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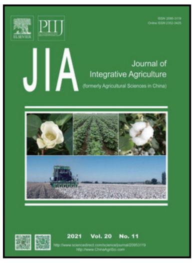

RESEARCH ARTICLE

Divergent responses of tiller and grain yield to fertilization and fallow precipitation: Insights from a 28-year long-term experiment in a semiarid winter wheat system

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Abstract

Tillering is an important phenological stage, which is strongly related to the yield in spike components and final grain yield during winter wheat growth. Precipitation during the fallow season (fallow precipitation) influences tillering in winter wheat on the semi-arid Chinese Loess Plateau. However, little work has been done regarding tiller number changes under various types of fertilization and amounts of fallow precipitation on a long-term scale. Effects of fallow precipitation and fertilization on tiller were investigated in a winter wheat (*Triticum aestivum* L.) system in a 28-year field study (1990 to 2017) in a semiarid agro-ecosystem. Tiller number, spike number and grain yield were measured in four fertilization conditions: control without fertilizer (CK); mineral nitrogen fertilizer alone (N); mineral phosphorus fertilizer alone (P); mineral nitrogen and phosphorus fertilizer together (NP). Based on the long-term annual fallow precipitation, dry years (<mean annual fallow precipitation) and wet years (>mean annual fallow precipitation) were distinguished. Phosphorus fertilization alone significantly increased the mean annual tiller number (23%), and the increase in tiller number was higher in wet years (29%) than in the dry years (17%). However, nitrogen fertilization alone had little effect on mean tiller number, while nitrogen and phosphorus together significantly increased mean annual tiller number (30%), mean tiller number in wet years (45%) and mean tiller number in dry years (17%). Tiller number was significantly and positively correlated with fallow precipitation in dry years for all fertilizer treatments, whereas it was weakly and either positively or negatively correlated with fallow precipitation in wet years depending on the treatment. This study found positive correlations between tiller number and fallow precipitation in the CK and NP treatments, and it found negative correlations between tiller number and fallow precipitation in the treatments with nitrogen fertilization alone or phosphorous fertilization alone in wet years. Understanding the impacts of fallow precipitation

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and fertilization on tiller development shed light on ways to improve crop production in rain-fed agricultural regions.

Keywords: tiller, grain yield, nutrient deficiency, fallow precipitation, winter wheat

1. Introduction

Tillering is an important phenological stage during the winter wheat growth progress. A greater number of tillers has been found to increase the leaf area index, resulting in the canopy intercepting more solar radiation, which consequently influences the amount of dry matter accumulated by the crop (Rodriguez *et al.* 1998b), and tillering is also strongly related to spike development (Rodriguez *et al.* 1999). Therefore, the dynamics of tillers are crucial to the final yield in winter wheat (Ishag and Taha 1974; Davidson and Chevalier 1990; Prystupa *et al.* 2003). Water shortage and nutrient deficiency are typically two primary factors in tillering of winter wheat in arid and semiarid regions (Li *et al.* 2009; Guo *et al.* 2012b). Until now, long-term effects of fertilization and precipitation on grain yield have been well-documented in the dryland system (Guo *et al.* 2012b; Wang *et al.* 2018). However, there is limited information about tillering dynamics and its relationship to grain yield under varied nutrients and precipitation in a winter wheat cropping system. Exploring the dynamics of tillers in relation to nutrient deficiency and precipitation will considerably enhance our understanding of the potential factors for influencing grain yield of winter wheat systems in arid and semiarid regions.

