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Shifts in nitrogen and phosphorus uptake and allocation in response to selection for yield in Chinese winter wheat

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Abstract. This study assessed changes in nitrogen (N) and phosphorus (P) uptake and partitioning in response to selection for yield in milestone varieties of Chinese winter wheat (*Triticum aestivum* L.). We established a factorial trial combining 11 nutrient–water regimes with three (2013–14) and five (2014–15) varieties released from 1970 to 2005. Grain yield increased at a rate of 0.46% year^{-1}, with no apparent increase in the uptake of nutrients. Nitrogen harvest index did not change, and P harvest index increased at a rate of 0.15% year^{-1}. Consequently, yield per unit N uptake and yield per unit P uptake increased at similar rates (0.4% year^{-1}) at the expense of nutrient concentration in grain, which declined at a rate of 0.47% year^{-1} for N and 0.31% year^{-1} for P. No trends in N nutrition index were found. Selection for yield in wheat increased the yield per unit nutrient uptake at the expense of grain nutrient concentration. Further gains in yield need to be matched by increasing N uptake to maintain grain protein. Dilution of P in grain needs to be considered in terms of the putatively undesirable role of phytate for human nutrition, and the need for P reserves in seed for crop establishment.

Additional keywords: breeding, grain nutrient concentration, nitrogen use efficiency, phosphorus use efficiency.

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Introduction

Globally, wheat breeding has significantly increased grain yield over the last five decades but at a declining relative rate (Fischer *et al*. 2014). The impact of selection for yield on the nitrogen (N) economy of wheat has been compared for breeding programmes in Australia, UK, Italy and Argentina (Sadras *et al*. 2016). During the last five decades in Australia, the rate of increase in N uptake matched the rate of increase in grain yield, leading to unchanged yield per unit N uptake. In addition, N harvest index (i.e. ratio of N in grain to N in total biomass) and grain protein concentration remained stable. By contrast, selection for yield of bread wheat in UK and Argentina and selection for yield of durum wheat in Italy did not increase N uptake, or where it did, the rate of increase was lower than the rate of increase in grain yield. Consequently, yield per unit N uptake increased while grain protein declined (Sadras *et al*. 2016). Tian *et al*. (2016) found similar results in China, when comparing cultivars developed between the 1950s and 2000s; the rate of change in yield (0.8% year^{-1}) was higher than the rate of increase in N uptake (0.27% year^{-1}), leading to decreased grain N concentration. In their experiment, however, crops where grown under two N rates and a single phosphorus (P) rate, and interactions between variety and N supply were not reported (Tian *et al*. 2016). In France, modern varieties had higher N uptake and N harvest index but grain N concentration decreased compared with older varieties (Brancourt-Hulmel *et al*. 2003).

Fewer studies have reported the effects of breeding for yield on P uptake and allocation in wheat. In Argentina, breeding for yield did not increase P uptake, hence the increase in yield per unit P uptake. In addition, P harvest index increased but at a low rate compared with yield, resulting in a decrease in grain P concentration (Calderini *et al*. 1995*b*). Egle *et al*. (1999) compared three new wheat varieties and one old variety released by CIMMYT. The new varieties had higher P uptake, while yield per P uptake improved slightly and grain P content did not decline significantly.

Nitrogen and P have differences in their soil and crop dynamics; therefore, it could be interesting to analyse the N and P economies in past wheat selection (Calderini *et al*. 1995*b*). Here we report field experiments in two successive seasons (2013–14, 2014–15) using three and five milestone cultivars, respectively, of winter wheat (*Triticum aestivum* L.) released between 1970 and 2005 in the Guanzhong region of Shaanxi province, and grown under contrasting nutrient and water supply in long-term fertiliser trials. The objective was to investigate the uptake and allocation of N and P to grain in response to variety, nutrient supply and their interaction.

Material and methods

Experimental design, varieties and environments

The experiments have been described in Wang *et al*. (2017) in a paper focusing on yield. Here we summarise key aspects of the study, with emphasis on N and P. Briefly, the experiment was conducted in Yangling, on the Guanzhong Plain, near the southern edge of the Loess Plateau (34°17′51″N, 108°00′48″E; 534 m a.m.s.l.). Two long-term fertiliser experiments, which are managed by the Chinese National Soil and Fertilizer Efficiency Monitoring Base for Loessial Soil, provided the background to this study. The history of fertilisation and crop rotation in these experiments was reported previously (Yang *et al*. 2011*a*, 2011*b*).

The soil is a silt clay loam (clay 32%, silt 52%, sand 16%) Anthrosol with a terric horizon derived from manure and loess material (FAO 2014). The experimental setup and growing conditions have been described (Wang *et al*. 2017). Briefly, the design was a split-plot with three replicates, where fertiliser and water inputs were assigned to the main plot (Table 1) and wheat varieties to the subplots. Varieties (and their release dates) were Aifeng 3 (1970), Xiaoyan 6 (1980), Shaan 229 (1993), Xiaoyan 22 (2003) and Xinong 979 (2005). Varieties had similar height and phenology (Wang *et al*. 2017). In 2013–14, we factorially combined three varieties (Xiaoyan 6, Xiaoyan22 and Xinong 979) and 11 growing conditions. In 2014–15, we factorially combined all five varieties and 11 growing conditions.

Measurements

Soil samples were taken before fertiliser input at sowing by using a hand auger to a depth of 200 cm in 20-cm layers. Nitrate-N was extracted from 4 g fresh soil with 50 mL of 1 M KCL and was determined with an AutoAnalyzer3 (AA3; SEAL Co., Germany) continuous flow analyser.

