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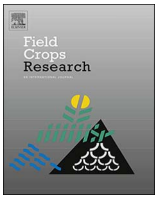

Synergy between breeding for yield in winter wheat and high-input agriculture in North-West China

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ABSTRACT

The aims of this paper were to explore the response of winter wheat grain yield and its components to supply of resources (nutrients, water), and how this response changed with varieties selected for yield in north-west China between 1970s and 2010s. Three varieties representing the decades 1980, 2000, and 2010 in season 2013–14, and five varieties representing the decades from 1970 to 2010 in season 2014-15 were combined factorially with 11 input levels (9 nutrient treatments under irrigation and 2 nutrient treatments in rainfed condition), returning a range of environmental mean yield from 1.1 to 7.3 t ha^{-1}. Yield ranged from 0.9 t ha^{-1} for the oldest variety under rainfed conditions and low input of nutrients to 8.3 t ha^{-1} for the newest variety under irrigation and high supply of nutrients, biomass ranged from 2.3 to 18.2 t ha^{-1}, and harvest index ranged from 0.33 to 0.49. The interactions between varieties and supply of resources were analysed from the perspective of phenotypic plasticity, quantified as the unitless slope of linear models relating the trait for each variety and the environmental mean of the trait. Plasticity of yield and plasticity of grain number increased with year of cultivar release, reflecting the enhanced ability of newer varieties to capture the benefits of higher inputs. Plasticity of harvest index declined with year of release, highlighting the stability of harvest index of newer varieties compared to their older counterparts. Our study demonstrates the synergy between breeding and agronomy whereby selection for yield has improved the ability of winter wheat to capture the benefits of higher inputs that has been a major feature of Chinese agriculture over the last six decades.

1. Introduction

World-wide, increase in crop yield on historical time scales has largely resulted from a combination of improved genetics and increased availability of nitrogen and water (Sinclair and Rufty, 2012), reflecting the synergy between breeding and agronomy (Fischer, 2009). Breeding and agronomy have dramatically increased productivity of Chinese agriculture over the last six decades; some synergies have been demonstrated but many have been overlooked (Zhang et al., 2015).

Genetic gains in wheat yield, and the changes in crop phenotype in response to breeding for yield have been quantified all over world, e.g. China (Zhou et al., 2007; Tian et al., 2011; Xiao et al., 2012; Sun et al., 2014), UK (Austin et al., 1980; Shearman et al., 2005), the United States (Donmez et al., 2001), Canada (Iqbal et al., 2016), Australia (Siddique et al., 1989; Sadras and Lawson, 2011), France (Brancourt-Hulmel et al., 2003), Spain (Sanchez-Garcia et al., 2013), Chile (del Pozo et al., 2014), Iran (Miri, 2009; Khodarahmi et al., 2010) and Argentina (Slafer and Andrade, 1989). A global comparison showed absolute genetic gain (kg ha^{-1} y^{-1}) for wheat has been larger in higher-yielding environments, with higher supply of water and nitrogen (Sadras et al., 2016).

Many studies have focused on the interaction between genetic improvement in wheat and fertilizer rates (Ortiz-Monasterio et al., 1997; Brancourt-Hulmel et al., 2003; Sylvester-Bradley and Kindred, 2009; Tian et al., 2011; Sadras et al., 2016). In France, 14 wheat cultivars released from 1946 to 1992 were tested in 26 environments; modern varieties had a good response to both high and low inputs (N rate, fungicide). Nevertheless, in solo N-input treatments, old varieties achieved a higher yield at low N rate, while modern cultivars achieved higher yield at high N rate (Brancourt-Hulmel et al., 2003). A similar cross over interaction was found for wheat varieties released between 1950 and 1985 in Mexico (Ortiz-Monasterio et al., 1997). In the UK, Sylvester-Bradley and Kindred (2009) found that the rate of N to achieve peak yield was greater in new cultivars (174 kg N ha^{-1}) than in the old ones (146 kg N ha^{-1}). In the Yangtze River Basin of China, wheat yield increased linearly with year of release from 1950s to 2000s and the annual rate of increment was higher at the highest N rate (Tian et al., 2011). Sadras et al. (2016) compared the impact of breeding for

