Changes in winter wheat (*Triticum aestivum* L.) phenotype in response to breeding for yield and in-furrow fertilizer

by

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Abstract

The grain yield of winter wheat (*Triticum aestivum* L.) increased over time through plant breeding, and preliminary research suggested that yield response to fertilizer differs in modern versus historical genotypes. However, this response is not universal. We hypothesize selection for yield may have unintentionally modified the dynamics of nutrient uptake and partitioning in the plant. Thus, our objectives were to identify the key shifts in crop phenotype, in above-ground biomass and in dynamics of nutrient uptake and partitioning during vegetative and reproductive phases in response to selection for yield and to in-furrow fertilizer. Field experiments were conducted in four Kansas environments in a factorial trial combining eight winter wheat varieties released between 1920 and 2016, and two fertilizer practices (control versus 112 kg ha^{-1} in-furrow 12-40-0-10-1). Grain yield and grain N-removal increased non-linearly with year of release (YOR), with greater increases between 1966 and 2000. In-furrow fertilizer increased yield in ~300 kg ha^{-1} with no variety × fertility interactions. Grain protein concentration (GNC) related negatively to yield, and the residuals of this relationship were unaffected by YOR. Yield increase in semi-dwarf varieties were associated with shorter vegetative period and longer grain filling period, and more kernels m^{-2} derived from more kernels head^{-1}. Historical varieties were taller, had thinner stems, and allocated more biomass to the stem than semi-dwarf varieties. At grain filling and maturity, shoot biomass was similar among varieties but semi-dwarf varieties allocated more dry matter to the kernels, suggesting that increases in yield derived from greater harvest index (HI) rather than greater biomass. Whole plant nutrient concentration negatively related to whole plant biomass and increased over decades for N, P, and S and decreased for K. In-furrow fertilizer increased the concentration of all nutrients. Grain-N, P, K, and S uptake increased from historical to semi-dwarf varieties; thus, nutrient HI increased with YOR, with greater increases between 1966 and 2000. Nutrient HI decreased with in-furrow fertilizer as the fertilizer increased biomass allocation to the vegetative tissues more than to the grain. Nutrient allocation rate to the head related positively to whole plant uptake rate, and YOR increased the head allocation rate for N, K, and S. There were positive and significant relationships between NHI and the HI of P, K, and S. Whole plant N uptake and P, K, and S uptake were also positively related, with ratios of 9.2, 1.1, and 15.4 for N:P, N:K, and N:S. Direct selection for grain yield modified the dynamics of nutrient uptake and partitioning over time, with semi-dwarf varieties allocating more N, P, K, and S to the grain. The ability of modern varieties to allocate more biomass and nutrients to the grain, coupled to an early maturity and longer grain filling period, increased grain yield and grain N-removal over time. However, increases in yield were greater than those in N-removal, reducing GNC. In-furrow fertilizer increased grain yield, biomass, and grain N, P, K, S uptake; nonetheless, the lack of variety × fertility interaction suggested variety response to fertility was similar.

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Chapter 1 - Changes in Winter Wheat Phenotype in Response to Breeding for Yield and In-Furrow Fertilizer.I. Biomass, Yield, and Grain Protein Concentration

Introduction

Global wheat production often surpasses 750 Mt harvested from about 220 Mha, with an average yield of 3.4 Mg ha^{-1} (FAOSTAT, 2018a). The development of semi-dwarf wheat varieties (Evenson, 2003) coupled with N fertilizer was responsible for large proportion of the yield advances over decades (Bell et al., 1995). The successful introduction of dwarfing genes carrying the alleles Rht1-B1b (Peng et al., 1999) allowed for plants with reduced height, greater response to fertilizer, and higher yields (Evenson, 2003). For irrigated spring wheat in Mexico, genetic improvement accounted for 28% and increased use of N fertilizers for 48% of the yield improvement between 1968 and 1990 (Bell et al., 1995). For dryland winter wheat in Kansas (U.S.) between 1977 and 2006, these estimates are 79 and 21%, respectively (Nalley et al., 2008).

Comparison of wheat varieties released during different historical eras returned rates of genetic gains from 0.3 to 1.1% (Austin et al., 1989; Battenfield et al., 2013; Brancourt-Humel et al., 2003; Fischer et al., 2014; Sayre et al., 1997). However, some studies also showed that rates of yield gain can differ over time, and has typically decreased in recent years. For instance, genetic gain greater than 0.5% yr^{-1} during the 1960s to 2000s period was reported in the U.S., Australia, and Chile (Fufa et al., 2005; Sadras and Lawson, 2011; Del Pozo et al., 2014). Meanwhile, the genetic gain in modern wheat varieties decreased or were non-significant in recent years in Spain, Brazil, and Argentina (Acreche et al., 2008; Beche et al., 2014; Lo Valvo et al., 2017).

Wheat yield gain is often associated with improved harvest index , kernels m^2, kernels per head, reduced plant height, shoot biomass and kernel weight (Brancourt-Humel et al., 2003; Zhou et al., 2007a; Fischer and Edmeades, 2010; Sadras and Lawson, 2011; Sanchez-Garcia et al., 2013; Beche et al., 2014; Wu et al., 2014; Aisawi et al., 2015; Lo Valvo et al., 2017). More recently, genetic gain in yield correlated with shoot biomass at maturity in some breeding programs (Beche et al., 2014; Donmez et al., 2001; Shearman et al., 2005; Wu et al., 2014; Xiao et al., 2012). However, previous research has not evaluated the dynamics of biomass accumulation and partitioning during the growing season of historical versus modern varieties.