Crop phenology was monitored regularly by using the scale of Zadoks *et al*. (1974). Shoots were sampled at anthesis to determine the N nutrition index (sample area 0.25–0.5 m^2) (Hoogmoed and Sadras 2016) and at maturity (sample area 0.5–5.8 m^2) to determine biomass and nutrient content. Samples were separated into organ components (leaf, stem and spike at anthesis; leaf, stem, grain and chaff at maturity), which were dried in a forced-air oven at 65°C for 36 h, weighed, then milled through a 1-mm sieve. Milled samples were digested with concentrated sulfuric acid (98%) and hydrogen peroxide (≥30%). Nitrogen concentration was determined by micro-Kjeldahl and P concentration by the vanadate–molybdate method (Kitson and Mellon 1944). Uptake of N and P (grain + straw) at maturity was calculated as a function of concentration and biomass in different organs.

Table 1. Eleven growing environments from the combination of nutrient and water inputs, and the nitrogen (N), phosphorus (P) and potassium (K) application rates (kg ha^{-1}) in each environment

Treatments from Control to M2N2P2 are irrigated; dControl and dMNPK are rainfed; M, nutrients derived from manure. Table was published previously (Wang *et al*. 2017)

Treatment	Manure			Fertiliser			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

Data analyses

Following the definitions of Moll *et al*. (1982) and Gastal *et al*. (2015), we calculated N uptake efficiency, N and P utilisation efficiency, N and P harvest index, and N nutrition index. Biomass and yield data used in the calculations were reported previously (Wang *et al*. 2017). Nitrogen uptake efficiency was calculated as the ratio between N uptake at maturity and N supply in the soil calculated as the sum of initial nitrate-N in soil and fertiliser (Table 1); mineralisation of N was not measured. Nitrogen and P utilisation efficiency was calculated as the ratio between yield and N or P uptake at maturity. Nitrogen and P harvest indices were calculated as the ratio between N or P in grain and total N or P uptake at maturity. The N nutrition index was calculated as the ratio between actual and critical N concentration in the shoot at anthesis, using the N dilution curve for wheat reported by Justes *et al*. (1994). Because this curve was derived for well-watered crops, we restricted the calculation of the N nutrition index to our irrigated treatments (Hoogmoed and Sadras 2016).

For each season, we used two-way analysis of variance to assess the response of N- and P-related traits to treatment, variety and treatment × variety interaction.

The rate of change in yield and N- and P-related traits was calculated as the slope of the least-square linear regression expressed as a percentage of the value of the latest released variety for each treatment (Fischer *et al*. 2014; Sadras *et al*. 2016).

Results

Growing conditions

Environmental conditions during the experiment were described in Wang *et al*. (2017). Briefly, seasonal precipitation was 303 mm in 2013–14 and 239 mm in 2014–15, compared with 57-year rainfall average (1957–2013) of 266 mm. No extreme temperatures were apparent during the critical period of yield determination from stem elongation to 10 days after flowering (Fischer 1985). The combination of growing conditions and treatments generated a yield range of 0.9–8.3 t ha^{-1} during the two experimental seasons (Wang *et al*. 2017).

Nitrogen traits

Treatment, variety and interaction effects on N traits in the first and second season are summarised in Tables 2 and 3, respectively. In both seasons, treatments affected N uptake per unit available N and biomass per unit N uptake. Nitrogen uptake per unit soil N responded to variety only in 2013–14; note, however, that soil N did not include mineralisation, and this might introduce bias, particularly in the treatments with manure. Yield per unit N uptake, N harvest index and grain N responded to variety in both seasons. Interaction effects were detected for N uptake per unit soil N, yield per unit N uptake and N harvest

Table 2. Season 1 (2013–14): nitrogen (N) uptake per unit soil N available, biomass per unit N uptake, yield per unit N uptake, N harvest index, grain N concentration, and N nutrition index (ratio between actual and critical N concentration in the shoot at anthesis) of winter wheat varieties grown under different nutrient and water inputs

Significance of treatments (T), varieties (V) and interaction (T × V) indicated as: $*P < 0.05$; $**P < 0.01$; $***P < 0.001$; n.s., not significant ($P > 0.05$). Means followed by the same letter are not significantly different (using Fischer's l.s.d. at $P = 0.05$): lower case letters for comparison among treatments, and upper case letters for comparison among varieties. Treatments are as in Table 1

