Effects of Different Nutrient Ratios on Sorghum Root Growth and Nutrient Uptake: Postprint

Authors: Cui Peipei, Liu Peng, Liu Jiaqi, Wang Jinsong, Wu Ailian, Dong Erwei, Ding Yuchuan, Jiao Xiaoyan

Date: 2017-11-08T00:00:00+00:00

Abstract

To investigate the responses of sorghum nutrient uptake and root growth to nitrogen, phosphorus, and potassium stress, a long-term field experiment was conducted under sorghum/maize rotation conditions to study the effects of different nutrient ratios (NPK, PK, NK, NP, CK) on sorghum root growth and nutrient uptake. The results showed that, compared with NPK, long-term nitrogen omission (PK) increased total root length by 18.29%, decreased total root volume by 26.52%, and roots were mainly distributed in the 0–10 cm soil layer, with a significant increase in the proportion of fine roots with diameter less than 0.5 mm. Phosphorus omission (NK) significantly inhibited sorghum root growth, with total root length, total root surface area, and total root volume decreasing by 24.03%, 27.48%, and 41.29%, respectively. Potassium omission (NP) had a significant inhibitory effect on fine root growth. Omission of nitrogen (PK), phosphorus (NK), and potassium (NP) all reduced the uptake and accumulation of corresponding nutrients in sorghum; nitrogen omission promoted the translocation of nitrogen and potassium from vegetative organs to grains, while phosphorus or potassium omission inhibited the translocation of nitrogen, phosphorus, and potassium. Nutrient uptake, accumulation, and translocation in sorghum were related to root morphology, and the relationships between accumulation/translocation of different nutrients and root morphology varied: nitrogen and potassium accumulation and translocation showed a good correlation with root morphology, and the correlation between nitrogen accumulation/translocation and plant biomass and yield was greater than that of phosphorus and potassium. In summary, sorghum root morphology and nutrient uptake responded differently to nitrogen, phosphorus, and potassium stress, and this study can provide a theoretical basis for efficient sorghum cultivation in nutrient-poor soils.

Full Text

Effect of Different Nutrient Combinations on Root Growth and Nutrient Accumulation in Sorghum

CUI Peipei[1], **LIU Peng**[3], **LIU Jiaqi**[1], **WANG Jinsong**[2], **WU Ailian**[2], **DONG Erwei**[2], **DING Yuchuan**[2], JIAO Xiaoyan[2]**

[1]College of Bioengineering, Shanxi University, Taiyuan 030006, China
[2]Institute of Agricultural Environment & Resources, Shanxi Academy of Agricultural Sciences, Taiyuan 030031, China
[3]Institute of Sorghum Research, Shanxi Academy of Agricultural Sciences, Yuci 030600, China

Abstract: Sorghum, one of the world' s important grain crops, exhibits strong adaptability to low-fertility soils. To understand how sorghum root growth and nutrient accumulation respond to nitrogen (N), phosphorus (P), and potassium (K) stress, a long-term experiment was initiated in 2011 under a sorghum/maize rotation system with five treatments (NPK, PK, NK, NP, and CK). The treatments created distinct differences in soil N, P, and K availability before sorghum sowing in 2016. Compared with the NPK treatment, the PK treatment increased total root length by 18.29% but decreased total root volume by 26.53%, with roots primarily distributed in the 0–10 cm soil layer and a significantly increased proportion of fine roots (<0.5 mm diameter). The NK treatment significantly inhibited root growth, reducing total root length, surface area, and volume by 24.03%, 27.48%, and 41.29%, respectively. The NP treatment notably suppressed fine root growth. Omitting N, P, or K each reduced the absorption and accumulation of the corresponding nutrient. N omission enhanced N and K translocation from vegetative organs to grains, while P or K deficiency inhibited the translocation of N, P, and K. Nutrient absorption, accumulation, and translocation were related to root morphology, though the relationships differed among nutrients: N and K accumulation and translocation showed stronger correlations with root morphology than P, and N accumulation and translocation were more closely correlated with biomass and grain yield than P or K. In summary, sorghum root morphology and nutrient absorption respond differently to N, P, and K stress. These findings provide a theoretical basis for efficient sorghum cultivation in nutrient-poor soils.

Keywords: Sorghum; Nutrient combination; Root growth; Nutrient uptake; Nutrient translocation

Sorghum [*Sorghum bicolor* (L.) Moench] is an important food, feed, and energy crop that also serves as a raw material for traditional brewing industries. Its superior tolerance to drought, waterlogging, poor soil conditions, and salinity compared with other crops has led to its establishment as a pioneer crop on marginal lands with poor soil fertility and water scarcity in China. However, with the rapid development of China' s brewing and feed processing industries, demand for sorghum has surged dramatically, reaching 6.65 million tons of imported sorghum in 2016 alone. Consequently, research on how nutrient stress affects sorghum root growth and nutrient absorption is urgently needed to ensure high yield and efficiency on poor soils.