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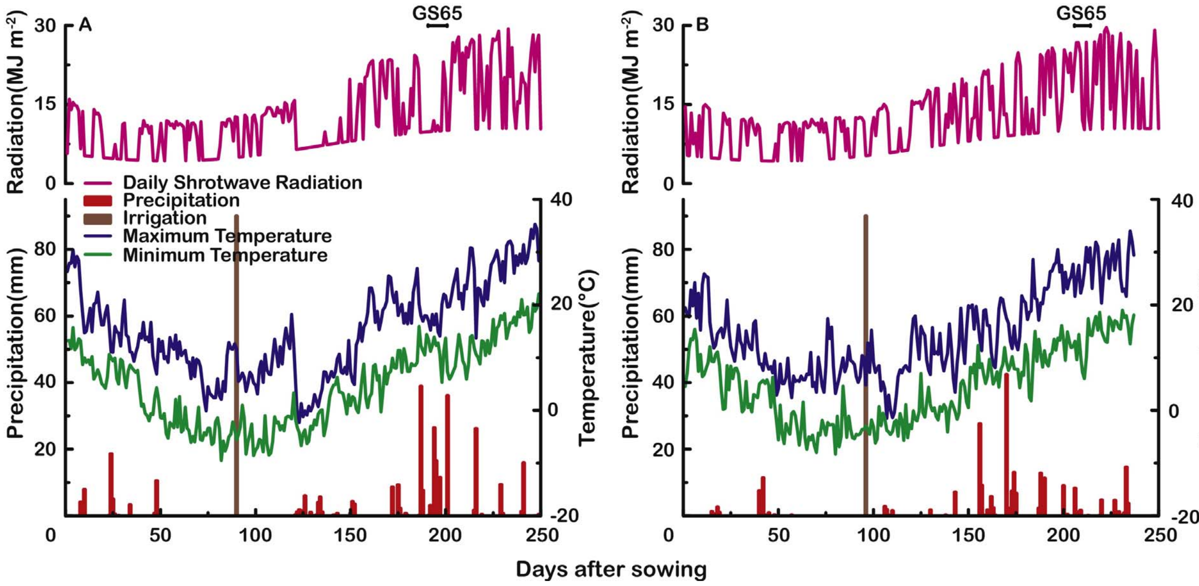

Fig. 1. Daily shortwave radiation, maximum and minimum temperatures, rainfall and irrigation during the period of wheat growth in 2013–2014 (A) and 2014–2015 (B). The horizontal bar represents the range of anthesis (GS65) for all the varieties.
Source: National Meteorological Observing Station in Yangling, Shaanxi province, China.

Table 1
Eleven growing environments from the combination of nutrient and water inputs Application rates are in kg ha^{-1}. Top 9 treatments from Control to M2N2P2 are irrigated, dControl and dMNPK are rainfed. Fertilizers were applied 2–3 days before sowing.

Treatment	Manure			Fertilizer			Total		
	N	P	K	N	P	K	N	P	K
Control	0	0	0	0	0	0	0	0	0
N1P1	0	0	0	75	13	0	75	13	0
N2P2	0	0	0	120	26	0	120	26	0
M1	75	31	34	0	0	0	75	31	34
M1N1P1	75	31	34	75	13	0	150	44	34
M1N2P2	75	31	34	120	26	0	195	57	34
M2	120	50	55	0	0	0	120	50	55
M2N1P1	120	50	55	75	13	0	195	63	55
M2N2P2	120	50	55	120	26	0	240	76	55
dControl	0	0	0	0	0	0	0	0	0
dMNPK	95	39	43	40	47	56	135	87	99

Table 2
Winter wheat varieties released in Guanzhong Plain between 1970s and 2010s. Plant height and flowering time (mean ± s.e.) are reported for the lowest (dControl: rainfed, unfertilised) and highest input (M2N2P2 receiving 240 kg N ha^{-1}, 76 kg P $ha^{-1}$and 55 kg K ha^{-1} under irrigation) environments. In 2013–2014 we used the varieties released in 1980s, 2000s and 2010s; all five varieties were used in 2014–2015.

Variety	Year of release	Plant height (cm)		Flowering time (days after sowing)	
		dControl	M2N2P2	dControl	M2N2P2
Aifeng 3	1970s	56 ± 1.9	77 ± 1.7	202 ± 0.7	196 ± 0.0
Xiaoyan 6	1980s	65 ± 2.9	87 ± 3.2	202 ± 0.6	196 ± 0.6
Shaan 229	1990s	58 ± 2.8	79 ± 2.6	202 ± 0.3	198 ± 0.0
Xiaoyan 22	2000s	59 ± 0.8	85 ± 1.2	202 ± 0.6	196 ± 0.3
Xinong 979	2010s	52 ± 1.7	80 ± 2.4	202 ± 0.6	196 ± 0.3

yield in the nitrogen economy of wheat in Australia, UK, Italy and Argentina. They found that the rate of increase in nitrogen uptake matched the rate of increase in grain yield with genetic improvement only in Australia. In the UK, Italy and Argentina, the rate of change in nitrogen uptake was lower than the rate of increase in yield, and this resulted in lower protein concentration in grain.

More broadly, where the combined effects of breeding and agronomy have been tested, yield gains have often been larger under more favorable conditions (Lobell et al., 2014; Richards et al., 2014), e.g. for wheat in Australia, yield increased at 9 kg ha^{-1} $year^{-1}$ under drought and 13.2 kg ha^{-1} $year^{-1}$ under more favorable conditions (Richards et al., 2014). For sorghum in Australia, however, combined breeding and agronomy improved yield faster under drought than under more favorable conditions (Potgieter et al., 2016). The direction of the interaction between availability of resources and yield improvement as driven by breeding, agronomy or both is thus variable, and needs direct assessment.