Variety release date	Control	N1P1	N2P2	M1	M1N1P1	M1N2P2	M2	M2N1P1	M2N2P2	dControl	dMNPK
N uptake per unit soil N available (T***, V**, T × V*)											
1980	0.83aA	0.28dA	0.51bcA	0.631bA	0.51bcA	0.39cdA	0.71abA	0.53bcA	0.42cdA	0.27dA	0.51bcA
2003	0.95aA	0.34cA	0.41bcA	0.86aA	0.51bcA	0.32cA	0.60bA	0.57bcA	0.44bcA	0.32cA	0.59bA
2005	0.69aA	0.29eA	0.44cdA	0.65abA	0.45cdA	0.43dA	0.66abA	0.52cdA	0.46cdA	0.29eA	0.55bcA
Biomass per unit N uptake (T***, Vn.s., T × Vn.s.)											
1980	93.7cdeA	108.0abcA	94.5cdeA	123.2aA	101.8bcdA	92.9cdeAB	118.0abA	103.7bcA	86.3defA	78.8efA	71.9fA
2003	93.8bcA	92.3bcA	101.4bA	106.1bA	105.0bA	103.70bA	130.5aA	110.1abA	92.8bcA	72.9cAB	77.7cA
2005	93.9cA	95.8cA	99.4bcA	120.6aA	124.7aA	86.4cdB	117.9aA	113.9abA	92.0cA	68.0eB	71.7deA
Yield per unit N uptake (T***, V***, T × V**)											
1980	36.4cdA	42.1bcA	34.6deB	49.5aA	37.0cdB	32.59defC	44.5abB	36.0cdB	28.1efgB	26.6fgB	24.2gB
2003	43.0bcdA	42.7bcdA	47.9bcA	50.7bA	49.5bcAB	46.5bcA	61.9aA	50.6bA	40.4cdeA	32.3eA	34.5deA
2005	40.5dA	44.2cdA	46.9bcdA	53.2abA	56.6aA	39.9dB	51.1abcB	53.6abA	42.3dA	27.0eB	32.1eA
N harvest index (T**, V*, T × V**)											
1980	0.83abA	0.79abA	0.76abA	0.80abA	0.75abA	0.73abcA	0.76abA	0.70bcA	0.58dB	0.75abA	0.63cdB
2003	0.792aA	0.80aA	0.80aA	0.67cB	0.80aA	0.77abA	0.79aA	0.80aA	0.69bcA	0.83aB	0.77abA
2005	0.84aA	0.82aA	0.83aA	0.80aA	0.74abA	0.66bA	0.77aA	0.78aA	0.75abA	0.77aA	0.74abA
Grain N g kg^{-1} (T***, V**, T × Vn.s.)											
1980	22.8bcA	19.0cdeA	22.1bcA	16.4eA	20.3cdeA	22.6bcA	17.3deA	19.4cdeA	20.8cdA	28.2aA	26.3abA
2003	18.5cA	18.7cA	16.8cdB	13.5deA	16.4cdB	16.7cdB	12.7eA	15.9cdeA	17.4cA	25.7aA	22.4bA
2005	20.9bcA	18.7cdA	17.6cdeB	15.2defA	13.1fC	16.6defB	15.4defA	14.8efA	17.83cdeA	28.9aA	23.0bA
N nutrition index (T***, Vn.s., T× Vn.s.)											
1980	0.25cA	0.53bcA	0.74abA	0.33cA	0.53bcA	0.92aA	0.44bcA	0.64abA	0.67abA		
2003	0.21eA	0.40cdeA	0.63bcAB	0.33deA	0.60bcA	0.81abA	0.47cdA	0.57cA	0.92aA		
2005	0.22fA	0.43deA	0.57bcB	0.31efA	0.49cdA	0.75aA	0.37deA	0.67abA	0.79aA		

Table 3. Season 2 (2014–15): nitrogen (N) uptake per unit soil N available, biomass per unit N uptake, yield per unit N uptake, N harvest index, grain N concentration, and N nutrition index (ratio between actual and critical N concentration in the shoot at anthesis) of winter wheat varieties grown under different nutrient and water inputs

Significance of treatments (T), varieties (V) and interaction (T × V) indicated as: $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$; n.s., not significant ($P > 0.05$). Means followed by the same letter are not significantly different (using Fischer's l.s.d. at $P = 0.05$): lower case letters for comparison among treatments, and upper case letters for comparison among varieties. Treatments are as in Table 1

Variety release date	Control	N1P1	N2P2	M1	M1N1P1	M1N2P2	M2	M2N1P1	M2N2P2	dControl	dMNPK
N uptake per unit soil N available (T**, Vn.s., T × V**)											
1970	0.43abA	0.40bcA	0.33bcA	0.46bcdeA	0.32bA	0.43abA	0.40bcA	0.33bcA	0.46bcdeA	0.32bA	0.43abA
1980	0.42abA	0.40bcA	0.52aA	0.40defA	0.47aA	0.42abA	0.40bcA	0.52aA	0.40defA	0.47aA	0.42abA
1993	0.46abA	0.61aA	0.55aA	0.55abcA	0.51aA	0.46abA	0.61aA	0.55aA	0.55abcA	0.51aA	0.46abA
2003	0.47abA	0.44bcA	0.44abA	0.40defA	0.41abA	0.47abA	0.44bcA	0.44abA	0.40defA	0.41abA	0.47abA
2005	0.48abA	0.45bA	0.51abA	0.57abA	0.50aA	0.48abA	0.45bA	0.51abA	0.57abA	0.50aA	0.48abA
Biomass per unit N uptake (T**, V*, T × Vn.s.)											
1970	115.1cA	108.2cA	137.0abA	125.1abcA	117.0bcB	107.5cAB	139.3aA	114.2cA	114.4cAB	105.5cA	103.3cAB
1980	112.2abA	108.4bA	99.1bB	123.3abA	140.5aA	119.1abA	118.4abB	120.8abA	122.3abA	114.0abA	118.7abA
1993	104.7aA	112.8aA	113.5aAB	122.1aA	122.4aAB	117.0aA	113.1aB	117.0aA	103.9aB	107.4aA	109.5aAB
2003	114.1bcA	127.8aA	107.4cB	138.3aA	113.6bcB	101.0cdB	129.8aAB	109.5bcA	115.1bAB	102.6bcdA	93.1dB
2005	128.6abA	130.8abA	117.7abcAB	140.1aA	118.0abcB	108.8bcAB	126.1abcAB	109.2bcA	113.8bcAB	102.7cA	113.6bcAB
Yield per unit N uptake (T***, V***, T × V**)											
1970	47.8bcdA	46.3cdA	62.9aA	57.81abBC	51.9bcA	46.5cdAB	55.1abcA	52.3bcAB	45.9cdAB	39.5dAB	46.7cdA
1980	49.1abA	48.7abA	43.7bB	49.7abC	54.2aA	44.7bB	54.2aA	46.7abB	44.2bB	41.1bB	45.7abA
1993	51.9abA	51.9abA	56.5aA	53.9aC	50.1abA	50.1abAB	52.0abA	51.4abAB	44.0bB	50.1abA	46.9abA
2003	54.1bcdA	58.8bcA	52.8cdeAB	67.9aA	54.0bcdA	46.6efAB	60.1bA	48.8defAB	47.8defAB	46.4efAB	43.9fA
2005	52.6bcA	57.5abcA	55.5bcAB	66.2aAB	57.2abcA	50.8bcA	59.1abA	53.0bcA	52.4bcA	47.0cAB	50.3bcA
N harvest index (T**, V***, T × V*)											
1970	0.80abA	0.80abA	0.75cB	0.83aA	0.80abA	0.79abcA	0.76bcB	0.82aA	0.76bcA	0.80abAB	0.80abA
1980	0.82aA	0.82aA	0.82aA	0.77abA	0.74bB	0.74bA	0.82aA	0.75abB	0.70bB	0.77abB	0.75abAB
1993	0.84aA	0.80abcdA	0.81abcdA	0.80abcdA	0.78bcdeAB	0.76defA	0.82abcA	0.74efB	0.72fAB	0.83abA	0.77cdefAB
2003	0.81abA	0.77cdA	0.81abA	0.80abcA	0.81abA	0.79bcA	0.81abA	0.77cdB	0.75dAB	0.82aAB	0.77cdAB
2005	0.76abA	0.76abA	0.80abAB	0.77abA	0.80abA	0.78abA	0.81abA	0.81aA	0.77abA	0.81aAB	0.74bB
Grain N g kg^{-1} (T***, V**, T × Vn.s.)											
1970	16.9abA	17.5abA	12.3cB	14.3bcAB	15.6bcA	17.0abA	13.9bcA	15.7bcA	16.6bA	20.4aA	17.1abA
1980	17.2abA	16.9abAB	19.0aA	15.7abA	13.6bA	16.5abA	15.3abA	16.1abA	15.9abA	18.8aA	16.7abA
1993	16.8aA	15.8aAB	14.3aB	14.9aA	15.5aA	15.2aA	15.8aA	14.3aA	16.4aA	16.7aA	16.6aA
2003	15.0cdeA	13.2efB	15.4bcdeAB	11.9fB	14.9cdeA	16.9abcA	13.5defA	15.7abcdA	16.0abcA	17.9aA	17.7abA
2005	14.5bcA	13.4bcAB	14.4bcB	11.8cB	14.0bcA	15.3abA	13.8bcA	15.5abA	14.8abA	17.4aA	14.6abcA
N nutrition index (T***, Vn.s., T × Vn.s.)											
1970	0.28fA	0.49cdeA	0.63abA	0.39efA	0.43deA	0.67aA	0.44deA	0.55bcdAB	0.61abcB		
1980	0.30eA	0.49bcA	0.60abA	0.35deA	0.55abcA	0.63aA	0.43cdA	0.59abA	0.54abcB		
1993	0.26dA	0.47bcA	0.59bA	0.35cdA	0.49bcA	0.62abA	0.38cdA	0.49bcB	0.79aA		
2003	0.24cA	0.49abA	0.62aA	0.40bcA	0.63aA	0.68aA	0.40bcA	0.56abAB	0.63aB		
2005	0.28dA	0.44bcA	0.65aA	0.32cdA	0.53abA	0.61aA	0.34cdA	0.53abAB	0.56abB		