The number of tillers produced per plant has been found to be affected either directly by limited nutrients or indirectly by inhibiting the supply of assimilates required for growth (Longnecker *et al.* 1993). Phosphorus and nitrogen have been recognized as important nutrients that can limit tiller emergence and development (Rodriguez *et al.* 1998b, 1999; Prystupa *et al.* 2003). Previous studies have shown that both phosphorus deficiency and nitrogen deficiency limited the tiller number (Batten *et al.* 1999; Fageria and Baligar 1999). Phosphorus deficiency reduced the leaf area of the crop and consequently limited light interception (Radin and Eidenbock 1984; Cromer *et al.* 1993), thereby reducing the photosynthetic capacity of leaves (Jacob and Lawlor 1991), which impacted tiller number (Rodriguez *et al.* 1998a). Nitrogen deficiencies restricted tillering in wheat (Fischer *et al.* 1966; Longnecker *et al.* 1993; Prystupa *et al.* 2003) and influenced the timing and rate of tiller development and mortality (Bauer *et al.* 1984; Maidl *et al.* 1998; Tilley *et al.* 2019).

Approximately 75% of wheat production is from dryland agricultural areas (Li 2004), where precipitation is typically a primary factor in winter wheat production, especially in arid and semiarid regions (Li *et al.* 2009). The tillering stage of wheat is sensitive to water stress, which can reduce tiller production, stomatal conductance and cell expansion in the leaves of winter wheat (Gutierrez-Boem and Thomas 1998; Aidoo *et al.* 2017). In addition, nutrient-moving diffusion and mobility decreased due to soil water stress (Nye and Tinker 1977), with a consequent negative impact on tiller production (Gutierrez-Boem and Thomas 1998).

The Loess Plateau is located in northwestern China, covering an area of 640 000 km^2. It has a continental monsoon climate and shows dramatic inter-annual fluctuations in precipitation (Lin and Wang 2007; Guo *et al.* 2012b). Agricultural ecosystems in this area face the threats of drought and nutrient deficiency. Capturing the synergetic effect of water stress and nutrient deficiency on tillering is beneficial for the understanding and prediction of crop growth in the rain-fed agricultural system on a long-term scale. In the present study, we examined the tiller number, spike number, and grain yield based on a 28-year (1990–2017) field experiment with four fertilization treatments. The objectives of this study were to: 1) characterize the response of tillers to N and P nutrients and fallow precipitation, and 2) explore the contributions of N and P nutrients to tiller, spike and grain yield development during different growth stages.

2. Materials and methods

2.1. Experimental site

The field experiment was established in 1984 at the Changwu State Key Agro-Ecological Experimental Station (35°12´N, 107°40´E, altitude 1 220 m), which is located in the rain-fed cropping region of the Loess Plateau in China. It has a semiarid and continental monsoon climate with an annual mean temperature of 9.1°C. The distribution of precipitation is characterized by strong inter-annual and seasonal variations. The groundwater has a depth of approximately 60 m (Huang *et al.* 2003a, b).

The soil is described as a loam, Cumulic Haplustoll (SSS 2010), originating from parent material of calcareous loess. The initial main properties of topsoil (0–20 cm) were as follows: clay 24% (<0.002 mm), $CaCO_3$ 10.5%, organic carbon 6.5 g kg^{-1}, total nitrogen 0.80 g kg^{-1}, total phosphorous 640 mg kg^{-1}, NH_4OAc-extractable K 200 mg kg^{-1}, soil pH 8.4 (1:1, soil:H_2O suspension), water-holding capacity 0.29 $cm^3\ cm^{-3}$ (v/v) and bulk density 1.3 Mg m^{-3}.

2.2. Experimental design

The long-term experimental design is described in Guo *et al.* (2012a) and Huang *et al.* (2003a, b). Four treatments were selected from the long-term experiment: (1) control without fertilizer (CK), (2) mineral nitrogen fertilizer alone (N), (3) mineral phosphorus fertilizer alone (P) and (4) mineral nitrogen and phosphorus fertilizer together (NP). The nitrogen and phosphorus fertilizers were applied in the form of urea (120 kg N ha^{-1} yr^{-1}) and superphosphate (26 kg P ha^{-1} yr^{-1}), which were incorporated into the plots one week prior to sowing wheat. Potassium fertilizers were not applied because of the high background. Winter wheat (*Triticum aestivum* L.) was sown (150 kg seeds ha^{-1}) with 20-cm intervals between rows in late September each year. As practised locally, the plots were ploughed to 20-cm depth after harvest (in July) to increase water infiltration and storage of the soils due to the absence of irrigation. Crop cultivation and field management, including pest and weed control among others, were performed according to local farming practices.