In this study, we quantified the interaction between breeding for yield and availability of resources in a setting of long-term soil fertility experiments (Yang et al., 2011a,b). We compared three (season 2013–2014) and five (season 2014–2015) milestone cultivars released from 1970s to 2010s in the Guanzhong region of Shaanxi province. Varieties factorially combined with 11 levels of input each season: nine long-term fertilizer treatments under irrigation and two fertilized treatments under rainfed conditions. The irrigated fertilizer experiment was established in 1980 (Yang et al., 2011a) and the rain-fed trail was established in 1990 (Yang et al., 2011b).

2. Materials and methods

2.1. Experimental site and crop husbandry

Experiments were conducted in Yangling, on the Guanzhong Plain, near the southern edge of Loess Plateau (34°17′51″N, 108°00′48″E, 534 m asl) during two seasons. Crops were hand-sown on October 10, 2013 and October 14, 2014, with stand density of 270 plants m^{-2}. Weeds were controlled by hand, insecticides for control of aphids were applied during grain filling, and no disease symptoms were apparent.

The soil is a silt clay loam Anthrosols (clay 32%, silt 52% and sand 16%) with a terric horizon derived from manure and loess material (FAO, 2014). The site is managed by the Chinese National Soil and Fertilizer Efficiency Monitoring Base for Loessial Soil (Yang et al., 2011a,b). Two long-term fertilizer experiments provided the background to this study. The first was set up in the summer of 1980 and involved a winter wheat/summer maize (*Triticum aestivum* L., *Zea mays* L.) double cropping system with irrigation. The second was set up in the autumn of 1990 and involved rainfed winter wheat/summer fallow. As a result of these long-term treatments, soil organic matter ranged from

Table 3

Yield (mean ± s.e.) of winter wheat varieties released in Guanzhong Plain between 1970s and 2010s under lowest (Control and dControl) and highest input of nutrients (M2N2P2 and dMNPK) under irrigated and rainfed conditions. In 2013–2014 we used the varieties released in 1980s, 2000s and 2010s; all five varieties were used in 2014–2015.

Season	Variety	Mean	Irrigated		Rainfed	
			Control	M2N2P2	dControl	dMNPK
2013–2014	1980s	3374 ± 793	1106 ± 124	4528 ± 221	929 ± 148	4314 ± 100
	2000s	4567 ± 1160	1470 ± 110	6651 ± 381	1362 ± 186	7158 ± 67
	2010s	4454 ± 1298	1056 ± 181	7503 ± 412	1018 ± 194	6231 ± 198
2014–2015	1970s	4850 ± 1301	1497 ± 332	7268 ± 258	1231 ± 147	6056 ± 32
	1980s	4385 ± 1124	1368 ± 121	6460 ± 419	1398 ± 140	5741 ± 152
	1990s	4834 ± 1219	1195 ± 141	6569 ± 36	1493 ± 21	6383 ± 219
	2000s	5287 ± 1347	1823 ± 205	6999 ± 269	1625 ± 87	7140 ± 202
	2010s	5250 ± 1485	1219 ± 169	8322 ± 334	1071 ± 98	7733 ± 227