The rates of genetic gain are often greater in well-fertilized, well-watered crops than in the counterparts with water and nutrient deficiency (Austin et al., 1980; Barraclough et al., 2010; Brancourt-Humel et al., 2003; De Vita et al., 2007; Giunta et al., 2007; Gizzi and Gambin, 2016; Slafer and Andrade, 1989; Tian et al., 2011; Wang et al., 2017b). In-furrow fertilization with N, P, S, and Zn can improve early-season wheat tillering, biomass production, and yield (Lollato et al., 2013; Rodríguez et al., 1999, 1998; Valle et al., 2009). Nitrogen can increase grain yield (Grant et al., 2016; May et al., 2008) through kernels $head^{-1}$ (Asif et al., 2012), heads m^2, and kernels m^2 (Marino et al., 2009). Phosphorus improves plant leaf area (Rodríguez et al., 1998) and tillering (Sato et al., 1996). Sulfur can increase grain yield and protein concentration (Tao et al., 2018), and Zn can increase pollen viability (Nautiyal et al., 2011).

The combination of improved yield potential and management resulted in yield increases worldwide; however, limited information exists on the interaction between historical and modern wheat varieties and in-furrow fertilization. Thus, our objectives were to determine the rate of genetic grain yield of wheat adapted to Kansas, USA, and its interaction with in-furrow fertilizer, as well as the underlying changes in phenology, morphological and physiological traits.

Materials and Methods

Sites, treatments structure, and experimental design

Fields experiments were conducted in four environments resulting from the combination of two seasons and two locations in Kansas. In 2016-17, experiments were established on a Belvue silt loam (coarse-silty, mixed, superactive, nonacid, mesic Typic Udifluvents) in Ashland Bottoms, (39°08'37.8"N, 96°37'59.8"W, elevation 315 m) and on a Crete silt loam (fine, smectitic Pachic Udertic Argiustolls) in Belleville (39°48'54.1"N 97°40'16.7"W, elevation 469 m). In 2017-18, experiments were conducted on an Ost loam (fine-loamy, mixed, superactive, mesic Udic Argiustolls) near Hutchinson (37°55'52.4"N 98°01'47.8"W, elevation 471 m) and again in Belleville.

Eight hard red winter wheat varieties released between 1920 and 2016 (Table 1 - 1) were combined factorially with two fertilization treatments. The experimental design was a split-plot with four replications, with whole plots arranged as randomized complete block design and subplots completely randomized within whole plots. Varieties were assigned to plots and fertilizer treatment to subplots.

Varieties were selected based on large adoption by growers in the period following their release. Kharkof and Scout 66 carry the alleles Rht1-B1a-Tall and will hereafter be referred to as ‘tall varieties’; the remaining varieties carry the alleles Rht1-B1b-Short and will be referred to as ‘semi-dwarf varieties’. Due to seed germination issues, we excluded the data from Jagger during the first year of the study.

Fertilizer treatments were i) control and ii) in-furrow 13 N, 45 P, 0 K, 11 S, and 1 kg Zn ha^{-1} fertilizer. The control treatment followed current soil fertility recommendations for P as per the nutrient "sufficiency" approach (Leikam et al., 2003), in which no P fertilizer was applied as the study locations had Mehlich-3 P above 25 mg kg^{-1} (Table 1 - 2). On the fertilization treatment, in-furrow fertilizer was applied at sowing through the drill with the seed.

Agronomic management

Seeds were treated with insecticide and fungicide (15.24 ml 100 kg seed^{-1} of imidacloprid[1] and with 0.74 ml 100 kg seed^{-1} of tebuconazole[2]) to control early-season insects and diseases. Wheat was sown 18 October 2016 at Ashland Bottoms, 3 October 2016 and 2 October 2017 at Belleville, and 19 October 2017 at Hutchinson. All locations followed a previous wheat crop and were conducted under conventional tillage with surface residue cover below 10%. Plots were sown with a commercial drill (Great Plains 606-NT drill) at a seeding rate of 67.25 kg ha^{-1} (approximately 2.1 million seeds ha^{-1}). Subplots were 9.1-m long by 2.66-m wide, consisting of fourteen 0.19-m spaced rows. Half of the subplot (9.1-m x 1.33-m) was used for destructive sampling of biomass. The other half was used for non-destructive measurements (i.e., stem diameter and plant height), and harvested for yield.