Roots are the primary organs for water and nutrient uptake, and their growth and development are influenced not only by genetic factors but also by environmental conditions such as soil nutrients, moisture, and temperature. Soil nutrient status significantly affects root growth, and when N, P, and K are deficient, root morphology and distribution undergo adaptive changes that subsequently influence nutrient uptake and, ultimately, aboveground growth and yield. Previous studies have shown that root responses to N, P, and K deficiencies differ: roots elongate to adapt to N deficiency, with increased root-to-shoot ratios observed in soybean [*Glycine max* L.] and significant increases in total root length and surface area in maize [*Zea mays* L.]. P deficiency inhibits primary root growth in wheat [*Triticum aestivum* L.] and *Arabidopsis* but induces proteoid root formation in white lupin [*Lupinus albus* L.] and increases lateral root numbers in rice [*Oryza sativa* L.], *Arabidopsis*, and *Malus hupehensis*, though extremely low P stress can reduce lateral root density. K deficiency significantly inhibits root elongation. Additionally, N and P deficiencies significantly reduce N, P, and K accumulation in wheat leaves, stems, and grains, while N deficiency increases the allocation rate of N to grains. To date, few studies have examined sorghum root growth and nutrient uptake responses to nutrient deficiency. Since sorghum is not suitable for continuous cropping and yield reductions occur even under normal management, the Loess Plateau region commonly uses rotation systems to overcome continuous cropping obstacles. To investigate adaptive changes in sorghum growth under N, P, and K stress while avoiding continuous cropping effects, this study examined long-term effects of different fertilizer combinations on sorghum root growth and nutrient uptake under a sorghum/maize rotation system. The objective was to clarify adaptive changes in sorghum root morphology and nutrient uptake to N, P, and K stress, providing a basis for rational fertilization on poor soils.

1.1 Experimental Design

The experiment was conducted at the Dongyang Experimental Base of the Shanxi Academy of Agricultural Sciences in Yuci District, Jinzhong City, Shanxi Province. The site is at 802 m elevation with an average annual temperature of 9.7 °C and average annual precipitation of 450 mm, with over 70% of rainfall concentrated from June to September. The soil is a fluvo-aquic soil with a clay-loam texture. The experiment began in 2011 with baseline topsoil nutrient contents of 11.24 $g \cdot kg^{-1}$ organic matter, 7.38 $mg \cdot kg^{-1}$ available phosphorus (Olsen-P), 219 $mg \cdot kg^{-1}$ available potassium, and 1.10 $g \cdot kg^{-1}$ total nitrogen. Five treatments were established: NPK, PK, NK, NP, and CK, with annual application rates of N 225 $kg \cdot hm^{-2}$, P_2O_5 75 $kg \cdot hm^{-2}$, and K_2O 75 $kg \cdot hm^{-2}$. Urea was used as the N source, calcium superphosphate as the P source, and potassium sulfate as the K source. P and K fertilizers were applied as basal fertilizers, while half of the N fertilizer was applied basally and the remaining half was topdressed at the jointing stage. The experiment used a randomized block design with three replications, each plot measuring 15 m × 5 m (75 m^2). From 2011 to 2016, the cropping sequence was maize-sorghum-maize-sorghum-maize-sorghum, with one season per year and identical fertilization and management each year. Soil chemical properties before sowing in 2016 are shown in Table 1. Compared with NPK, the PK treatment showed reduced soil total nitrogen and nitrate-N content, while the NK treatment had significantly lower available phosphorus and the NP treatment had significantly lower available potassium. Sorghum cultivar 'Jinzhong 0592' was sown on May 13, 2016, and harvested on September 28, with a plant density of 191,800 plants per hectare and a growth period of 138 days.

1.2 Root Sampling and Measurement

Roots were sampled at the flowering stage (August 1). In each plot, four uniformly growing representative adjacent plants were selected, and all roots within a soil volume of 50 cm along the row, 40 cm perpendicular to the row, and 40 cm deep were excavated. Eighty small soil blocks (10 cm × 10 cm × 10 cm) were collected using a root sampler. All roots from each block were carefully extracted with tweezers, placed in labeled ziplock bags, and stored at -4 °C for later analysis. For measurement, roots were washed with distilled water and placed without overlap in transparent resin trays containing 3–4 mm of pure water for scanning with a double light source. Root images were analyzed using WinRHIZO Pro(S) v. 2004b software (Regent Instruments Inc., Canada) to obtain total root length, root diameter, total root surface area, total root volume, and the length, surface area, and volume of roots in three diameter classes: 0–0.5 mm, 0.5–4 mm, and >4 mm. Root biomass was determined after oven-drying at 105 °C for 30 minutes, followed by drying at 70 °C to constant weight.