Table 4. Season 1 (2013–14): phosphorus (P) uptake, biomass per unit P uptake, yield per unit P uptake, P harvest index, grain P concentration and grain nitrogen (N) : P ratio of winter wheat varieties grown under different nutrient and water inputs

Significance of treatments (T), varieties (V) and interaction (T × V) indicated as: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; n.s., not significant ($P > 0.05$). Means followed by the same letter are not significantly different (using Fischer's l.s.d. at $P = 0.05$): lower case letters for comparison among treatments, and upper case letters for comparison among varieties. Treatments are as in Table 1

Variety release date	Control	N1P1	N2P2	M1	M1N1P1	M1N2P2	M2	M2N1P1	M2N2P2	dControl	dMNPK
P uptake kg ha^{-1} (T***, V*, T × Vn.s.)											
1980	4.52gA	10.0fA	18.7deA	15.6eA	23.9bcdB	26.1abcA	21.2cdA	26.8abA	30.6aA	3.80gA	20.2deA
2003	5.03fA	10.81eA	14.6deA	16.3dA	23.2bcB	25.0abA	19.1cdA	28.1abA	30.2aA	4.14fA	25.5abA
2005	4.03eA	10.4dA	17.3cA	17.8cA	28.2bA	27.9bA	20.0cA	29.6bA	36.1aA	3.30eA	22.2cA
Biomass per unit P uptake (T***, V**, T × Vn.s.)											
1980	644.7abA	724.4aA	632.7abA	415.6dB	491.9cdAB	550.1bcA	389.9dA	468.6cdB	458.5cdA	743.2aA	642.0bA
2003	644.9aA	686.7aA	730.2aA	475.2bcA	514.8bcA	526.0bA	401.7cA	511.4bcA	506.0bcA	746.4aA	637.5aA
2005	623.0bA	626.5bA	635.6bA	379.4dB	447.6cdB	518.5cA	381.8dA	461.5cdB	458.0cdA	769.7aA	634.9bA
Yield per unit P uptake (T***, V**, T × V**)											
1980	248.4abB	282.2aA	231.8bB	167.1deB	178.0cdeB	191.1cdB	147.1eB	162.5deB	149.6eB	250.8abB	215.2bcA
2003	296.1abA	318.3abA	344.9aA	227.3dA	242.8cdA	236.0cdAB	190.6dA	234.8cdA	221.3dA	331.4abA	282.9bcA
2005	266.6abAB	290.1aA	299.8aAB	167.5dB	203.1cdB	239.8bcA	165.4dB	217.2cA	210.7cdA	305.0aA	284.7abA
P harvest index (T***, V***, T × V**)											
1980	0.87aA	0.87aA	0.85abA	0.70cdeB	0.76cdB	0.76cdB	0.64eB	0.71cdeC	0.68deA	0.78bcB	0.73cdA
2003	0.90aA	0.89abA	0.90abA	0.84abcdA	0.89abA	0.83bcdAB	0.79cdA	0.85abcA	0.81cdA	0.83bcdA	0.78dA
2005	0.89aA	0.87abA	0.87abA	0.71dB	0.81bcAB	0.86abA	0.69dAB	0.80bcB	0.80bcA	0.84abcA	0.77cdA
Grain P g kg^{-1} (T***, V***, T × Vn.s.)											
1980	3.54cdA	3.10dA	3.68bcdA	4.24abA	4.27abA	4.02abcA	4.35abA	4.40aA	4.51aA	3.13dA	3.41cdA
2003	3.04cA	2.81cA	2.66cB	3.73abA	3.67abA	3.55bA	4.15aA	3.64abB	3.66abB	2.51cB	2.79cB
2005	3.37cdeA	3.04defA	2.94efAB	4.21aA	4.03abA	3.58bcdA	4.19aA	3.68abcB	3.82abcB	2.75fAB	2.72fB
Grain N : P (T***, Vn.s., T × Vn.s.)											
1980	6.52bcA	6.23bcdA	6.02bcdA	3.91eA	4.78cdeA	5.76cdeA	3.96eA	4.39deA	4.62cdeA	9.14aA	7.82abA
2003	6.17cdA	6.74bcA	6.50cA	3.65efA	4.46efA	4.77deA	3.06fB	4.37efA	4.78deA	10.24aA	8.06bA
2005	6.33cA	6.27cA	6.05cA	3.59dA	3.28dB	4.64dA	3.64dAB	4.04dA	4.66dA	10.50aA	8.47bA