Composite soil samples consisting of 15 individual soil cores were collected at two depths (0-15 cm and 15-60 cm) prior to sowing and analyzed for nutrient concentration (Table 1 - 2) The soil pH was analyzed through the procedure with water, P through Mehlich-3, K, Ca, Mg, Na through ammonium acetate extraction, $S0_4$-S through calcium phosphate extraction, Zn

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[1] Imidacloprid: 1-[(6-Chloro-3-pyridinyl) methyl]-N-nitro- 2-imidazolidinimine), 0.95 ml 100 kg seed^{-1} of metalaxyl: N-(2,6-dimethylphenyl)-N-(methoxyacetyl) alanine methyl ester

[2] Tebuconazole: alpha-[2-(4-chlorophenyl) ethyl]-alpha- (1,1-dimethyl-ethyl)-1H-1,2,4-triazole-1- ethanol)

through DTPA extraction, cation exchange capacity (CEC) through summation, organic matter through loss of ignition, and NO_3-N through N KCl extraction. Results were used to determine N fertilizer needs for a yield goal of 6 Mg ha^{-1} (Leikam et al., 2003), resulting in different total inorganic N amount in each site depending on the profile NO_3-N content. Topdress N was applied as urea (46-0-0) early spring (GS 31) under favorable weather conditions to minimize N losses, and to ensure that N deficiency was not a limiting factor. Two foliar fungicide applications (i.e., 65.77 ml ha^{-1} of picoxystrobin[3] at jointing (GS 31) and 89.15 ml ha^{-1} of picoxystrobin[1] plus 35.63 ml ha^{-1} cyproconazole[4] at anthesis (GS 65)) ensured that genetic resistance to fungal diseases was not a confounding factor. Herbicides were sprayed during the fall of both growing seasons to ensure weeds were not a limiting factor. There was no significant insect pressure so no insecticide was applied.

Plots were machine-harvested for grain yield on 22 June 2017 at Ashland Bottoms, 28 June 2017 and 24 June 2018 at Belleville, and 6 June 2018 at Hutchinson using a Hege 140 self-propelled small-plot combine. Grain moisture was measured at harvest and grain yield was corrected for 13% moisture content.

Vegetative development evaluations

Phenological stages using Zadoks scale (Zadoks et al., 1974) were determined when about 50% of the plants in the experimental unit achieved a particular stage. Shoot biomass was collected from the middle rows at tillering (GS 26), jointing (GS 31), anthesis (GS 65) soft dough stage of grain development (GS85); and physiological maturity (GS92) using an electric clipper (Gardena 8893-U, Gardena Co., Ulm, Germany). The sampled area was 0.76, 0.76, 0.38,

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[3] Picoxystrobin (Methyl (∝E)- ∝-(methoxymethylene)-2-[[[6-(trifluoromethyl)-2 pyridinyl]oxy]methyl]benzeneacetate

[4] Cyproconazole ∝-(4-chlorophenyl)- ∝-(1-cyclopropylethyl)-1H-1,2,4-triazole-1-ethanol

0.19, and 0.19 m^2, respectively, at an average stand of 185 plants m^2. Varieties differed in maturity and thus sampling occurred on different calendar days. Dry mass was determined after drying the samples at 65^0C until constant weight. Whole shoot weight was determined at GS 26; stem and leaf weights were determined at GS 31; stem, leaf, and chaff weights were determined at GS 65; and stem, leaf, grain, and chaff weights were determined at GS 85 and GS 92. Plant parts were separated manually, except for grain and chaff, which were separated with thresher (Wheat Head Thresher, PM Precision Machine Co. Inc., Lincoln, NE).

Stem diameter was measured at GS 85 using OriginCal IP54 digital caliper (Igaging, San Clement, CA) approximately 2.5 cm aboveground on the main stem of ten randomly selected plants per subplot. Plant height was measured at GS 92 from the soil surface until the tip of the awns of three plants per subplot. Yield components (harvest index, heads m^2, kernels $head^{-1}$, kernels m^2, and individual kernel weight) were measured in the sample collected at physiological maturity. Grain protein concentration (g kg^{-1}) was measured in whole kernel samples collected at harvest using near-infrared reflectance spectroscopy with a Perten DA 7250 (Perten Instruments Inc., Springfield, Illinois) and was reported on a 130 g kg^{-1} water basis. Grain-N removal was calculated as the product between grain yield and grain nitrogen concentration (Lollato et al., 2019).

Data analysis

Two-way analyses of variance (ANOVA) were performed to determine significant difference among treatments using PROC GLIMMIX in SAS version 9.4 (SAS Institute, Cary, NC). To determine whether site-years could be combined, we performed an ANOVA on the residuals of the combined analysis considering year, location, variety, and fertility, and their interactions, as fixed effects. Year was a significant effect for both biomass ($p < 0.05$) and grain yield (*p* = 0.08); thus, we performed all remaining analysis across locations within year. Variety, fertility, and variety × fertility were fixed effects; and replication, sites, replication nested within site, and variety × replications nested within site were random effects. We used the LINES statement for pairwise comparisons.

To evaluate historical trends across the entire dataset, we calculated trait deviation from the mean of each environment (Sadras and Lawson, 2011) and fitted seven models to the deviation data as a function of year of release (i.e., logarithm, logistic, piecewise, linear, quadratic, sigmoidal, and cubic). Models were fitted with SigmaPlot version 13.0 (Systat Software, San Jose, CA). The best model was selected using two statistical criteria, the Akaike information criterion (AIC) and coefficient of determination (R^2), and also considering the agronomic significance of alternative models. To determine when major differences occurred across varieties and variety × fertility interactions we performed an ANOVA on the deviation data across all site-years and used the LINES statement. If the interaction of variety and fertility was not significant, we analyzed the residuals of these relationships for the fertilizer effect (Sadras and Moran, 2012). Because grain protein concentration is dependent on yield (Bogard et al., 2010; Oury and Godin, 2007; Simmonds, 1995), we first fitted a linear regression between deviations of grain protein and yield. Then, we analyzed the residuals of this relationship against year of variety release and fertilizer practice (Ortez et al., 2018).