1.3 Plant Sampling and Nutrient Determination

Aboveground plant samples were collected at the flowering stage (August 1) and harvest (September 28). In each plot, three uniformly growing representative plants were combined into one sample. Plants were separated into leaves, stems, and grains, oven-dried at 105 °C for 30 minutes, then at 70 °C to constant weight to determine biomass of each part. Dried samples were ground for N, P, and K analysis. Total N was determined by the Kjeldahl method after digestion with concentrated H_2SO_4 using an automatic Kjeldahl analyzer. Total P and K were determined after digestion with a 1:3 mixture of concentrated $HClO_4$ and HNO_3; P was measured by the vanadium molybdate yellow method using a UV spectrophotometer, and K was measured by flame photometry. Nutrient accumulation, translocation, and translocation rate were calculated as follows:

Nutrient accumulation in each part = Biomass of each part × Nutrient content

of each part (1)
Nutrient translocation from vegetative organs = Nutrient accumulation in vegetative organs at flowering stage - Nutrient accumulation in vegetative organs at harvest (2)
Nutrient translocation rate = (Nutrient translocation from vegetative organs / Nutrient accumulation in vegetative organs at flowering stage) × 100 (3)

1.4 Harvest Investigations

At harvest, each plot was harvested separately to determine aboveground total biomass, grain yield, and yield components (spike number, grain weight per spike, and 1000-grain weight). Harvest index and soil nutrient natural supply capacity were calculated. Harvest index is the ratio of economic yield to aboveground total biomass. Soil nutrient natural supply capacity refers to the percentage of yield achieved without a particular nutrient relative to the full fertilization yield when other nutrients are adequately supplied.

1.5 Statistical Analysis

Data were organized and analyzed using Microsoft Excel 2010. Single-factor ANOVA and correlation analysis were performed using SPSS 20.0, with multiple comparisons among treatments conducted using Duncan' s method at a significance level of $\alpha = 0.05$. Data in tables and figures are presented as means ± standard error (mean ± SE) of three replications.

2.1.1 Effects on Sorghum Root Morphology and Biomass

As shown in Table 2, compared with NPK, the PK and NK treatments significantly affected total root length ($P < 0.05$), with PK increasing it by 18.29% and NK decreasing it by 24.03%. Although NP and CK treatments showed decreases and increases in total root length, respectively, these were not significant ($P > 0.05$). Total root volume under PK, NK, and CK treatments was significantly lower than under NPK and NP ($P < 0.05$). Compared with NPK, root surface area decreased by 27.48%, 7.90%, and 2.47% under NK, NP, and CK, respectively, while PK increased it by 3.47%. PK, NK, NP, and CK treatments did not affect average root diameter ($P > 0.05$) but all reduced total root dry weight. Root biomass under NK was significantly lower than under NPK, NP, and CK ($P < 0.05$), with no significant differences among other treatments. These results indicate that N deficiency significantly increased total root length and showed a trend toward increased total root surface area while significantly reducing total root volume. P deficiency had the greatest impact on roots, significantly reducing all morphological indices and biomass. K deficiency also inhibited root growth, though not significantly.

2.1.2 Effects on Root Morphology in Different Soil Layers

As shown in Table 3, compared with NPK, NK, and NP treatments, PK and CK significantly increased total root length and surface area in the 0–10 cm soil layer ($P < 0.05$). For root length, 63.61% and 63.84% of roots were distributed in the 0–10 cm layer under PK and CK, respectively, compared with 43.40%, 44.89%, and 45.52% under NPK, NK, and NP. For root surface area, 60.01% and 59.90% were in the 0–10 cm layer under PK and CK, compared with 45.52%, 46.67%, and 48.36% under NPK, NK, and NP. For root volume, 64.56% and 64.81% were in the 0–10 cm layer under PK and CK, compared with 61.62%, 63.42%, and 63.78% under NPK, NK, and NP. These results demonstrate that N omission led to shallow root distribution, while P or K omission had little effect on root distribution. NK and NP treatments reduced root morphological indices at all soil layers, with NK showing greater reductions than NP, indicating that P or K deficiency inhibited root growth across all soil layers, with P deficiency having a greater impact than K deficiency.