2.3. Crop sampling

Tiller number and spike number per unit (1-m long) were counted manually in mid-November and before harvest with three replications, respectively. Then, spike number was transformed into spike number per hectare. Aboveground plant biomass at physiological maturity (in late June) was harvested annually from the central half area of each plot manually, and a grain-thresher was used to separate the grains. Grains were air-dried to a constant moisture content (about 12–14%), and the weight was recorded to obtain the final grain yield, which was then transformed into the grain yield per hectare.

2.4. Statistical analysis

The fallow precipitation is the precipitation that occurred from July to September, when the fallow season occurred for the winter wheat cropping system. Based on the mean fallow precipitation (314 mm), dry year (<mean annual fallow precipitation) and wet year (>mean annual fallow precipitation) were distinguished. The effects of fertilization treatments on tiller number, spike number and grain yield were evaluated with a one-way analysis of variance (ANOVA), and significant differences between treatments were determined using the least significant difference test at the 0.05 probability level. The effects on yield and its components from precipitation and fertilization were analyzed using a linear regression model with the SigmaPlot 10.0 Software, based on the data for 1990–2017 (except for 2004 (extreme precipitation), 2007 and 2009 (data missing). The precipitation use efficiency (PUE) was estimated by the changes of tiller number, spike number or grain yield per unit fallow precipitation. All these statistical analyses were performed with Statistical Analysis System ver. 8.0 (SAS Institute Inc., Cary, NC) unless otherwise indicated.

3. Results

3.1. Inter-annual variations of precipitation distribution

Fallow precipitation ranged from a low of 104 mm in 1995 to a high of 608 mm in 2004, with a 28-year average of 314.6 mm and a coefficient of variation (CV) of 35% (Fig. 1). Based on the ratio of precipitation and mean precipitation, the two types of dry and wet years were distinguished. The mean precipitation in wet years (395 mm calculated by averaging 16 years) was 63% higher than that in the dry years (242 mm calculated by averaging 12 years). The frequencies of dry and wet seasons were generally similar to those of the two corresponding types of years, respectively.

3.2. Fertilization influence on tiller number, spike number and grain yield

Fertilization practices influenced tiller number, spike number and grain yield differentially (Table 1). Phosphorus alone significantly increased tiller number by 29.0% in wet years (4.0±0.8) and increased this number by 17.2% in dry years (3.4±0.8) compared with the CK treatment in the same years (3.1±0.7 and 2.9±0.8, respectively), whereas P treatment had less effect on spike number and grain yield. Nitrogen alone had less effect on tiller number and spike number, but N treatment increased grain yield by 29.4% in wet years ((2.2±0.8) t ha^{-1}), which retained its levels in dry years ((1.3±0.5) t ha^{-1}) when compared with the CK treatment ((1.7±0.6) and (1.2±0.3) t ha^{-1}, respectively). The NP combination significantly increased tiller number, spike number and grain yield either in wet years or in dry years. Mean tiller number in the NP treatment was increased by 45.2% in wet years (4.5±0.6) and increased by 17.2% in dry years (3.4±0.9). Spike number and grain yield were increased 77.0 and 176.5% in wet years and increased 60.0 and 175.0% in dry years in the NP treatment compared to the CK treatment, respectively.

3.3. Fallow precipitation influence on tiller number, spike number and grain yield

Tiller number, spike number, and grain yield were also highly influenced by fallow precipitation during the 28-year experimental period (Fig. 2). Tiller number was positively