Table 5. Season 2 (2014–15): phosphorus (P) uptake, biomass per unit P uptake, yield per unit P uptake, P harvest index, grain P concentration and grain nitrogen (N) : P ratio of winter wheat varieties grown under different nutrient and water inputs

Significance of treatments (T), varieties (V) and interaction (T × V) indicated as: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; n.s., not significant at $P = 0.05$. Means followed by the same letter are not significantly different (using Fischer's l.s.d. at $P = 0.05$): lower case letters for comparison among treatments, and upper case letters for comparison among varieties. Treatments are as in Table 1

Variety release date	Control	N1P1	N2P2	M1	M1N1P1	M1N2P2	M2	M2N1P1	M2N2P2	dControl	dMNPK
P uptake kg ha^{-1} (T***, V*, T × Vn.s.)											
1970	5.33eA	9.22dA	16.8cA	18.8bcA	22.0bA	32.4aA	20.6bcA	33.6aB	31.3aAB	3.28eAB	19.9bcD
1980	5.33dA	8.46dA	19.5cA	16.9cA	26.5bA	26.8abA	20.9cA	28.7abB	32.4aAB	4.35dA	27.6abB
1993	3.71eA	10.8dA	20.4cA	16.9cA	27.1abA	27.5abA	19.8cA	21.7bcC	29.3aB	4.03eAB	23.1bcC
2003	6.35deA	9.06dA	18.3cA	15.4cA	25.0bA	33.4aA	19.4cA	31.5aB	31.3aAB	4.00eAB	25.2bBC
2005	4.43gA	11.0fA	19.5eA	18.3eA	21.8deA	26.4cdA	19.1eA	39.7aA	36.3abA	2.72gB	30.8bcA
Biomass per unit P uptake (T***, V**, T × Vn.s.)											
1970	687.6bcdA	740.0bcA	829.1bA	446.5eA	581.3cdeA	551.2deA	476.23eA	466.9eB	581.1cdeA	999.6aA	676.1bcdA
1980	609.4cdA	776.8bA	675.6bcA	446.9eA	554.0cdeA	612.0cdA	410.6eA	512.2deB	552.1cdeA	911.2aA	538.9cdeC
1993	659.1bcA	793.2abA	669.9abcA	452.0eA	527.7cdeA	607.6cdA	507.7deA	651.3bcdA	531.8cdeA	805.2aA	643.8cdAB
2003	626.1bcA	829.6aA	697.9bA	512.8cdA	597.2bcdA	541.8cdA	483.7dA	524.45cdB	546.2cdA	906.6aA	600.4bcdBC
2005	710.4abcA	821.8abA	675.0abcA	440.4deA	639.1bcdA	601.3cdeA	432.7deA	406.9eB	502.6cdeA	873.1aA	567.9cdeC
Yield per unit P uptake (T***, V**, T × V**)											
1970	282.6bcdA	316.3abA	381.7aA	206.4eB	257.2bcdeAB	238.4cdeA	188.7eA	214.3deB	232.5deA	375.4aAB	305.7bcA
1980	267.5aA	349.6bA	298.0cA	181.4cB	212.8cB	231.8cA	189.5cA	198.2cB	200.9abA	327.6cB	207.8cC
1993	325.9abA	365.0aA	333.4abA	199.7fB	214.9efB	259.2cdeA	233.4cdefA	285.8bcA	225.3defA	375.5aAB	277.8bcdAB
2003	295.2cA	382.3abA	343.1bA	251.0cdeA	284.7cdA	249.9cdeA	224.1eA	233.6deB	223.4eA	410.1aA	283.2cdAB
2005	284.6cdA	358.1abA	318.0bcA	208.5eB	309.2bcA	279.3cdA	202.7eA	196.9eB	231.3deA	394.9aAB	251.4deB
P harvest index (T***, V***, T × V**)											
1970	0.84abcA	0.85abA	0.84abcA	0.80cdA	0.86aA	0.82abcA	0.71eB	0.80bcdA	0.78dA	0.84abcAB	0.78dA
1980	0.88aA	0.86aA	0.87aA	0.74bcB	0.78bB	0.79bA	0.71cB	0.74bcB	0.75bcA	0.79bB	0.72cC
1993	0.88aA	0.86abA	0.87abA	0.75deB	0.80cdAB	0.81bcA	0.74eAB	0.76cdeAB	0.75deA	0.87abA	0.75eB
2003	0.87aA	0.86abA	0.86abA	0.81bcdA	0.85abcAB	0.81cdeA	0.76eAB	0.77deAB	0.77deA	0.84abcAB	0.78deA
2005	0.84abA	0.86aA	0.86aA	0.82abA	0.82abAB	0.81abA	0.78bA	0.79abAB	0.80abA	0.87aA	0.77bA
Grain P g kg^{-1} (T***, V***, T × Vn.s.)											
1970	2.99bcA	2.73cdA	2.65cdAB	3.88aA	3.36abAB	3.47abA	3.80aA	3.76aA	3.35abA	2.23dA	2.56cdC
1980	3.38abA	2.49cA	2.92bcA	4.09aA	3.66abA	3.44abA	3.86aA	3.75abA	3.76abA	2.43cA	3.47abA
1993	2.70bcA	2.37cA	2.61bcB	3.77aAB	3.73aA	3.15abA	3.27abA	2.75bcB	3.34abA	2.37cA	2.72bcBC
2003	3.03abcA	2.26deA	2.51cdeB	3.28abB	3.03abcAB	3.24abA	3.41aA	3.30abAB	3.46aA	2.07eA	2.77bcdBC
2005	3.08bcA	2.41cdA	2.72bcdAB	3.96aA	2.71bcdB	2.97bcdA	3.88aA	4.01aA	3.47abA	2.20dA	3.08bcAB
Grain N : P (T***, Vns, T × Vn.s.)											
1970	5.67bcdA	6.52bcA	4.73deA	3.69eAB	4.69deAB	4.93cdeA	3.66eA	4.22deAB	4.97cdeA	9.12aA	6.77bA
1980	5.16bA	6.86aA	6.53aA	3.83bA	3.73bB	4.83bA	4.14bA	4.31bAB	4.31bA	7.76aA	4.84bAB
1993	6.20abcA	6.63abA	5.50abcdA	3.95dA	4.19cdAB	4.84bcdA	5.00bcdA	5.40abcdA	4.95bcdA	7.32aA	6.23abcAB
2003	5.14abcA	5.83abA	6.16abcdA	3.65dAB	4.99cdAB	5.23bcdA	3.98bcdA	4.76abcdAB	4.69bcdA	8.65aA	6.38abcAB
2005	4.82bcdA	5.54bA	5.29bcA	2.99eB	5.29bcA	5.38bA	3.55deA	3.87cdeB	4.27bcdeA	8.01aA	4.76bcdB