2.1.3 Effects on Different Diameter Roots

Sorghum roots were classified into three diameter classes: fine roots ($0 < D \leq 0.5$ mm), medium roots ($0.5 < D \leq 4$ mm), and coarse roots ($D > 4$ mm). As shown in Table 4, compared with NPK, PK and CK significantly increased fine root length ($P < 0.05$), while NK and NP significantly decreased it ($P < 0.05$). Fine root surface area under PK increased by 20.97% compared with NPK ($P < 0.05$), while NK and NP decreased it by 26.74% and 25.63%, respectively ($P < 0.05$). No significant differences in fine root volume were observed among the four nutrient-deficient treatments and NPK. Compared with NPK, PK significantly increased medium root length ($P < 0.05$), while NK significantly decreased it ($P < 0.05$). Only NK treatment showed significantly lower medium root surface area and volume than NPK ($P < 0.05$), with no significant differences among NPK, PK, NK, and CK. For coarse roots, PK, NK, and CK consistently and significantly reduced coarse root length, surface area, and volume compared with NPK ($P < 0.05$), while NP showed decreasing trends without significant differences. These results indicate that N deficiency increased fine roots and decreased coarse roots; P deficiency significantly reduced fine, medium, and coarse roots; and K deficiency decreased fine roots without significantly affecting medium and coarse roots.

2.2 Effects of Nutrient Combinations on Nutrient Uptake and Translocation

Table 5 shows that, compared with NPK, PK and CK significantly reduced N accumulation in vegetative organs at flowering, in vegetative organs at harvest, and in grains ($P < 0.05$). NK and CK significantly reduced P accumulation in these tissues ($P < 0.05$). PK, NK, NP, and CK significantly reduced K accumulation in vegetative organs at flowering; PK, NK, and CK significantly reduced K accumulation in vegetative organs at harvest ($P < 0.05$), while NP showed no significant change. All four nutrient-deficient treatments reduced K accumulation in grains, with only NK and CK showing significant reductions. These results demonstrate that N deficiency inhibited N and K absorption and accumulation, P deficiency inhibited P and K absorption and accumulation, and K deficiency inhibited K absorption and accumulation at flowering.

Compared with NPK, PK, NP, and CK significantly reduced N translocation from vegetative organs to grains ($P < 0.05$), but PK and CK significantly increased N translocation rate. PK, NK, and CK significantly reduced P translocation ($P < 0.05$), though no treatment significantly affected P translocation rate. NP and CK significantly reduced K translocation ($P < 0.05$), while PK showed the highest K translocation rate ($P < 0.05$) and NP the lowest. These results indicate that N deficiency reduced N and P translocation amounts but increased N and K translocation rates; P deficiency reduced P translocation; and K deficiency inhibited N and K translocation.

2.3 Effects of Nutrient Combinations on Yield and Components

As shown in Table 6, compared with NPK, PK and CK significantly reduced grain yield ($P < 0.05$), while NK and NP showed yield reductions without significant differences ($P > 0.05$). Yield reductions under PK, NK, NP, and CK were 35.76%, 3.79%, 6.56%, and 36.74%, respectively. Aboveground biomass followed similar trends, with reductions of 24.55%, 4.40%, 0.56%, and 23.53% under PK, NK, NP, and CK, respectively. Regarding yield components, treatments did not significantly affect spike number per unit area but significantly reduced grain weight per spike ($P < 0.05$) by 37.26%, 8.92%, 8.54%, and 42.15% under PK, NK, NP, and CK, respectively. PK and CK significantly increased 1000-grain weight ($P < 0.05$), while NK and NP had no significant effect. PK and CK significantly reduced harvest index ($P < 0.05$), while no significant differences were observed among NK, NP, and NPK. Based on yield results, the soil nutrient supply capacities for N, P, and K after six years of differential fertilization were 64.24%, 96.21%, and 93.44%, respectively. These results indicate that N fertilizer was the primary limiting factor for sorghum yield and its components in this region, followed by P and K fertilizers.

2.4 Correlations Between Nutrient Uptake, Accumulation, Translocation and Root Morphology and Yield

Table 7 shows that total root length was significantly negatively correlated with N accumulation in vegetative organs at both sampling stages, total root surface area was significantly negatively correlated with N translocation amount, and total root volume was significantly positively correlated with N accumulation in vegetative organs at harvest and significantly negatively correlated with N translocation rate. Only total root surface area was significantly positively correlated with grain P content at harvest. Total root volume was significantly positively correlated with K accumulation in vegetative organs at harvest and significantly negatively correlated with K translocation rate, while average root diameter was extremely significantly negatively correlated with both K translocation amount and rate. These results indicate that nutrient uptake, accumulation, and translocation are regulated by root morphology, with weaker correlations between P accumulation/translocation and root morphology compared with N and K.