Shoot biomass as affected by thermal time (growing degree days, GDD°C base temperature 0°C, Gallagher (1979)) was first evaluated using the ANOVA procedure described above at each growth stage for whole plant biomass, and afterwards, for each individual plant component at each growth stage. Crop growth rate was calculated as the difference in shoot biomass between two successive samplings, divided by the intervening thermal time. Non-linear models and historical trends were fitted with SigmaPlot version 13.0 (Systat Software, San Jose, CA).

We analyzed the entire dataset to identify the environmental influences on grain yield, as well as the relationships between yield and the measured traits. We tested seven statistical procedures (stepwise, forward, backward, least angle regression (LAR), least squared shrinkage operator (LASSO), elastic net, and conditional inference trees) using grain yield as a dependent variable and measured traits and environmental conditions as independent variables. The first six models were built in PROC GMSELECT in SAS version 9.4 (SAS Institute, Cary, NC). The conditional inference tree was built using the *partykit* package in R (R development Core team, 2016). Intermediate node and terminal node included a minimum of 10% of total observations. A sensitivity analysis allowed less observations to form nodes, but the model fit was improved in less than 10% so the most parsimonious model was selected. Environmental conditions evaluated were average maximum and minimum temperatures, cumulative precipitation, cumulative solar radiation, and photothermal quotient for different developmental windows, including the entire cycle, the 30-d period prior to anthesis, and the grain filling period.

Results

Weather conditions

Seasonal precipitation ranged between 281 and 472 mm. Seasonal differences were more apparent during the fall and winter, with spring precipitation ranging between 169 and 262 mm at both growing seasons (Table 1 - 3). These conditions led to lower biomass production in 2016-17, precluding a combined analysis of the data. Despite lower seasonal total precipitation, favorable spring weather led to greater grain yield in 2017-18.

Grain yield, grain-N removal, and grain protein concentration

There were significant variety and fertility effects on wheat grain yield in both seasons, with no variety × fertility interaction (Table 1 - 4). Grain yield ranged from 1.7 to 4.9 Mg ha^{-1} for tall varieties and from 3.4 to 6.3 Mg ha^{-1} for semi-dwarf varieties. Within growing season, tall varieties yielded 2.1 to 5.9 Mg ha^{-1} less than semi-dwarf varieties.

In-furrow fertilizer increased mean yield by 0.2 to 0.4 Mg ha^{-1} in relation to control. Grain yield increased non-linearly with year of release (Fig. 1 - 1A), with three distinct rates. A low yield-gain period between 1920 and 1966 (17 kg ha^{-1} yr^{-1}), followed by a steep yield gain between 1966 and 2000 (62 kg ha^{-1} yr^{-1}), and a slower yield gain phase after 2000 (8 kg ha^{-1} yr^{-1}).

There were significant variety and fertility effects on grain-N removal (Table 1 - 4). Grain-N removal increased from tall to semi-dwarf varieties (c.a., 64 to 130 kg ha^{-1} in 2016-17 and 127 to 155 kg ha^{-1} in 2017-18). In-furrow fertilizer increased grain-N removal by 6 to 9 kg ha^{-1}. Similar to grain yield, grain-N removal deviation varied non-linearly with year of release, with linear rates of 0.44, 1.28, and 0.11 kg ha^{-1} yr^{-1} for the corresponding periods.

In 2016-17, there was a significant interaction between variety and fertility on grain protein concentration (Table 1 - 4) as most varieties increased grain protein concentration in response to in-furrow fertilizer except by the semi-dwarf varieties Fuller and KanMark (data not shown). Typically, tall varieties had greater grain protein concentration than the semi-dwarf varieties. In 2017-18, grain protein concentration in tall varieties was 142 to 150 g kg^{-1} compared to 129 to 140 g kg^{-1} in semi-dwarf varieties. In-furrow fertilizer decreased grain protein concentration (Table 1 - 4). Grain protein deviation declined linearly with grain yield deviation

(Fig. 1 - 2A), and the residuals of this relationship were unrelated to year of release ($p > 0.37$, Fig. 1 - 2B).

Yield components

There was a non-linear relationship between heads m^2 and year of release, with modern varieties resulting in less heads m^2 (greater differences between late 1980s until early 2000s, Fig. 1 - 3A). Tall varieties had 872 and 767 heads m^2 while semi-dwarf varieties had 741 and 680 heads m^2 during 2016-17 and 2017-18 (Table 1 - 4). As heads m^2 decreased over time, kernels head^{-1} increased, with greater increases after 1980s from 12-18 kernels head^{-1} in tall varieties to 21-27 kernels head^{-1} in semi-dwarf varieties (Fig. 1 - 3B and Table 1 - 4). Due to the contrasting trends in heads m^2 and kernels head^{-1}, the increase in kernels m^2 was slower but also significant (Fig. 1 - 3C). The tall variety Kharkof had the lowest kernels m^2 (i.e., 9383 and 12852 kernels m^2) while the semi-dwarf variety KanMark had the highest (i.e., 17904 and 21041 kernels m^2).