index in both seasons, and for biomass per unit N uptake in 2014–15.

Interactions did not affect grain protein or N nutrition index. Nitrogen dilution curves may be influenced by wheat variety and growing condition (Hoogmoed and Sadras 2016). Therefore, we compared the N nutrition index calculated by using the N dilution curve reported by Justes *et al.* (1994), which is widely used, and a curve reported by Li *et al.* (2015), which was developed under an environment similar to that of our study and with variety Xiaoyan 22, released in 2003. The N nutrition index calculated with the Li *et al.* (2015) curve was higher than that obtained with the Justes *et al.* (1994) curve, but the ranking of varieties and treatments was similar (Supplementary material fig. 1, available at the journal's website).

Phosphorus traits

Treatment, variety and interaction effects on P traits are summarised in Table 4 (2013–14) and Table 5 (2014–15). Most traits responded to variety, except for biomass per unit P uptake in 2014–15 and grain N : P ratio in 2013–14. Interaction effects were found for yield per unit P uptake and P harvest index in both seasons and for P uptake in 2014–15.

Time trends in nitrogen and phosphorus traits

In order to elucidate the season-dependent responses and interactions outlined above, we adopted the framework of Sadras *et al.* (2016) to analyse changes in N and P traits resulting from selection for yield, using a relative scale as recommended by Fischer *et al.* (2014). The rate of change in yield varied with growing conditions; it was lowest in the unfertilised treatment and peaked at 0.83% year^{-1} for crops receiving 135 kg N ha^{-1}. For our global analysis where the aim was to compare rates of change of different traits, we calculated rates for the pooled treatments because these were more robust than for individual treatments (Fig. 1). Selection for yield increased yield at a rate of 0.46% year^{-1}, with no changes in the rate of nutrient uptake and hence a significant increase in the rate of yield per unit N and yield per unit P uptake (0.42% and 0.40% year^{-1}, respectively). Further tests for individual treatments showed that the rate of change in N uptake with year of release was not different from zero for either the treatment with highest ($P = 0.32$) and lowest ($P = 0.14$) N supply. Likewise, the rate of change in P uptake with year of release was not different for zero for either the treatment with highest ($P = 0.08$) and lowest ($P = 0.29$) P supply. The P harvest index increased at a rate of 0.15% year^{-1}, whereas there was no change in N harvest index. Concentrations of N and P in grain decreased at rates of 0.47% and 0.31% year^{-1}, respectively, whereas the N : P ratio in grain did not change over time. The N nutrition index did not change with year of variety release.

Next, we placed these findings in a broader context by comparing them with breeding systems worldwide (Fig. 2). Plots of rate of change in nutrient uptake *v.* rate of change in yield show two clusters. For Australia and for 0 kg N ha^{-1} in Mexico, the points scatter around the $y = x$ line, whereas for our data in China and for breeding systems in UK, Italy, Argentina and Mexico, the rate of change in yield has been larger than rate of change in nutrient uptake (Fig. 2*a*). The mismatch between the rate of change in nutrient uptake and the rate of change in yield per unit nutrient uptake in our study is then reflected in the shifts in grain nutrient concentration along the $y = -x$ line in Fig. 2*b*.

Discussion

A previous review compared the rate of yield gain *v.* rate of change in N uptake, and the rate of change in grain N concentration *v.* rate of change per unit N uptake of diverse breeding systems (Sadras *et al.* 2016). Here we expanded the comparison in two aspects.