N accumulation in vegetative organs at flowering, in vegetative organs at harvest, and in grains, as well as N translocation amount, were all extremely significantly positively correlated with yield. Whole-plant biomass was significantly positively correlated with N translocation amount and extremely significantly positively correlated with N accumulation at both stages, while N translocation rate was extremely significantly negatively correlated with both yield and whole-plant biomass. P accumulation in vegetative organs at flowering was significantly positively correlated with yield and whole-plant biomass, and P translocation amount was significantly positively correlated with yield. K accumulation in vegetative organs at flowering was significantly positively correlated with yield, and K accumulation in vegetative organs at harvest was extremely significantly positively correlated with both yield and whole-plant biomass. These results demonstrate that nutrient uptake, accumulation, and translocation are closely related to final yield, with N accumulation and translocation showing much stronger correlations with yield and plant biomass than P or K.

3.1 Effects of Nutrient Combinations on Sorghum Root Growth

Crop roots absorb required nutrients, with total root length and surface area reflecting passive absorption capacity. Deficiencies in N, P, and K all inhibited sorghum root growth to varying degrees, but root morphology showed different adaptive responses to each nutrient deficiency. Studies on soybean, maize, wheat, *Malus hupehensis*, and *Isatis indigotica* have demonstrated that N deficiency promotes root elongation, increases root-to-shoot ratio, and reduces root activity. This study also showed that sorghum increased total root length and surface area to expand contact with N and enhance passive absorption capacity to compensate for reduced active absorption under stress, ultimately promoting efficient N uptake. However, reduced total root volume and dry weight indicated that absorbed N remained insufficient for normal growth. Some studies suggest that P stress induces root remodeling, with P deficiency promoting root growth in rapeseed, potato, and soybean but significantly reducing root length and surface area in barley and sweet potato. Other research indicates that both K application and deficiency can inhibit crops, with K application significantly reducing total root length, surface area, and volume in cotton, and K deficiency inhibiting root growth in wheat, rice, and watermelon. In this study, P deficiency significantly reduced sorghum total root length, surface area, and volume, decreasing overall root absorption capacity and ultimately inhibiting root growth. K deficiency also inhibited root growth, though not significantly.

Deep root systems enhance nutrient absorption and utilization, with root mass in deep layers significantly contributing to yield improvement. This study' s stratified root analysis showed that N deficiency caused sorghum roots to be primarily distributed in the shallow 0–10 cm layer, while P or K deficiency had little effect on root distribution but inhibited root growth in all soil layers, with P deficiency having a greater impact than K deficiency. Different diameter roots serve different functions: fine roots primarily control water and nutrient uptake, while coarse roots control root penetration and robustness. Studies have shown that low N stress increases the proportion of fine roots (0–0.2 mm) in maize. This study's root classification analysis demonstrated that N deficiency increased fine roots ($ $0.5 mm) and decreased coarse roots (>4 mm); P deficiency significantly reduced fine, medium, and coarse roots; and K deficiency decreased fine roots without significantly affecting medium and coarse roots. These results indicate that under N deficiency, sorghum produces more fine roots to enhance nutrient uptake capacity, but shallow root distribution hinders utilization of deep soil nutrients. P deficiency inhibited root growth across all soil layers and diameter classes. K deficiency had less impact on sorghum root growth than N or P deficiency, but reduced fine roots would affect nutrient uptake.

Previous research suggests that adaptive changes in root morphology to nutrient deficiency are genetically regulated physiological processes possibly related to carbohydrate redistribution and regulation by endogenous hormones such as auxin, cytokinin, and ethylene. In rose seedlings, N or P deficiency promotes translocation of aboveground dry matter to roots, significantly increasing root length and number and enlarging root surface area. In this study, when sorghum roots sensed N deficiency, aboveground assimilates were translocated to roots, stimulating new root formation and promoting root elongation and surface area expansion. P deficiency inhibited root growth, which differs from some previous results, possibly because sorghum is a P-loving gramineous crop with strong P demand, especially under dense planting conditions. K affects root growth through different mechanisms than N and P, directly participating in photosynthesis and serving as an activator for multiple enzymes in protein, carbohydrate, and respiratory metabolism. K deficiency affects photosynthesis and assimilate translocation, reducing assimilate synthesis and accumulation and ultimately inhibiting fine root growth.