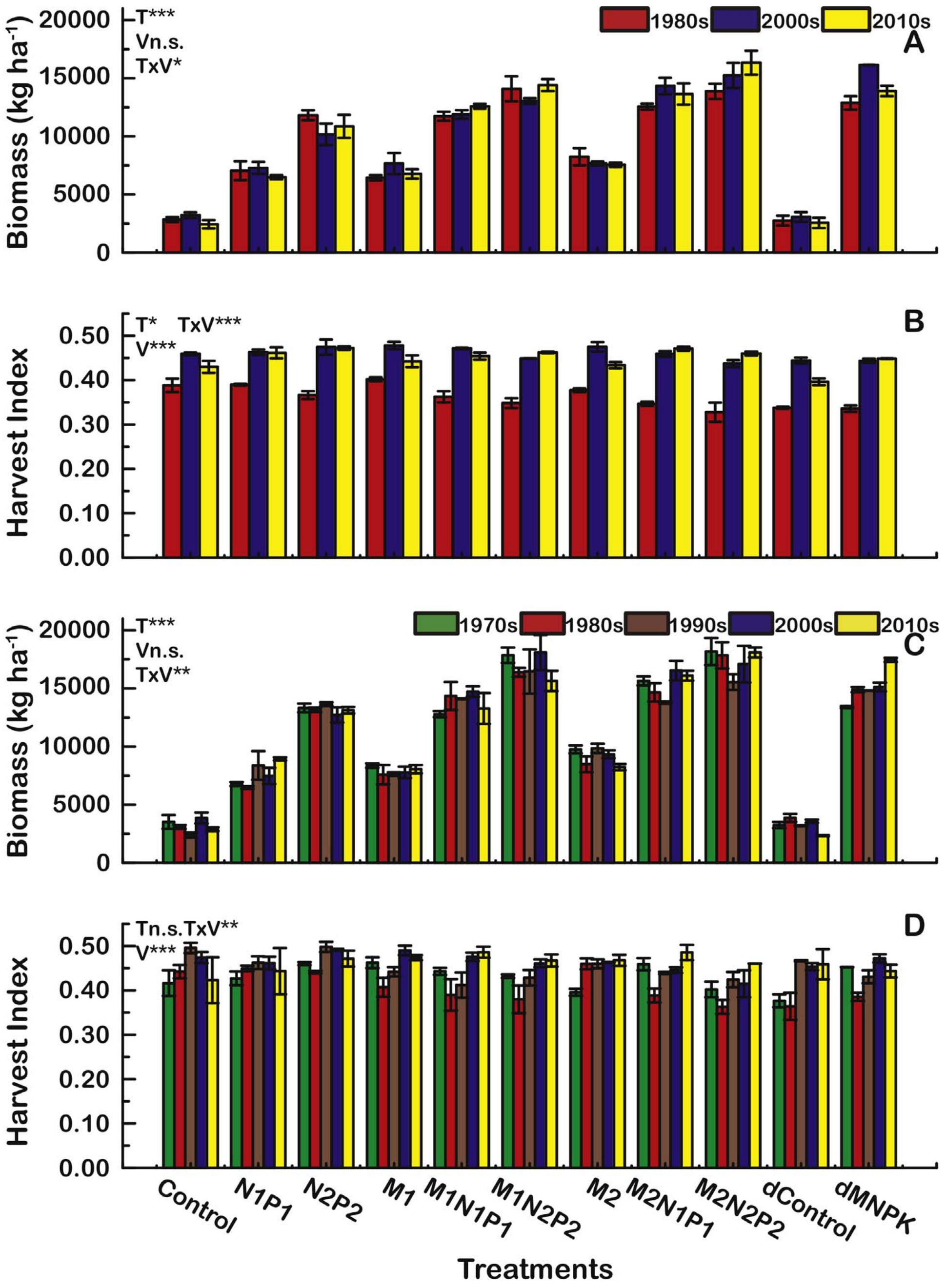

Fig. 2. Biomass and harvest index of winter wheat cultivars released in different decades under different nutrient and water inputs in season 2013–2014 and 2014–2015. Treatment codes are in Table 1. The error bars are two standard errors of the means. Significance of treatments (T), varieties (V) and interaction (TxV) is indicated as *, **, *** for $p < 0.05$, $p < 0.01$ and $p < 0.001$, respectively.

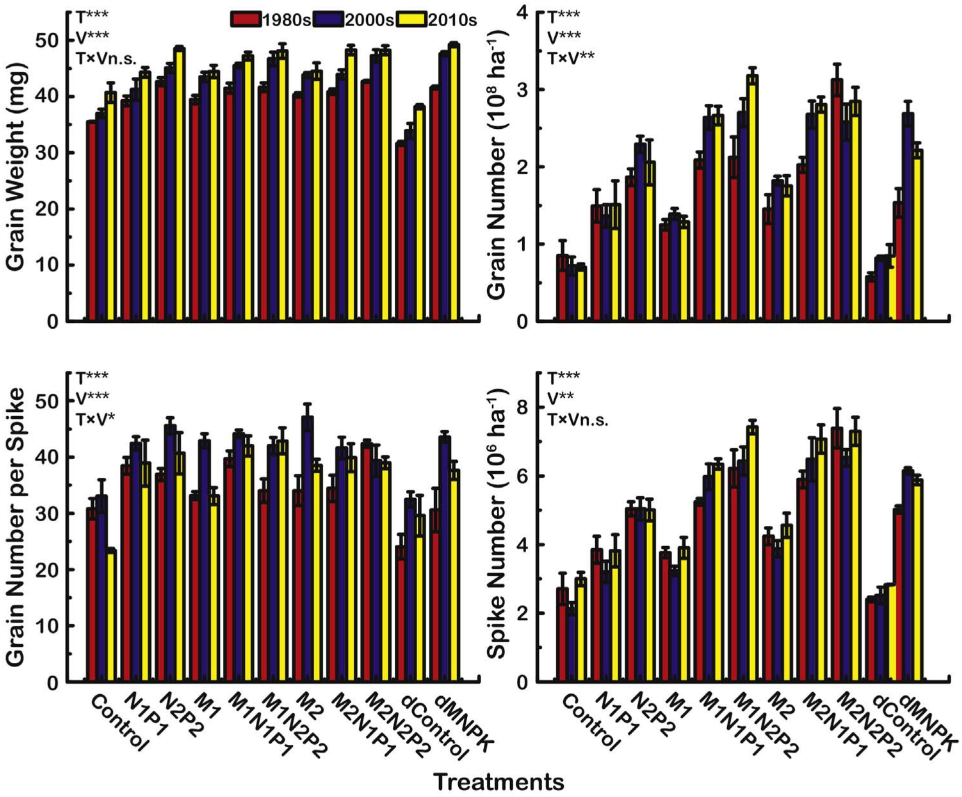

Fig. 3. Yield components of winter wheat cultivars released in different decades under different nutrient and water inputs in season 2013–2014. Treatment codes are in Table 1.The error bars are two standard errors of the means. Significance of treatments (T), varieties (V) and interaction (TxV) is indicated as *, **, *** for $p < 0.05$, $p < 0.01$ and $p < 0.001$, respectively.