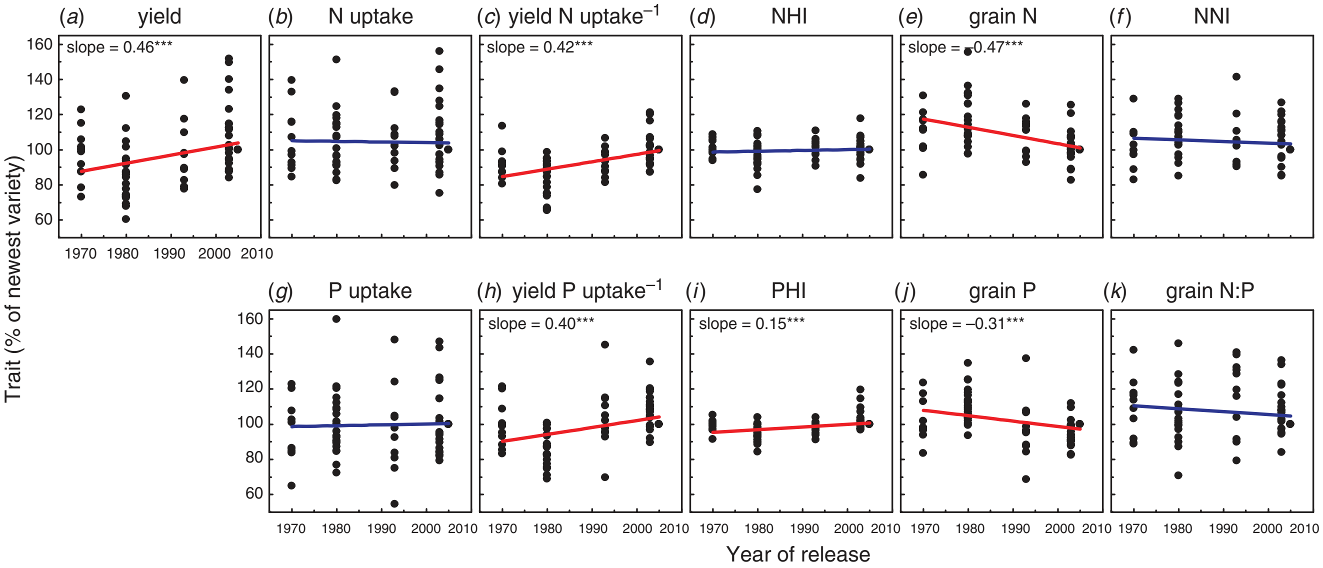

Fig. 1. Changes in yield and nutrient-related traits of wheat in China, in response to selection for yield. Data are pooled across growing conditions. NHI, Nitrogen harvest index; PHI, phosphorus harvest index; NNI, N nutrition index. Traits are relative to the newest variety (Fischer *et al.* 2014). ***$P < 0.001$: for significance of slope from least-square regression.

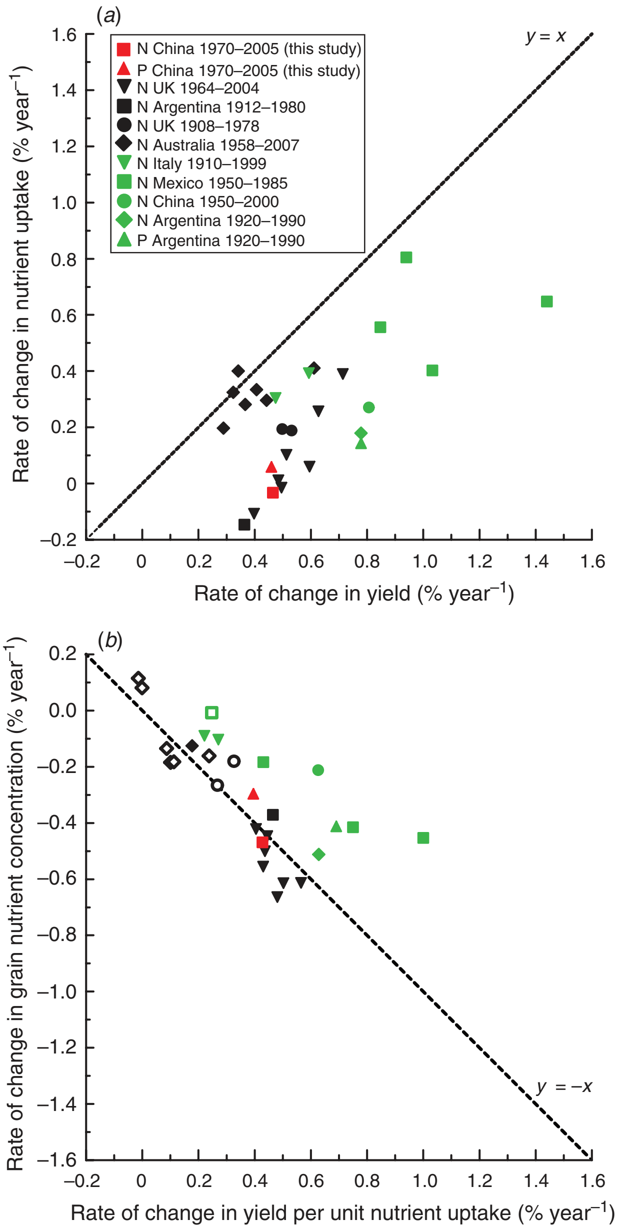

Fig. 2. Comparison of rates of change in wheat traits in response to selection for yield: (*a*) nutrient uptake *v.* yield; (*b*) grain nutrient concentration *v.* yield per unit nutrient uptake. In (*b*), open symbols indicate that rates of change in grain protein or phosphorus concentration are not different from zero, and solid symbols indicate significant rates ($P < 0.05$). Sources: Austin *et al.* (1980) (UK 1908–1978); Slafer *et al.* (1990) (Argentina 1912–1980); Calderini *et al.* (1995*a*) (Argentina 1920–1990); Calderini *et al.* (1995*b*) (Argentina 1920–1990); Ortiz-Monasterio R *et al.* (1997*a*) (Mexico 1950–1985); Ortiz-Monasterio R *et al.* (1997*b*) (Mexico 1950–1985); Giunta *et al.* (2007) (Italy 1910–1999); Barraclough *et al.* (2010) (UK 1908–1978); Sadras and Lawson (2013) (Australia 1958–2007); Tian *et al.* (2016) (China 1950–2000).