3.2 Effects of Nutrient Combinations on Nutrient Uptake and Translocation

Root morphology and distribution affect nutrient uptake, accumulation, and translocation. Previous research on banana plantation soil showed that N omission significantly reduced sorghum N uptake but increased P and K uptake, while P omission reduced P uptake but increased K uptake. In contrast, this study found that N omission inhibited N and K absorption and accumulation, P omission inhibited P and K absorption and accumulation, and K omission inhibited K absorption and accumulation at flowering. The inconsistent effects of N or P omission on K uptake between studies may be related to differences in soil type and sorghum variety and requires further investigation. This study confirmed that omitting any one of N, P, or K inhibited absorption and accumulation of the corresponding nutrient. Under N deficiency, increased translocation rates of N and K from vegetative organs ensured normal growth of newly formed sink tissues, but excessive translocation reduced leaf photosynthesis and accelerated leaf senescence, ultimately decreasing yield. P deficiency reduced P translocation amount, and K deficiency inhibited N and K translocation, indicating that P and K deficiency directly affected nutrient translocation and was unfavorable for grain nutrient accumulation.

3.3 Effects of Nutrient Combinations on Yield and Components

Previous studies have shown that N is the primary nutrient factor affecting sweet sorghum and forage sorghum yield. This study also demonstrated that N fertilizer was the primary limiting factor for grain sorghum biomass, grain yield, and yield components, followed by P and K fertilizers. N omission significantly reduced aboveground biomass, grain yield, grain weight per spike, and harvest index, but increased 1000-grain weight. The increased 1000-grain weight resulted from significantly reduced grain weight per spike, which decreased competition among grains. Other researchers have also concluded that grain size contributes little to sorghum yield, with spike number and grain weight per spike being the decisive factors.

Soil nutrient natural supply capacity is an important indicator for evaluating soil fertility. Previous research found that soil nutrient supply capacity declines to a stable level after two years of continuous fertilization. After six years of continuous differential fertilization in this study, soil N, P, and K supply capacities were 64.24%, 96.21%, and 93.44%, respectively, indicating that N supplementation is far more critical for sorghum production than P or K. Correlation analysis also showed weaker relationships between P accumulation/translocation and root morphology compared with N and K, and N accumulation/translocation was much more closely correlated with yield and plant biomass than P or K. Therefore, although P deficiency significantly inhibited root growth, the yield reduction under N omission was significantly greater than under P omission.

Under N deficiency, sorghum increased total root length, root surface area, and fine root proportion to absorb more N, but shallow root distribution and reduced root volume inhibited N and K absorption and accumulation. Even with increased nutrient translocation rates, reduced translocation amounts ultimately caused yield loss. Low P stress significantly inhibited root growth, P and K accumulation, and P translocation. Low K stress significantly inhibited fine root growth, K accumulation, and N and K translocation. Although sorghum root growth and nutrient uptake showed different adaptive responses to N, P, and K stress, all ultimately led to yield reduction, demonstrating that N, P, and K fertilizers are all essential for sorghum cultivation on the Loess Plateau.

References

[1] Farré I, Faci J M. Comparative response of maize (*Zea mays* L.) and sorghum (*Sorghum bicolor* L. Moench) to deficit irrigation in a Mediterranean environment[J]. *Agricultural Water Management*, 2006, 83(1/2): 135-143.

[2] Wang X, Li Z Q, Gu W B, et al. Systemic regulation of anatomic structure and photosynthetic characteristics of developing leaves in sorghum seedlings under salt stress[J]. *Acta Agronomica Sinica*, 2010, 36(11): 1941-1949.

[3] Moore W J, Ditmore M, TeBeest D O. The effects of cropping history on grain sorghum yields and anthracnose severity in Arkansas[J]. *Crop Protection*, 2009, 28(9): 737-743.

[4] Wang J S, Jiao X Y, Ding Y C, et al. Response of nutrient uptake, yield and quality of grain sorghum to nutrition of nitrogen, phosphorus and potassium[J]. *Acta Agronomica Sinica*, 2015, 41(8): 1269-1278.

[5] Marschner H, Kirkby E, Cakmak L. Effect of mineral nutritional status on shoot-root partitioning of photoassimilates and cycling of mineral nutrients[J]. *Journal of Experimental Botany*, 1996, 47(S1): 1255-1263.

[6] Bonser A M, Lynch J P, Snapp S. Effect of phosphorus deficiency on growth angle of basal roots in *Phaseolus vulgaris*[J]. *New Phytologist*, 1996, 132(2): 281-288.

[7] Ma X F, Song F B, Zhang J Z. Advances of research of roots responses to environmental stress on soil[J]. *Chinese Agricultural Science Bulletin*, 2011, 27(5): 44-48.

[8] Ericsson T. Growth and shoot: Root ratio of seedlings in relation to nutrient availability[J]. *Plant and Soil*, 1995, 168-169(1): 205-214.

[9] Bonifas K D, Lindquist J L. Effects of nitrogen supply on the root morphology of corn and velvetleaf[J]. *Journal of Plant Nutrition*, 2009, 32(8): 1371-1382.