Kernel weight showed a significant bi-linear relationship with year of release (Fig. 1 - 3D), increasing at a higher rate until 1966 and remaining constant afterwards (Table 1 - 4). Harvest index increased non-linearly over time and ranged from 0.26 to 0.51 among locations (Fig. 1 - 3E). In 2016-17, harvest index increased from 0.15 in tall varieties to 0.33 in their semi-dwarf counterparts; differences were smaller in 2017-18 (Table 1 - 4). Variety affected grain volume weight in both growing seasons, both with no consistent time trends (Table 1 - 4).

In-furrow fertilizer increased heads m^2 (Fig. 1 - 3A) from 733 to 825 in 2016-17, and from 667 to 737 heads m^2 in 2017-18 (Table 1 - 4). However, it decreased kernels head^{-1} (Fig. 1 - 3B) from 20 to 17 in 2016-17 and from 26 to 24 in 2017-18 (Table 1 - 4). Fertilizer had no effect on kernels m^2 (Fig. 1 - 3C) and decreased kernel weight (Fig. 1 - 3D and Table 1 - 4) from 26.9 to 26.1 mg kernel^{-1} in 2016-17 and from 26.3 to 25.4 mg kernel^{-1} in 2017-18. There were no differences in harvest index between the fertilizer practices (Fig. 1 - 3E), and in-furrow fertilizer showed lower volume weight than control (Table 1 - 4).

Plant height, stem diameter, and chronological changes

Plant height decreased over time with a steep change around ~1970s from 122 cm for tall varieties to 93-100 cm in semi-dwarf ones (Fig. 1 - 4A, Table 1 - 4). Stem diameter ranged from 2.87 to 3.21 mm among locations and increased with year of release, particularly from 1960 to 2000s (Fig. 1 - 4B). Semi-dwarf varieties reached anthesis and physiological maturity earlier than tall varieties (Fig. 1 - 4CD), and had a longer period from anthesis to physiological maturity (Fig 1 - 4F). However, varieties released in the last 30-yr showed minimal developmental changes (Fig. 1 - 4).

Total biomass, crop growth rate, and biomass allocation to plant components

There was no clear pattern in the differences in biomass among varieties early in the season (i.e. at GS 26 and 31), but tall varieties had greater shoot biomass than semi-dwarf ones at anthesis (861-1087 g m^2 *versus* 658-888 g m^2). These differences were not apparent (2017-18) or were reversed (2016-17) at GS 85, when semi-dwarf varieties showed up to 30% greater biomass accumulation relative to tall varieties. Semi-dwarf varieties reached maximum dry weight at GS 85. There were no differences in biomass accumulation among varieties at maturity. In-furrow fertilizer increased biomass irrespective of growth stage.

Crop growth rate was low (c.a., 0.08 to 0.3 g m^2 GDD $°C^{-1}$) between tillering and jointing, and increased to about 1.3-1.5 g m^2 GDD $°C^{-1}$ between GS31 and GS65 (Table 1 - 5). There were no clear differences among varieties early in the season, although in-furrow fertilizer consistently increased growth rate. The growth rate in semi-dwarf varieties was as much as two times greater than in tall varieties from anthesis to soft dough in the first season (Table 1 - 5), decreasing after soft dough. Negative values suggest dry matter accumulated at maturity was less than that at soft dough (Table 1 - 5).

There were no clear patterns in the differences among varieties in their allocation of biomass towards leaves and stem early in the season (Table 1 - 6). However, 57 to 68% of the biomass in tall varieties was allocated to stem during anthesis, decreasing to 39 to 60% during soft dough. Meanwhile, stem biomass in semi-dwarf varieties accounted for c.a., 47 to 62% at anthesis and 36 to 47% at soft dough. Grain biomass at soft dough stage was greater in semi-dwarf varieties in both growing seasons, and dry matter partitioning to leaves and stem ceased at this stage regardless of year of release. Grain biomass at maturity accounted for as much as 46% of total biomass in semi-dwarf varieties, and no more than 36% for tall varieties (Table 1 - 6). For every g m^2 increase in whole plant biomass, semi-dwarf varieties allocated 0.35 g m^2 to grains while tall varieties allocated only 0.28 g m^2 (Fig. 1 - 5A). In-furrow fertilizer increased biomass accumulation relative to no fertilizer treatment irrespective of growth stage and plant component (Table 1 - 6); however, this biomass was more allocated to the vegetative tissues rather than to the grain (Fig. 1 - 5B – C).

Association between grain yield, weather variables, and measured traits

In-furrow fertilizer, plant height, year of release, and kernels m^2 were positively, and seasonal cumulative solar radiation was negatively associated with grain yield in at least 6 out of 7 models (inset table on Fig. 1 - 6). Grain yield related positively with kernel weight, head size, stem diameter, biomass growth rate between GS65 and GS 85, and maximum temperature during grain filling at least half of the studied models. Head number, seasonal minimum and maximum temperature, photothermal quotient during grain filling, cumulative precipitation thirty days before anthesis, and biomass rate at GS 92, were negatively associated with yield. Figure 1 - 6 suggests that kernels head^{-1} was among the most important determinants of yield, interacting with biomass rate at GS 92 and plant height when < 22 kernels head^{-1}. When > 22 kernels head^{-1}, fertilizer increased yield depending on photothermal quotient. In the absence of fertilizer, more kernels m^{-2} was related to greater yield.