First, we included data for China, where breeding has improved yield at a rate of 0.46% year^{-1} between 1970 and 2005 (Fig. 1*a*), and where fertiliser inputs have increased from 8.3 to 24.0 Mt N and from 2.2 to 8.3 Mt P between 1979 and 2012 (Zhang *et al.* 2015). Second, we expanded the comparisons to include P-related traits.

Shifts in nitrogen uptake and partitioning

Our data align with those for UK, Italy, Argentina and Mexico, where yield improvement was not accompanied by a proportional increase in N uptake or by improved partitioning of N to grain. This applied to both the pooled data and to the treatments with highest and lowest nutrient input. Selection for wheat in Australia remains the only reported case where the rate of improvement in N uptake matched the rate of increase in yield (Sadras and Lawson 2013; Sadras *et al.* 2016; Aziz *et al.* 2017). For wheat released in the UK between 1964 and 2000, the rate if change in N uptake was zero for crops fertilised with 0–200 kg N ha^{-1}, and positive but smaller than the rate of yield increase for crops with 350 kg N ha^{-1} (Barraclough *et al.* 2010). In Mexico, improvement in N uptake matched yield improvement in unfertilised crops, whereas yield increased faster than N uptake under heavy fertilisation (Fig. 2). Collectively, the increase in yield with no compensating changes in N uptake or allocation to grain led to a reduction in grain N concentration in our study. Increasing yield per unit nutrient uptake, a commonly used measure of efficiency, is thus achieved where yield, largely driven by grain number, increases faster than nutrient uptake, but at the expense of nutrient concentration in grain (Calderini *et al.* 1995*b*; Egle *et al.* 1999; Acreche and Slafer 2009; Foulkes *et al.* 2009; Tian *et al.* 2016).

The rate of change in grain nutrient concentration is tightly coupled with the rate of change in yield per unit nutrient uptake (Fig. 2*b*). To maintain N concentration in grain, the rate of increase in N uptake has to match the rate of yield gain (Sadras *et al.* 2016). A complementary view defines 'grain protein deviation' as the residual of the yield–protein relationship, and studies with winter wheat showed that grain protein deviation correlates with post-anthesis N uptake, thus allowing for improved grain yield and protein synchronously (Monaghan *et al.* 2001; Guttieri *et al.* 2015, 2017). To further improve wheat yield but maintain grain N concentration, either the N harvest index or N uptake, or both, must be improved (Barraclough *et al.* 2010). For the varieties under study, N harvest index was up to 0.8, suggesting limited scope for further improvement to 0.9 (Barraclough *et al.* 2010; Gorjanovic *et al.* 2011). Wheat breeding in China, we suggest, should focus on improving the ability of wheat to capture more N from soil. However, many factors influence N uptake and partitioning, including soil available N, and root and shoot traits (Semenov *et al.* 2007; Foulkes *et al.* 2009; Sylvester-Bradley and Kindred 2009; Barraclough *et al.* 2010, 2014). Root architecture can influence N acquisition, but root growth can be restricted by soil properties such as soil-water content, mechanical impedance or chemical constraints such as salinity (Clark *et al.* 2003; Ho *et al.* 2004; Sadras *et al.* 2005; Barraclough *et al.* 2010; Flavel *et al.* 2014). In winter-rainfall environments of south-eastern Australia, selection for yield increased crop N uptake and improved the N nutrition index of wheat despite a dramatic reduction in root-length density, more than compensated for by increased N uptake per unit root length (Sadras and Lawson 2013; Aziz *et al.* 2017). For the combination of wheat genotypes and environments investigated by Guttieri *et al*. (2017), plant height and time to anthesis correlated genetically with N-use efficiency traits, and N-uptake efficiency increased in response to selection for yield. However, plant height did not change with year of release in Guan Zhong Plain between 1970s and 2010s (Sun *et al*. 2014; Wang *et al*. 2017). In *Arabidopsis*, the overexpression of TGA4 (Zhong *et al*. 2015) improved the nitrate transport and N assimilation and NLP7 enhanced the N and carbon assimilation (Yu *et al*. 2016).

Shifts in phosphorus uptake and partitioning

The P harvest index increased, but not enough to maintain P concentration in the grain driven by large rates of yield increase. Similarly for wheat released between 1920 and 1990 in Argentina, yield increase in the absence of improved P uptake reduced seed P concentration despite enhanced allocation to grain.

In our study, grain P decreased at a rate of 31% year^{-1}. Reserves of P in seed can favour seedling water uptake and vigour, and plant growth and reproduction (Radin and Matthews 1989; Henery and Westoby 2001), but large amounts of phytate-P may play negative roles in both human and monogastric nutrition, for example, by reducing bioavailability of zinc and iron (Raboy 2009; White and Broadley 2009; Veneklaas *et al*. 2012). Undigested P in manure represents a potential environment risk (Sharpley *et al*. 1994). For a given amount of P in grain, the proportion or activity of phytase can be reduced (Raboy 2007, 2009), but the trade-off between available P, seedling vigour and crop establishment needs attention (Yuan *et al*. 2017). Reducing the P concentration of grain by ~20% through breeding did not affect barley yield (Bregitzer and Raboy 2006). Phosphorus in seed should support seedling growth until the root system is established (White and Veneklaas 2012); for example, a rye (*Secale cereale* L.) seed with 151 mg P could support seedling growth for 15 days after germination (White 1993; White and Veneklaas 2012).

Competing interests

The authors declare that they have no competing interests.

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