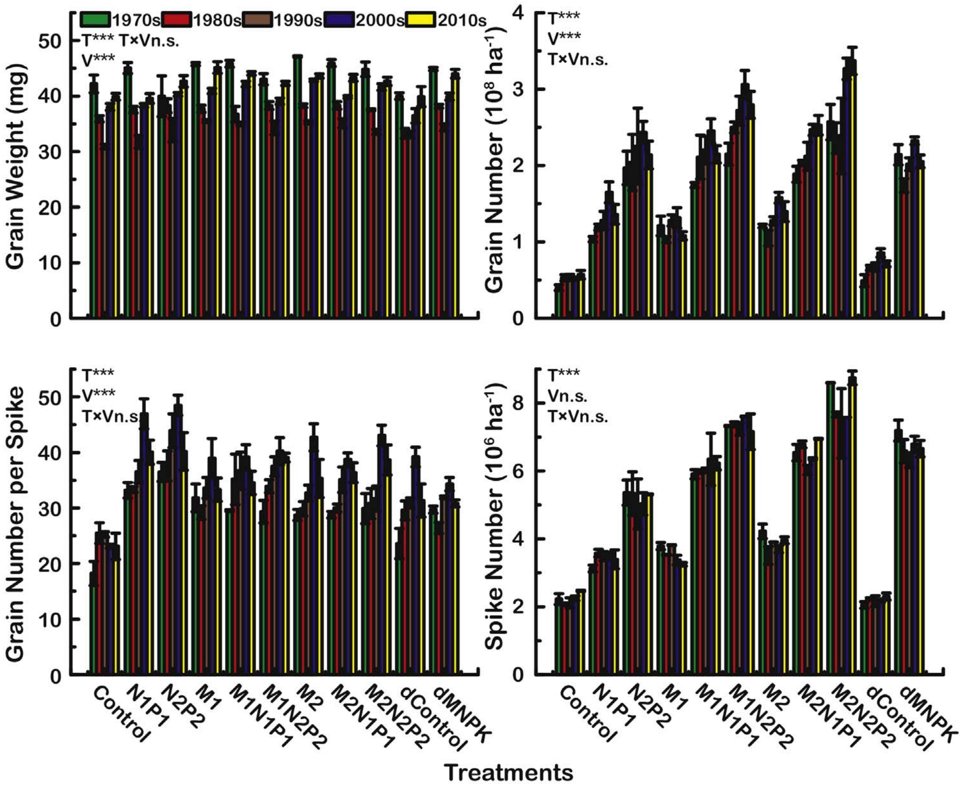

Fig. 4. Yield components of winter wheat cultivars released in different decades under different nutrient and water inputs in season 2014–2015. Treatment codes are in Table 1.The error bars are two standard errors of the means. Significance of treatments (T), varieties (V) and interaction (TxV) is indicated as *, **, *** for $p < 0.05$, $p < 0.01$ and $p < 0.001$, respectively.