[10] Wang S Q, Han X Z, Qiao Y F, et al. Root morphology and nitrogen accumulation in soybean (*Glycine max* L.) under different nitrogen application levels[J]. *Chinese Journal of Eco-Agriculture*, 2009, 17(6): 1069-1073.

[11] Jiang L L, Han L S, Han X R, et al. Effects of nitrogen on growth, root morphological traits, nitrogen uptake and utilization efficiency of maize seedlings[J]. *Plant Nutrition and Fertilizer Science*, 2011, 17(1): 247-253.

[12] Wu Y J, Shen Y F, Yan Q F, et al. Effect of N deficiency and N recovery treatment on root growth, root activity, content of NO_3^--N and amino acids[J]. *Acta Agriculturae Boreali-Occidentalis Sinica*, 2012, 21(12): 61-64.

[13] Chen L, Wang S F, Liu R L, et al. Changes of root morphology and rhizosphere processes of wheat under different phosphate supply[J]. *Plant Nutrition and Fertilizer Science*, 2012, 18(2): 324-331.

[14] Sánchez-Calderón L, López-Bucio J, Chacón-López A, et al. Phosphate starvation induces a determinate developmental program in the roots of *Arabidopsis*

thaliana[J]. *Plant and Cell Physiology*, 2005, 46(1): 174-184.

[15] Neumann G, Martinoia E. Cluster roots —an underground adaptation for survival in extreme environments[J]. *Trends in Plant Science*, 2002, 7(4): 162-167.

[16] Li H B, Xia M, Wu P, et al. Effect of phosphorus deficiency stress on rice lateral root growth and nutrient absorption[J]. *Acta Botanica Sinica*, 2001, 43(11): 1154-1160.

[17] Fan W G, Yang H Q, Han X J. Changes of root architecture and phosphorus uptake by roots of *Malus hupehensis* (Pamp) Rehd. under the condition of phosphorus-deficiency[J]. *Acta Horticulturae Sinica*, 2007, 34(6): 1341-1346.

[18] Wan H Y, Liu J J, Wang J X, et al. Effects of phosphorus spatial availability on root morphology and architecture in *Arabidopsis thaliana* (L.) Heynh[J]. *Plant Physiology Communications*, 2007, 43(3): 425-429.

[19] Zhang Z Y, Wang Q L, Li Z H, et al. Effect of potassium deficiency on root growth of cotton (*Gossypium hirsutum* L.) seedlings and its physiological mechanisms involved[J]. *Acta Agronomica Sinica*, 2009, 35(4): 718-723.

[20] Yang Y M, Zhang Q Y, Li J, et al. Effect of nutrient accumulation, distribution and use efficiency of Chuannong 16 and Chuanmai 42 under N, P and K stress[J]. *Southwest China Journal of Agricultural Sciences*, 2015, 28(4): 1675-1682.

[21] Fan F F, Wang J S, Dong E W, et al. Effects of sorghum continuous cropping on the growth of sorghum and soil environment[J]. *Soil and Fertilizer Sciences in China*, 2016, 21(3): 127-133.

[22] Bao S D. *Soil and Agricultural Chemistry Analysis*[M]. 3rd ed. Beijing: Agricultural Press China, 2000: 30-177.

[23] Yang H S, Zhang Y Q, Xu S J, et al. Characteristics of dry matter and nutrient accumulation and translocation of super-high-yield spring maize[J]. *Plant Nutrition and Fertilizer Science*, 2012, 18(2): 315-323.

[24] Men M X, Li X W, Xu H. Effects of long-term fertilization on crop yields and stability[J]. *Scientia Agricultura Sinica*, 2008, 41(8): 2339-2346.

[25] Cao X, Xia R X, Yang H Y, et al. Effects of P, K and Ca deficiency on the root morphology and nutrient absorption of *Poncirus trifoliata* seedlings[J]. *Journal of Plant Nutrition and Fertilizer*, 2014, 20(4): 981-988.

[26] Xie M L, Li Q, Zha L, et al. Effects of low nitrogen stress on the physiological and morphological traits of roots of different low nitrogen tolerance maize varieties at seedling stage[J]. *Chinese Journal of Eco-Agriculture*, 2015, 23(8): 946-953.

[27] Zhang X Q, Cao C F, Chen H, et al. Effect of long-term fertilization on root traits and root-shoot ratio of wheat in lime concretion black soil[J]. *Journal of*

Triticeae Crops, 2017, 37(3): 382-389.

[28] Qiao H T, Yang H Q, Shen W B, et al. Effect of nitrogen-deficient and iron-deficient on root architecture of young seedlings of *Malus hupehensis* (Pamp) Rehd[J]. *Acta Horticulturae Sinica*, 2009, 36(3): 321-326.