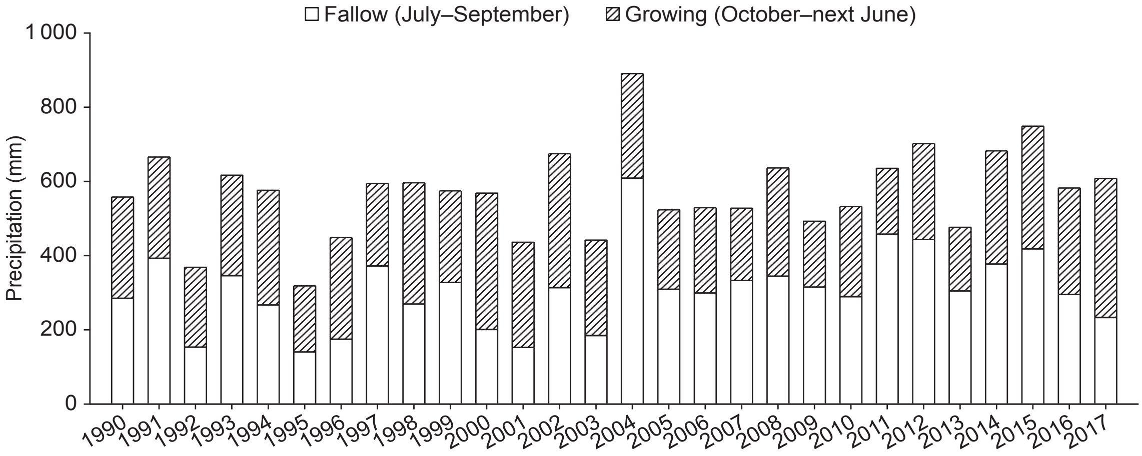

Fig. 1 Annual precipitation in fallow and growing seasons at the Changwu Station, Loess Plateau in China between 1990 and 2017.

Table 1 Variations of mean tiller number, spike number and grain yield during the 28-year experiment

Item	Treatment[1]	Dry year		Wet year		Total	
		Mean value	Increment (%)	Mean value	Increment (%)	Mean value	Increment (%)
Tiller (no.)	CK	2.9±0.8 a	–	3.1±0.7 a	–	3.0±0.8 a	–
	N	2.8±0.7 a	–3.4	3.1±0.5 a	0	2.9±0.7 a	–3.3
	P	3.4±0.8 ab	17.2	4.0±0.8 b	29.0	3.7±0.9 b	23.3
	NP	3.4±0.9 b	17.2	4.5±0.6 b	45.2	3.9±1.0 b	30.0
Spike ($\times10^4$ ha^{-1})	CK	205.0±43.4 a	–	258.9±37.0 a	–	228.0±48.3 a	–
	N	199.3±55.8 a	–2.7	245.2±59.2 a	–5.3	219.0±60.1 a	–3.9
	P	224.2±35.7 a	9.4	247.3±67.9 a	–4.4	234.1±51.8 a	2.7
	NP	328.3±80.9 b	60.0	458.9±104.4 b	77.0	384.3±111.0 b	68.6
Yield (t ha^{-1})	CK	1.2±0.3 a	–	1.7±0.6 a	–	1.4±0.5 a	–
	N	1.3±0.5 a	8.3	2.2±0.8 a	29.4	1.7±0.8 a	21.4
	P	1.0±0.3 a	–16.7	1.6±0.9 a	–5.9	1.3±0.7 a	–7.1
	NP	3.3±0.2 b	175.0	4.7±1.4 b	176.5	3.9±1.4 b	178.6

[1] CK, control without fertilizer; N, mineral nitrogen fertilizer alone; P, mineral phosphorus fertilizer alone; NP, mineral nitrogen and phosphorus fertilizer together.

Different letters indicate significant difference at $P<0.05$, and values are mean±SD ($n=3$).

correlated with fallow precipitation in dry years among all fertilization treatments. However, tiller number was weakly and either positively or negatively correlated with fallow precipitation in wet years depending on the treatment. Spike number was positively correlated with fallow precipitation in the NP treatment in both dry and wet years, and in the N treatment in dry years. There were negative correlations between spike number and fallow precipitation in the P treatment in both wet and dry years, and in the N treatment in wet years. No significant relationship between spike number and fallow precipitation in the CK treatment was found. The grain yield was also positively correlated with fallow precipitation in dry years, except for in the P treatment.