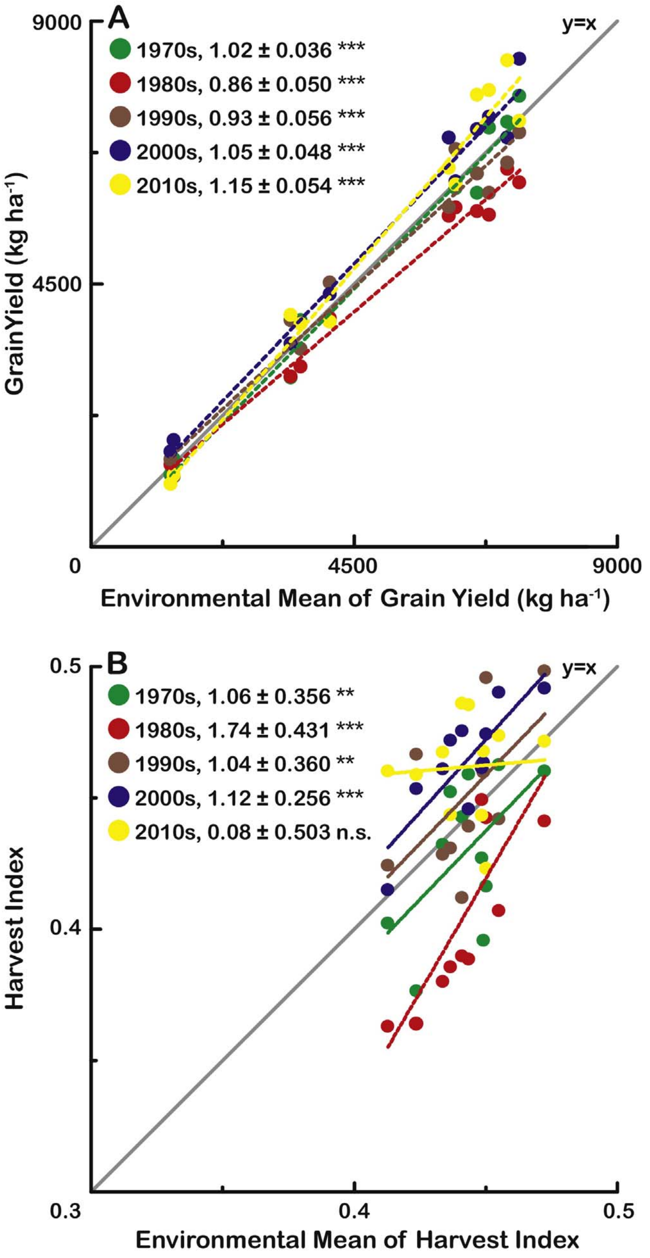

Fig. 5. Relationship between yield and harvest index and their corresponding environmental means in the second season 2014–2015. Numbers next to symbols are slopes ± standard error. Significance of slopes is indicated as ns, **, *** for $p > 0.05$, $p < 0.01$ and $p < 0.001$, respectively.

6.7 to 19.4 g kg^{-1} (Yang et al., 2011a,b).

Mean annual temperature is 13.0 °C, and a mean annual precipitation was 581 mm during 1957–2013, 54% of which fells between July and September (Dai et al., 2016). Fig. 1 shows the weather during the experiments. Seasonal precipitation (October–June) was 303 and 239 mm for 2013–2014 and 2014–2015, which were close to the 57-year average (1957–2013) (266 mm) (Dai et al., 2016). Rainfall from GS 65 to GS 92 accounted for 30% of seasonal rain in 2014, and 21% in 2015. Extreme temperatures during the critical period were not apparent.

2.2. *Varieties, inputs and experimental design*

The experiment has a factorial split-plot design with three replicates, where fertilizer and water inputs were assigned to the main plot (Table 1) and wheat varieties (Table 2) assigned to the subplots; both main plots and subplots were distributed randomly. In consultation with local breeders, five varieties were selected according to three criteria: they were agronomically well adapted to the region, widely used by growers, and they have a narrow range of phenology and plant height (Table 1).

In 2013–2014, we combined factorially three varieties (released in the 1980s, 2000s and 2010s) and eleven growing conditions, including nine fertilizer treatments under irrigation (flood irrigated with approx. 90 mm early in January) and two fertilizer treatments under rainfed conditions (Table 2). Under irrigation, the fertilizer treatments combined manure (M) and inorganic N and P fertilizers returning nine treatments (Table 1). In the rainfed condition, we compared unfertilized controls with high nutrient input combining manure and inorganic fertilizer. In 2014–2015, we combined factorially five varieties (Table 2) and eleven growing conditions, as in season 2013–2014. Individual plot size ranged from 30 to 499 m^2, and from 24 to 85 rows, spaced at 0.25 m.

2.3. *Measurements*

Crops were monitored regularly to establish key phenological stages using the scale of Zadoks et al. (1974). Plant height was measured from the ground to the top of plant with a ruler after anthesis (GS65). At maturity, a 0.5–5.8 m^2 area was harvested for each replicate to determine shoot biomass, grain yield and its components; the range in sample size reflects the original setting of the long-term trials (Yang et al., 2011a,b). Harvest index was calculated as the ratio of grain yield and shoot biomass at maturity. Grain number per spike was determined in a sample of 10 plants per replicate. Spike number was determined at grain filling (GS75) in 2014 and anthesis (GS65) in 2015. Grain number was quantified using grain number per spike multiplied by spike number and grain weight was measured in sub-samples.

2.4. *Statistical analysis*

We used ANOVA to assess yield traits response to treatments (T), varieties (V) and treatment × variety interaction. Interactions were further explored from the perspective of phenotypic plasticity (Sadras and Richards, 2014). Plasticity was quantified as the unitless slope of linear models relating the trait for each variety and their environmental mean of the trait (Finlay and Wilkinson, 1963). Environmental mean was the value of the trait averaged across varieties for each growing condition.

3. Results

3.1. *Grain yield*

In both seasons, yield responded to all three sources of variation, variety, treatment and their interaction (all $p < 0.0001$). Yield ranged from 0.9 t ha^{-1} for the oldest variety under rainfed conditions and low input of nutrients, to 8.3 t ha^{-1} for the newest variety under irrigation and high supply of nutrients (Table 3). Yield gains were significant under high input (M2N2P2) with rates of 0.55 ± 0.175% y^{-1} ($p = 0.0005$), or 37 kg ha^{-1} y^{-1} ($p = 0.03$), but rates were not significant ($p > 0.61$) under low input (dControl).