[29] Shi S L, Ye B Z, Zhang R Z, et al. Effect of N deficiency and N recovery on growth and nitrogen metabolism of *Isatis indigotica* seedlings[J]. *Acta Botanica Boreali-Occidentalis Sinica*, 2015, 35(3): 523-529.

[30] Sato A, Miura K. Root architecture remodeling induced by phosphate starvation[J]. *Plant Signaling & Behavior*, 2011, 6(8): 1212-1213.

[31] Wang S Q, Han X Z, Yan J, et al. Impact of phosphorus deficiency stress on root morphology, nitrogen concentration and phosphorus accumulation of soybean (*Glycine max* L.)[J]. *Chinese Journal of Soil Science*, 2010, 41(3): 644-649.

[32] Wang Y L, Almvik M, Clarke N, et al. Contrasting responses of root morphology and root-exuded organic acids to low phosphorus availability in three important food crops with divergent root traits[J]. *AoB Plants*, 2015, 7: 1-11.

[33] Ning Y W, Ma H B, Zhang H, et al. Effects of nitrogen, phosphorus and potassium on root morphology and endogenous hormone contents of sweet potato at early growing stages[J]. *Jiangsu Journal of Agricultural Sciences*, 2013, 29(6): 1326-1332.

[34] Pan Y H, Ma Z M, Lü X D, et al. Effects of different potassium nutrition on growth and root morphological traits of watermelon seedling[J]. *Chinese Journal of Eco-Agriculture*, 2012, 20(5): 536-541.

[35] Zhang Y Q, Bi R C, Pang C H, et al. Biological responses of the roots of different spring wheat varieties to low-potassium stress[J]. *Acta Botanica Boreali-Occidentalis Sinica*, 2006, 26(6): 1190-1194.

[36] Liu M, Wu G J, Lu D X, et al. Improvement of nitrogen use efficiency and the relationship with root system characters of maize cultivars in different years[J]. *Journal of Plant Nutrition and Fertilizer*, 2017, 23(1): 71-82.

[37] Sullivan W M, Jiang Z C, Hull R J. Root morphology and its relationship with nitrate uptake in Kentucky bluegrass[J]. *Crop Science*, 2000, 40(3): 765-772.

[38] Chen Z, Yi X, Chen F J, et al. Differential response of maize roots to heterogeneous local nitrogen and phosphorus supply and genotypic differences[J]. *Journal of Plant Nutrition and Fertilizer*, 2017, 23(1): 83-90.

[39] Sun Y B, Zhao C K, Zhang L, et al. Effect of N, P, K-deficiency on root architecture of young seedlings of *Rosa rugosa*[J]. *Soil and Fertilizer Sciences in China*, 2013, (3): 43-48.

[40] Liaoning Academy of Agricultural Sciences. *Chinese Sorghum Cultivation*[M]. Beijing: Agricultural Press, 1988: 243-244.

[41] Chen B L, Sheng J D, Jiang P A, et al. Effects of potassium nutrition on growth of cotton on liquid foster[J]. *Chinese Agricultural Science Bulletin*, 2008, 24(11): 267-271.

[42] Saengwilai P, Tian X, Lynch J P. Low crown root number enhances nitrogen acquisition from low-nitrogen soils in maize[J]. *Plant Physiology*, 2014, 166(2): 581-589.

[43] Yang B M, Yao L X, Li G L, et al. Effect of nutrient combination on uptake of nitrogen phosphorus and potassium of sorghum[J]. *Chinese Agricultural Science Bulletin*, 2008, 24(4): 282-290.

[44] Xu K Z. The dynamic changes of nitrogen content and photosynthesis and their correlations in pot rice leaves after anthesis[J]. *Acta Agronomica Sinica*, 1995, 21(2): 171-175.

[45] Wang Z C, Wang Y H, Chen J P, et al. Effects of combined application of nitrogen, phosphorus and potassium on yield and dry matter accumulation of sweet sorghum in saline alkali soil[J]. *Jiangsu Agricultural Sciences*, 2013, 41(11): 80-81.

[46] Zhou H P, Hao B P, Guan C L, et al. Effect of fertilizer application on nutritive quality and growth of hybrid sorghum grass[J]. *Chinese Journal of Eco-Agriculture*, 2009, 17(1): 60-63.

[47] Ciampitti I A, Vara Prasad P V. Historical synthesis-analysis of changes in grain nitrogen dynamics in sorghum[J]. *Frontiers in Plant Science*, 2016, 7: 275.

Note: Figure translations are in progress. See original paper for figures.