In addition, fertilization practices impacted the responses of tiller number, spike number and grain yield to fallow precipitation, and this was also evidenced by PUE. Precipitation use efficiency for tiller ($\mathrm{PUE}_{\mathrm{tiller}}$) and yield ($\mathrm{PUE}_{\mathrm{yield}}$) were higher under the NP condition than under either the N alone adequate supply or P alone adequate supply, whereas precipitation use efficiency for spike ($\mathrm{PUE}_{\mathrm{spike}}$) changed in various ways among fertilization practices (Fig. 2). Therefore, the increased $\mathrm{PUE}_{\mathrm{tiller}}$ and $\mathrm{PUE}_{\mathrm{yield}}$ under the NP condition can be largely attributed to the improvements of the nutrient conditions (both N and P), but N was the primary factor for the varied $\mathrm{PUE}_{\mathrm{spike}}$.

3.4. Relationships among grain yield, tiller number and spike number

This study indicated grain yield was positively influenced by spike number for all fertilization treatments (Fig. 3-B, E, H and K). However, spike number and grain yield were positively correlated with tiller number only in the N and NP treatments (Fig. 3-F and L), which means phosphorus had little effect on spike or yield. In addition, nitrogen fertilization alone did not increase the tiller number or the spike number,

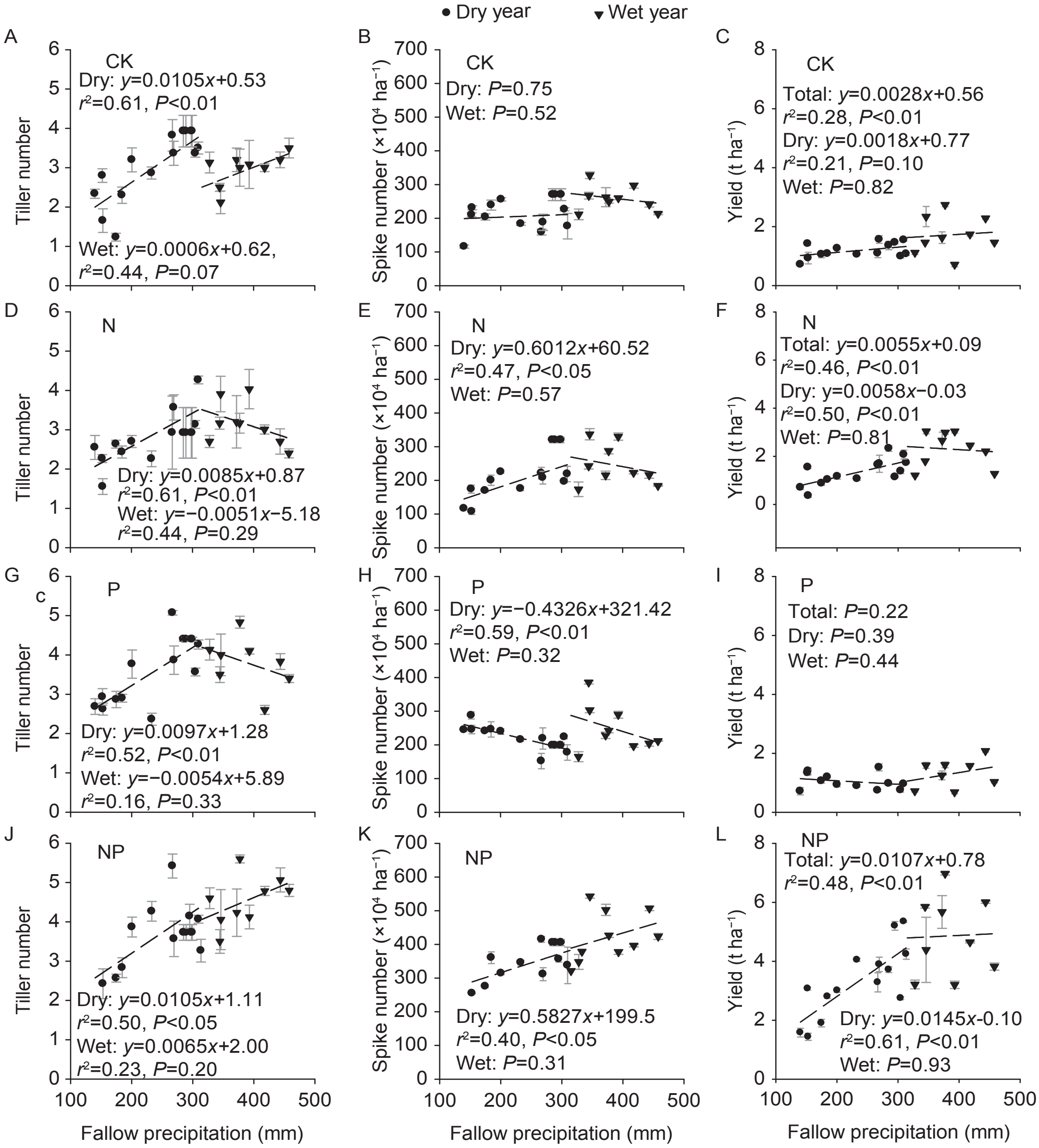

Fig. 2 Correlations of tiller number (A, D, G, and J), spike number (B, E, H, and K) and grain yield (C, F, I, and L) with fallow season precipitation among different fertilizer treatments. CK, control without fertilizer; N, mineral nitrogen fertilizer alone; P, mineral phosphorus fertilizer alone; NP, mineral nitrogen and phosphorus fertilizer together. Bars are SD (n=3).

but N treatment increased the grain number and thousand-grain weight, consequently promoting the proportion of spikes contributing to grain yield (Table 2).

4. Discussion

4.1. Divergent responses of tillers and yield to fertilization practices

Tillers determine spike development, and grain yield strongly depends on spikes in the winter wheat cropping system (Gutierrez-Boem and Thomas 1998; Prystupa *et al.* 2003; Golba *et al.* 2018; Ren *et al.* 2019). However, our study showed the responses of tiller, spike and yield to fertilization were different (Table 1). The significant increases in tiller number under the phosphorus addition treatments (P and NP) may be related to the following: first, calcareous soils on the Loess Plateau have a low availability of phosphorus (Olsen-P) in the soil (5.9 mg kg^{-1}) (Zhu *et al.* 1983; Peng and Peng 1998), and thus P treatment significantly increased