Discussion

Grain yield, grain-N removal, and grain protein concentration

A sample of winter wheat varieties released between 1920 and 2016 in the U.S. southern Great Plains revealed different rates in yield gain in different time periods, with a small yield gains until ~1970s, accompanied by greater yield gain through ~2000s, and smaller gains afterwards. However, our power to infer is low on account of most of the varieties studied were developed by the Kansas state wheat breeding program leading to potential bias. Historical sets of wheat varieties have been assessed to estimate the progress of breeding efforts and quantify the impact of management practices (Acreche et al., 2008; Brancourt-Humel et al., 2003; Del Pozo et al., 2014; Flohr et al., 2018; Lo Valvo et al., 2017). In some cases, similar historical trends occurred in different regions (Cox et al., 1988; Austin et al., 1980; Slafer and Andrade, 1989; Lo Valvo et al., 2017; Sanchez-Garcia et al., 2013; Beche et al., 2014; Flohr et al.; 2018). The greater yield improvement mid-century was a result of the introduction of the dwarfing genes, which allowed for less lodging and for the use of greater fertilizer rates (Evenson, 2003).

The trend in yield gain found in this study, however, contrasted with other studies that reported no clear tendency of leveling-off in yield progress (Donmez et al., 2001; Sadras and Lawson, 2011). This divergence might result from the genotype × environment interaction (Sanchez-Garcia et al., 2013), or environmental yield potential might also affect these results, especially when evaluating responses to management (Brancourt-Humel et al., 2003). Finally, the focus of the regional breeding programs may also affect the rate of yield gain (e.g., focusing solely in yield potential *versus* focusing in disease resistance and grain quality) (Fischer and Edmeades, 2010).

Crops yielded more with in-furrow fertilizer relative to unfertilized controls. Varieties yielding more in high-input environments were also shown by Wang et al. (2017) and Leikam et al. (1982). While higher rates of P fertilizer resulted in greater yield relative to no fertilizer application in some studies (Leikam et al., 1982; Lollato et al., 2019) initial soil P concentration was above the minimum critical values for wheat yield at all studied site-years (Leikam et al., 2003). This suggests that the yield increase in our research might have resulted from nutrients other than P (i.e., N, S, and Zn). Also, our results showed greater grain yield difference between tall and semi-dwarf varieties as compared to between fertilizer treatments, suggesting that genetic improvement might have contributed more to historical yield gains than agronomic management, corroborating with Nalley et al. (2008).

Modern varieties had greater grain-N removal and lower grain protein concentration than historical ones, suggesting that the decrease in grain protein concentration over time was due to greater improvements in grain yield relative to grain-N removal. This is similar to the suggestion by Sadras et al. (2016). As expected and reported (Bogard et al., 2010; Kibite and Evans, 1984; Lollato and Edwards, 2015; Oury and Godin, 2007), grain protein concentration showed a significant linear negative relationship with grain yield. The decrease in grain protein concentration at higher yielding environments is a dilution effect as a result of the increment on the amount of carbohydrate assimilated in the grain (Kibite and Evans, 1984). Nonetheless, when normalized for yield, grain protein concentration did not change with year of release.

Morphological and physiological components of yield increase

Heads m^2 decreased over time in our study, with similar findings reported by Tian et al. (2011) in China. Breeding programs directly selecting for yield in dry environments (e.g., Kansas or the North China Plain) might have indirectly selected for lower tillering and fewer heads per unit area as a soil water conservation strategy (van Herwaarden et al., 1998). In-furrow fertilizer increased heads m^2 by 7-10%, likely due to greater early-season wheat biomass (Lollato et al., 2013) and tillers plant^{-1} (Sato et al., 1996), increasing heads m^2 (Rodríguez et al., 1999). The effects of in-furrow fertilizer on yield components typically contrasted with the trends over time, perhaps explaining the inconsistent wheat yields response to in-furrow P in the region (e.g., Lollato et al., 2013; Lollato et al., 2019).

The increase kernels head^{-1} over time corroborates findings for other regions (De Vita et al., 2007; Del Pozo et al., 2014; Siddique et al., 1989a, 1989b). Sanchez-Garcia et al. (2013) reported that the increase in kernels head^{-1} was explained by an increase in spikelets head^{-1} and kernels spikelet^{-1}. The introduction of dwarfing genes can partially explain the increase in kernels head^{-1} (De Vita et al., 2007; Flintham et al., 1997), as these genes might be associated with enlargement of biomass partitioned into spikes (Abbate et al., 1998; Miralles et al., 1998), and changes into the heads (e.g., endurance of the floret primordia; Miralles et al., 1998). Interestingly, in-furrow fertilizer reduced kernels per head, perhaps because of the increased number of heads reducing average head size.