3.2. *Biomass and harvest index*

In 2013–2014, biomass and harvest index responded to all three sources of variation, except for lack of variety effect on biomass (Fig. 2). Biomass responses to treatments were generally similar to those described for yield. In all treatments, harvest index in the oldest variety was lower than in the newer varieties.

In 2014–2015, the responses of biomass and harvest index were similar to those in the first season, except for a lack of treatment effect

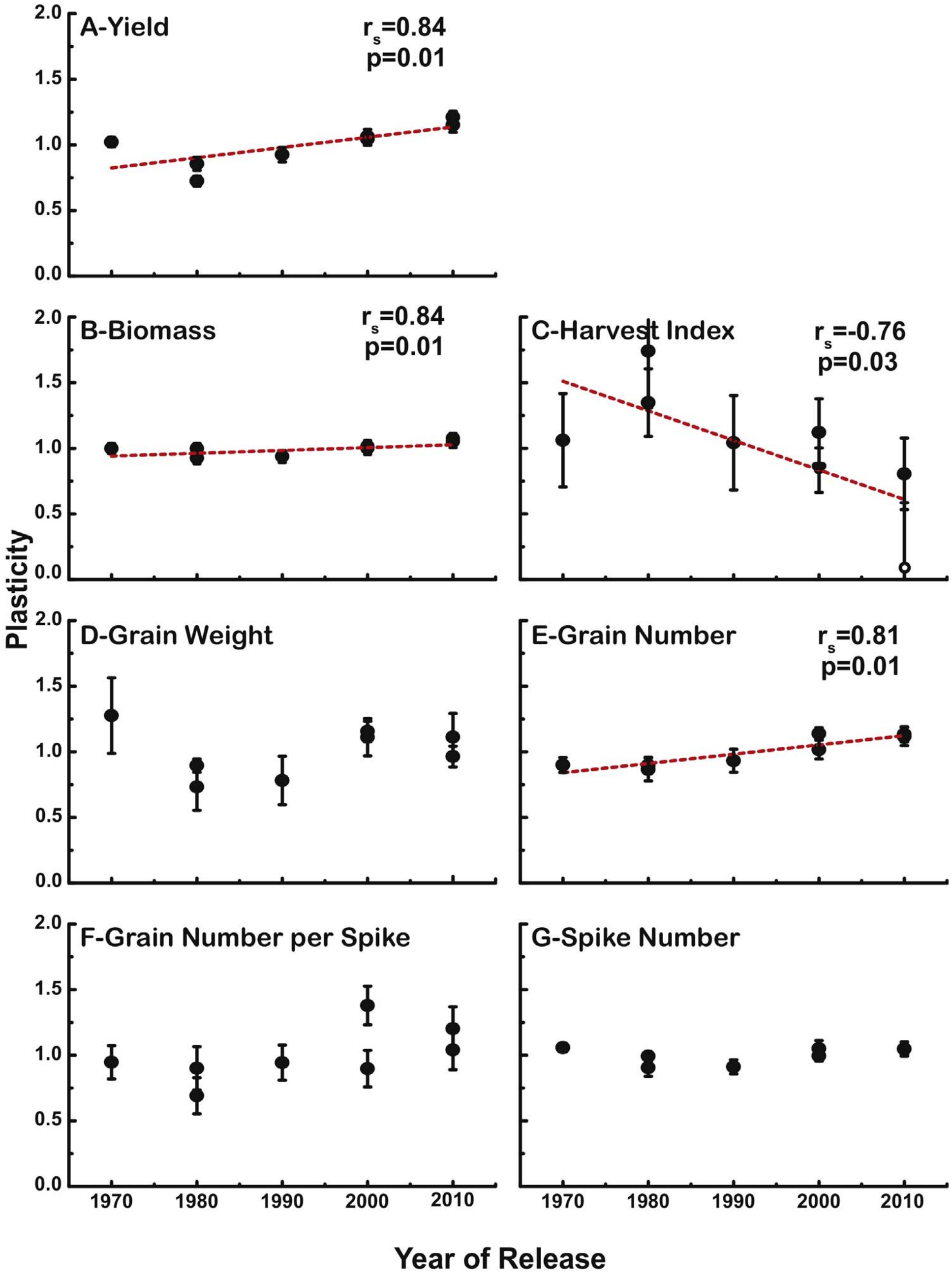

Fig. 6. Plasticity (± s.e.) of grain yield, biomass, harvest index and yield component in winter wheat released in different decades. Solid symbols represent significantly different from zero ($p < 0.05$); open symbol represents $p > 0.05$. Fitted lines are shown when Spearman correlation coefficient, r_s is significant ($P < 0.05$).

in harvest index (Fig. 2).

3.3. Grain number and grain weight

In 2013–2014, all yield components responded to treatments and varieties; interaction effects were detected for grain number and grain number per spike (Fig. 3). The variety released in the 1980s had a lower grain weight in all the treatments and lower grain number under high inputs.