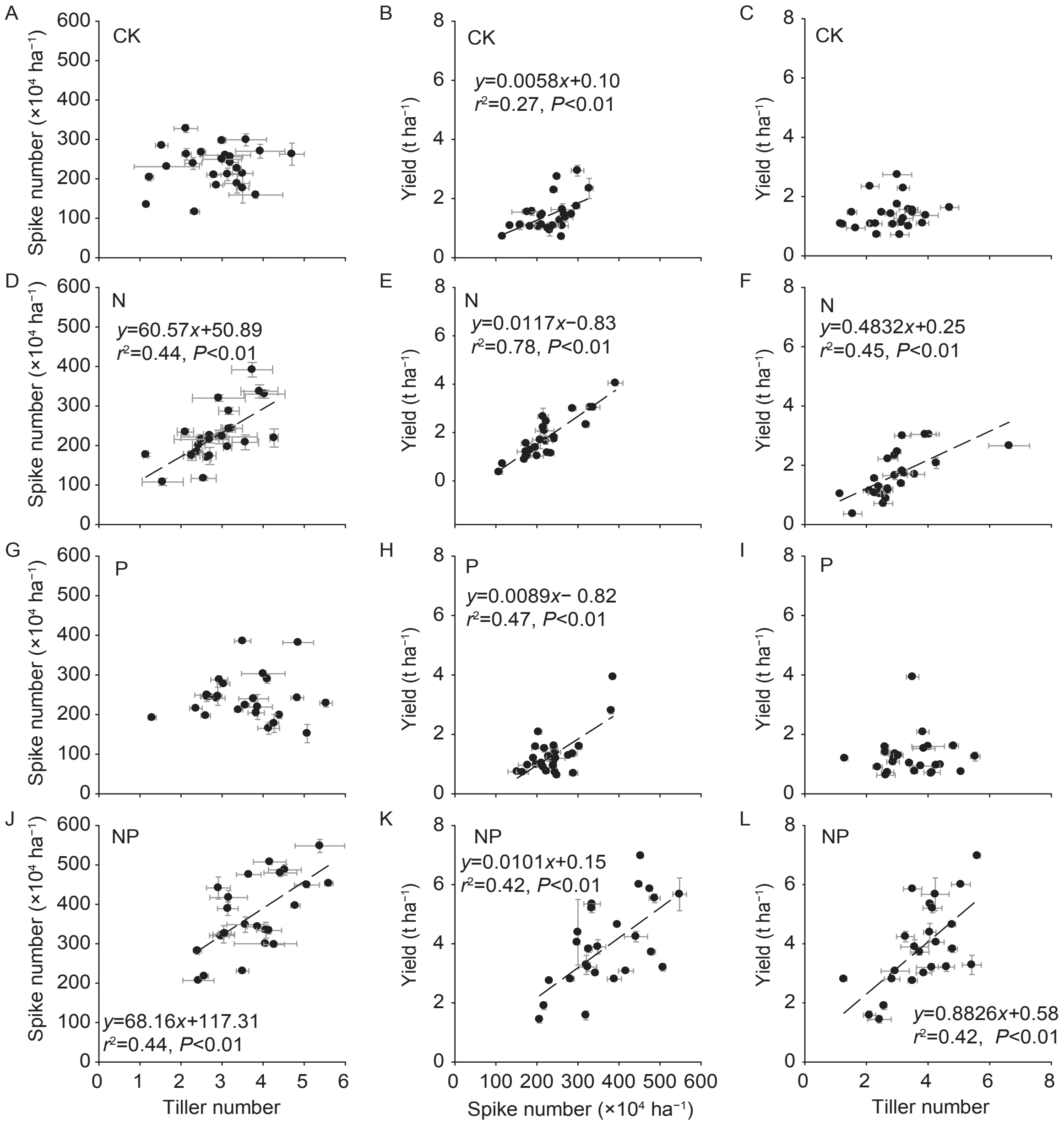

Fig. 3 Correlations between spike number and tiller number (A, D, G and J), between grain yield and spike number (B, E, H and K), and between grain yield and tiller number (C, F, I and L). CK, control without fertilizer; N, mineral nitrogen fertilizer alone; P, mineral phosphorus fertilizer alone; NP, mineral nitrogen and phosphorus fertilizer together. Bars are SD (n=3).

the available phosphorus content; second, the phosphorus deficiency either reduced the tiller appearance through the inhibition of cell division and expansion (Prystupa *et al.* 2003) or it reduced potential tiller sites as the phosphorus deficiency decreased the leaf appearance rates (Skinner and Nelson 1994); in addition, the lower stomatal conductance and mesophyll characteristics of crop leaves in soils with phosphorus deficiency could have resulted in the reduction of the number of tillers (Jacob and Lawlor 1991). However, P treatment did not increase the grain yield due to the unchanged spike number (Table 1). Furthermore, our study also showed the pronounced influence on the relationship of tiller number, spike number and grain yield under nitrogen deficiency or phosphorus deficiency. Although P treatment significantly promoted tiller emergence and development, nitrogen deficiency inhibited spike appearance and grain yield development. This was evidenced by the strong correlations among tiller number, spike number and grain yield in both nitrogen-supplied fertilizer treatments (N and NP) but the weak correlations among them without nitrogen

Table 2 Variation of mean grain number and thousand-grain weight among fertilization practices

Treatment[1)]	Grain number per spike (no.)	Thousand-grain weight (g)
CK	19.70±5.26 a	42.91±5.03 a
N	19.83±5.41 a	44.20±4.41 ab
P	18.50±5.03 a	44.56±3.73 ab
NP	22.91±5.73 b	46.00±4.63 b

[1)] CK, control without fertilizer; N, mineral nitrogen fertilizer alone; P, mineral phosphorus fertilizer alone; NP, mineral nitrogen and phosphorus fertilizer together.