Kernels m^2 is considered a coarse-regulator of wheat yield (Slafer et al., 2014). Its progress over decades was reported to relate to improvements in kernels head^{-1} (De Vita et al., 2007; Slafer and Andrade, 1989), head dry weight at anthesis (Acreche et al., 2008), the capability of varieties to partition more photoassimilates into the developing heads (Slafer and Andrade, 1989), and growth rate (Sadras and Lawson, 2011).

Kernel weight increased from 1920 until 1960s, with no major changes afterwards. This evaluation was performed under non-limiting photoassimilate conditions (slope and $r^2 = 0$ for kernel weight vs. kernels m^{-2}, data not shown), suggesting that selection for yield over time did not change kernel weight, maybe because kernel weight is a fine regulator of wheat yield (Slafer et al., 2014). Besides the variety effect, in-furrow fertilizer decreased average kernel weight, which agrees with Tian et al. (2011). This likely results from the more heads formed from later tillers due to in-furrow fertilization.

Harvest index has been associated with genetic yield gain in wheat (Royo et al., 2007; Slafer and Andrade, 1989; Zhou et al., 2007a). However, Austin et al. (1980) proposed that theoretical biological limit for harvest index in well-watered crops was ~0.62, suggesting that might have room for further improvement in modern hard red winter wheat varieties in the study region (i.e., harvest index ~0.44 for semi-dwarf varieties), but not as much as 0.62, as the studied regions are characterized as dry environments. Tall and semi-dwarf varieties at maturity presented similar whole plant biomass, suggesting that improvements in grain yield over time resulted from a greater ability of semi-dwarf varieties to allocate assimilates to the grain (Tian et al., 2011).

Plant height, stem diameter, and chronological changes

An optimum wheat plant height between 0.7-1.0 m was described by Richards (1992), which is shorter than the measurements in the current study. This indicates that there is still scope for shortening wheat varieties in U.S. southern Great Plains. Benefits of shorter varieties might include increases in harvest index (Acreche et al., 2008; Austin et al., 1980); standability;

less haying off (Van Hardewaarden et al., 1998); and perhaps improvements in grain yield (Brancourt-Humel et al., 2003; Donmez et al., 2001). Historical varieties with thinner stems were more prone to lodging (data not shown). Zuber et al. (1999) and Tripathi et al. (2003) found a strong negative relationship between stem diameter and lodging score. Lodging can decrease the stored photoassimilate reserves (Fischer and Stapper, 1987) and the N use efficiency (Brancourt-Humel et al., 2003), resulting in grain yield losses of as much as 35% (Fischer and Stapper, 1987).

Large variation for flowering thermal time in the varieties included in this study occurred between 1920 and 1988, with no substantial changes afterwards. The shorter cycle observed in semi-dwarf varieties derived from earliness in flowering time but similar or longer duration of grain fill. Early anthesis has been associated with genetic progress in grain yield of wheat in the U.S. Great Plains (Donmez et al., 2001), in the U.K. (Austin et al., 1980), and Mediterranean environments (De Vita et al., 2007; Giunta et al., 2007; Siddique et al., 1989a). Perhaps the lack of change in flowering time since 1990s suggests that modern varieties flower at the optimal time for the region, balancing higher risks of spring freeze injury in earlier flowering and greater risks for high temperatures and drought stresses during grain fill with later flowering (Khalil et al., 1995). Semi-dwarf varieties also reached maturity earlier than tall varieties, maybe due to greater growth rates (Kirby et al., 1989; Siddique et al., 1989a).

Total biomass, crop growth rate, and allocation to plant components

The majority of the studies comparing historical and modern wheat varieties report biomass at physiological maturity (Brancourt-Humel et al., 2003; Giunta et al., 2007; Sadras and Lawson, 2011; Wang et al., 2017b); fewer studies reported dynamics of shoot biomass (e.g., Austin et al., 1980; Siddique et al., 1989a; Shearman et al., 2005; Acreche et al., 2008; Flohr et al., 2018).

The similarity among wheat varieties in total biomass and initial growth rate suggests that the chronological changes in biomass accumulation responsible for greater grain yield occurred later in the season. At anthesis, tall varieties had greater total biomass, likely due to the longer period required to reach this growth stage as compared to shorter-cycled semi-dwarf varieties (Álvaro et al., 2008; Flohr et al., 2018). Despite a greater biomass, its partitioning into reproductive organs was less efficient in tall varieties. Reports by Slafer et al. (1990) and Álvaro et al. (2008) agreed with our findings and showed that biomass partitioning to the chaff in wheat varieties increased over time. The same levels of biomass with greater HI in semi-dwarf varieties suggests that yield increases in modern wheat varieties resulted from more efficient partitioning of assimilates to the grains rather than greater biomass. Previous studies have reported no substantial changes in biomass accumulation at maturity over the years, for instance (Acreche et al., 2008; Austin et al., 1980; D. F. Calderini et al., 1995; Kitonyo et al., 2017; Royo et al., 2007).