In 2014–2015, yield components responded to varieties and treatments but not to the interaction (Fig. 4). Newer varieties set more grain per unit area, particularly under high inputs, and this was mostly related to grain number per spike.

3.4. Phenotypic plasticity of grain yield and its components

Fig. 5 illustrates the analysis of plasticity for yield and harvest index. Across the environments and varieties, yield ranged from 1.1 to 8.3 t ha^{-1}, and plasticity of yield ranged from 0.86 to 1.15. The newest variety had the highest plasticity of yield. Plasticity of yield was mostly related to high responsiveness to high-yielding environments. Across the environments and varieties, harvest index ranged from 0.36 to 0.50, and plasticity of harvest index ranged from 0.08 in the newest variety to 1.74 for the variety released in the 1980s. The high plasticity of HI in this variety was mostly related to a severe reduction in HI under high input of nutrients in irrigated crops (Fig. 2).

The relationship between plasticity of yield-related traits and year release are shown in Fig. 6. There was a significant time-trend in the plasticity of four traits. Plasticity increased with year of release for yield, biomass and grain number, while it decreased for harvest index.

4. Discussion

Sustained differences in input of mineral nutrients and organic matter over long-term experiments change soil chemical and physical properties with direct implications for crop yield (Girma et al., 2007; Yang et al., 2011a). In our study, this is reflected in significant interactions between resources and varieties affecting grain yield, biomass and HI (Fig. 2 and Table 3). Previous studies in China showed lack of change in shoot biomass with breeding for yield (Tian et al., 2011), whereas recent improvements in biomass were reported for the UK and Australia (Shearman et al., 2005; Sadras and Lawson, 2011). Here we found breeding improved plasticity of biomass over the 1970–2010 period, but the rate of change was modest compared to the change in plasticity of harvest index (Fig. 6).

Genetic improvement for yield under high availability of resources might also improve yield under stress; however, this correlation depends on the particular combination of varieties and environments (Sadras and Richards, 2014). In our study, a cross-over at around 1.8 t ha^{-1} suggests a tradeoff between yield under high inputs and yield under stress for the varieties released in 1980s and 2010s (Fig. 5). However, this trade-off is of little agronomic significance in a region where yield average 3.5 t ha^{-1} (Zhang et al., 2013). Selection for yield increased yield plasticity from 1970s to 2010s (Fig. 6). Similarly, selection for yield increased yield plasticity (range from 0.64 to 1.37) of winter wheat in the North American Great Plains from 1874 to 2010 (Grogan et al., 2016).

Increased HI has been a common source of yield improvement in wheat (Brancourt-Hulmel et al., 2003; Shearman et al., 2005; Tian et al., 2011), and has been partially associated with reduced plant height after the introduction of dwarfing genes (Mathews et al., 2006; Zhou et al., 2007). In our study, we used cultivars spanning a narrow range of plant height (Table 1).

High plasticity of yield was associated with low plasticity of harvest index and high plasticity of grain number. Plasticity in harvest index reflected a large interaction between genotype and environment. First, it is important to note that low HI occurred with the highest input condition. Second, the newest variety had the lowest plasticity for HI, reflecting its capacity to maintain high allocation to grain under high input of nutrients and water. In comparison to ours, Tian et al. (2011)'s study in China included a broader set of varieties released from 1950 to 2005 and a narrow range of N fertilizer (0–225 kg per ha); under these conditions, cultivars released in recent two decades had a larger variability in HI from 0.20 to 0.48. Ortiz-Monasterio et al. (1997) compared wheat varieties released between 1950 and 1985 in Mexico under nitrogen fertilizer rates from 0 to 300 kg ha^{-1}. Similar to our findings, they reported higher stability of HI in newer varieties, and a drop in HI from 0.30 to 0.22 in response to nitrogen supply in their oldest variety. In their study, however, the oldest variety was previous to introduction of dwarfing gene.

Theory and empirical evidence show the high plasticity of seed number and the stability of seed weight (Sadras, 2007). Bradshaw (1965) initially defined a hierarchy of plasticities in the evolution of processes maximizing fitness, where different solutions may be developed in different plants. For all such solutions, an essential common character was that some traits, due to various reasons, held more or less constant, whereas others showed high plasticity. Sadras and Slafer (2012) used this notion to discussed the relationship among plasticity in wheat grain yield and its components. In our study, selection for yield increased plasticity of grain number but plasticity of grain weight remained unchanged. Spike number was positively associated with grain yield, biomass and their plasticity in previous studies (Sadras and Rebetzke, 2013; Slafer et al., 2014). Possibly small, non-significant trends for the spike number and grains per spike combined to generate a significant trend of grain number. Therefore, future breeding should focus on enhancing the plasticity of spike number and biomass emerging from an improved capacity to capture high inputs of resources; the tradeoff between yield under high and low input deserves attention.

In conclusion, the interaction between selection for yield and availability of resources in this study showed a synergy between breeding and agronomy whereby selection for yield has improved the ability of winter wheat to capture the benefits of higher inputs that has been a major feature of Chines agriculture over the last six decades.

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