Different letters indicate significant difference at $P<0.05$, and values are mean±SD ($n=3$).

being supplied (CK and P) (Fig. 3). Nitrogen promoted the process of tillers contributing to spike development; this was confirmed by the higher slope ratio of correlations between tillers and spikes in the nitrogen-supplied treatments (N and NP) in the present study (Fig. 3-D and J).

4.2. Divergent responses of tillers and yield to fallow precipitation

Soil water, mainly derived from the limited local precipitation, is typically a primary constraint for crop growth in drylands in arid and semiarid regions (Li *et al.* 2009; Guo *et al.* 2012b). Previous studies in the same experiment have shown dynamic variations of soil water under different fertilized soils, and wheat under fertilized soil must deplete more soil-water to keep a higher yield. Precipitation is the sole source of soil water supply for crop growth, and fallow precipitation which occurs from July to September therefore can account for up to 60% of the annual precipitation in the study region, thereby playing a key role in winter wheat growth (Guo *et al.* 2012b; Cao *et al.* 2017). Grain yield was significantly and positively correlated with fallow precipitation except in the P alone treatment (Fig. 2), which is consistent with previous studies (Guo *et al.* 2012b; He *et al.* 2016). Tiller and spike development are crucial to the final grain yield (Ishag and Taha 1974; Davidson and Chevalier 1990; Prystupa *et al.* 2003; Golba *et al.* 2018; Ren *et al.* 2019). In the present study, we systematically evaluated the responses of tillers and spikes to fallow precipitation and their contributions to final grain yield development (Figs. 2 and 3). Although tillers and spikes are strongly correlated with grain yield (Fig. 3), the responses of tillers and spikes to fallow precipitation were different from the responses of grain yield to fallow precipitation. Under adequate nutrient supply (NP), tillers and spikes increased with greater fallow precipitation, which was similar to the responses of grain yield to fallow precipitation variation. With P fertilization alone, only the number of tillers increased with fallow precipitation (less than 314 mm), while spike number and grain yield only slightly responded to fallow precipitation (Fig. 2). With N fertilization alone, tiller number, spike number and grain yield increased with greater fallow precipitation (less than 314 mm; Fig. 2).

Accurate simulation of winter wheat growth is not only crucial for predicting future yield under a changing climate but also for accurately predicting the nutrient and water cycles for winter wheat in the dominant regions (Lu *et al.* 2017). A mechanistic model of crop growth has been used in the past to simulate and predict the crop growth, such as the DeNitrification-DeComposition (DNDC), Community Land Model (CLM), crop estimation through the resource and environment synthesis-wheat model (CERES-Wheat), etc. (Li *et al.* 1992; Lu *et al.* 2017). However, most of these models were designed to directly simulate the leaf area index by using environmental factors and then predict the grain yield (DNDC and CLM) (Lu *et al.* 2017). In the present study, we found that fertilization and fallow precipitation significantly impacted the tillering of winter wheat, which could result in the variation of the leaf area index (Rodriguez *et al.* 1998b). Such variations of the leaf area index induced by tillering will decrease the accuracy of these aforementioned models for predicting crop growth. Incorporating the impacts of environmental factors in tiller phenological stages will help us to accurately understand and predict crop growth in rain-fed agricultural regions.

5. Conclusion

Tillering is an important process in the yield development of winter wheat. Phosphorus fertilization alone significantly increased tiller number, whereas N fertilization alone had less of an effect on tiller number. Nitrogen and P together significantly increased mean tiller number both in dry and wet years. Tiller number was significantly and positively correlated with fallow precipitation in dry years for all fertilizer treatments, whereas it was weakly and either positively or negatively correlated with fallow precipitation in wet years depending on the treatments. Our observations highlight the divergent responses of tiller number to fallow precipitation and fertilization.

Acknowledgements

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Declaration of competing interest

The authors declare that they have no conflict of interest.

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