Conclusions

Kansas winter wheat varieties increased grain yield over time, but there was a decrease on the pace of progress after 1990s. The selection of lines to move forward in breeding programs based on grain yield indirectly changed the yield components over decades, leading to greater kernels per area and kernels per head in modern semi-dwarf cultivars. Semi-dwarf varieties also flowered earlier than tall varieties, but had a longer grain filling period. Greater yield in semi-dwarf cultivars also resulted from a greater ability to allocate dry matter into the grain, as semi-dwarf cultivars had the same shoot biomass levels than tall varieties. The decrease in grain protein concentration over time was solely function of increases in grain yield, as there was no relationship between the residuals of grain protein concentration and grain yield versus year of release. While in-furrow fertilizer increased biomass and grain yield, the lack of interaction suggests that semi-dwarf varieties were not more responsive than tall varieties to in-furrow fertilizer. Future research could expand on the number of varieties studied on both tall and semi-dwarf groups to cover a greater number of year of release.

Figures

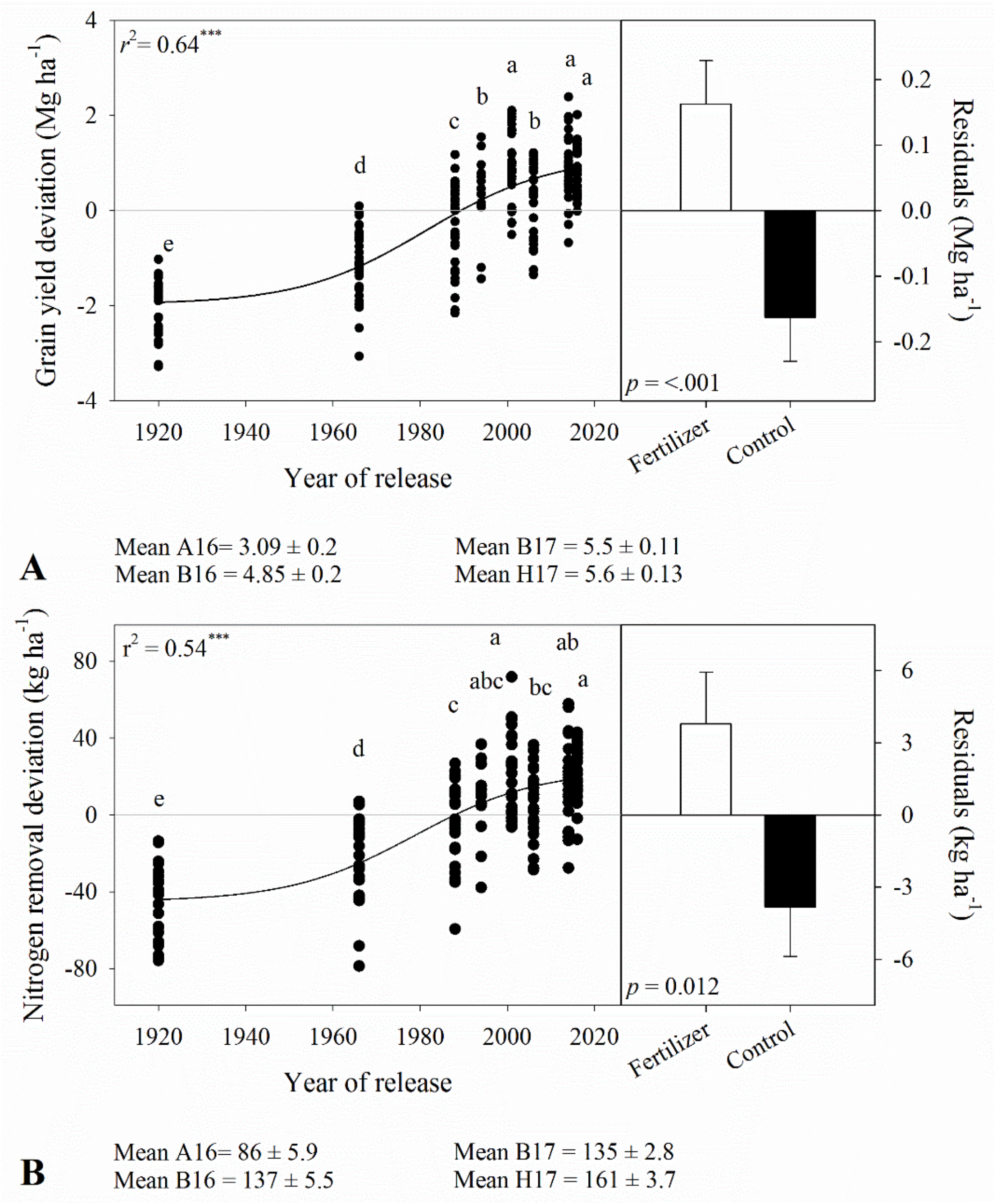


Figure 1.1 Relationship between year of release from wheat varieties released between 1920 and 2016 and grain yield deviation. Comparison of the regression residuals for in-furrow fertilizer treatment and no fertilizer (bars show mean and standard error). Values correspond to the data of four site-years during two growing seasons (2016-17 and 2017-18) (A). Relationship between year of release from wheat varieties released between 1920 and 2016 and nitrogen removal deviation. Comparison of the regression residuals for in-furrow fertilizer treatment and no fertilizer (bars show mean and standard error) (B). Mean for all varieties in each site and year. * Significant ($P<0.05$); ** significant ($P<0.01$); * significant ($P<0.001$); ns non-significant ($P>0.05$).**

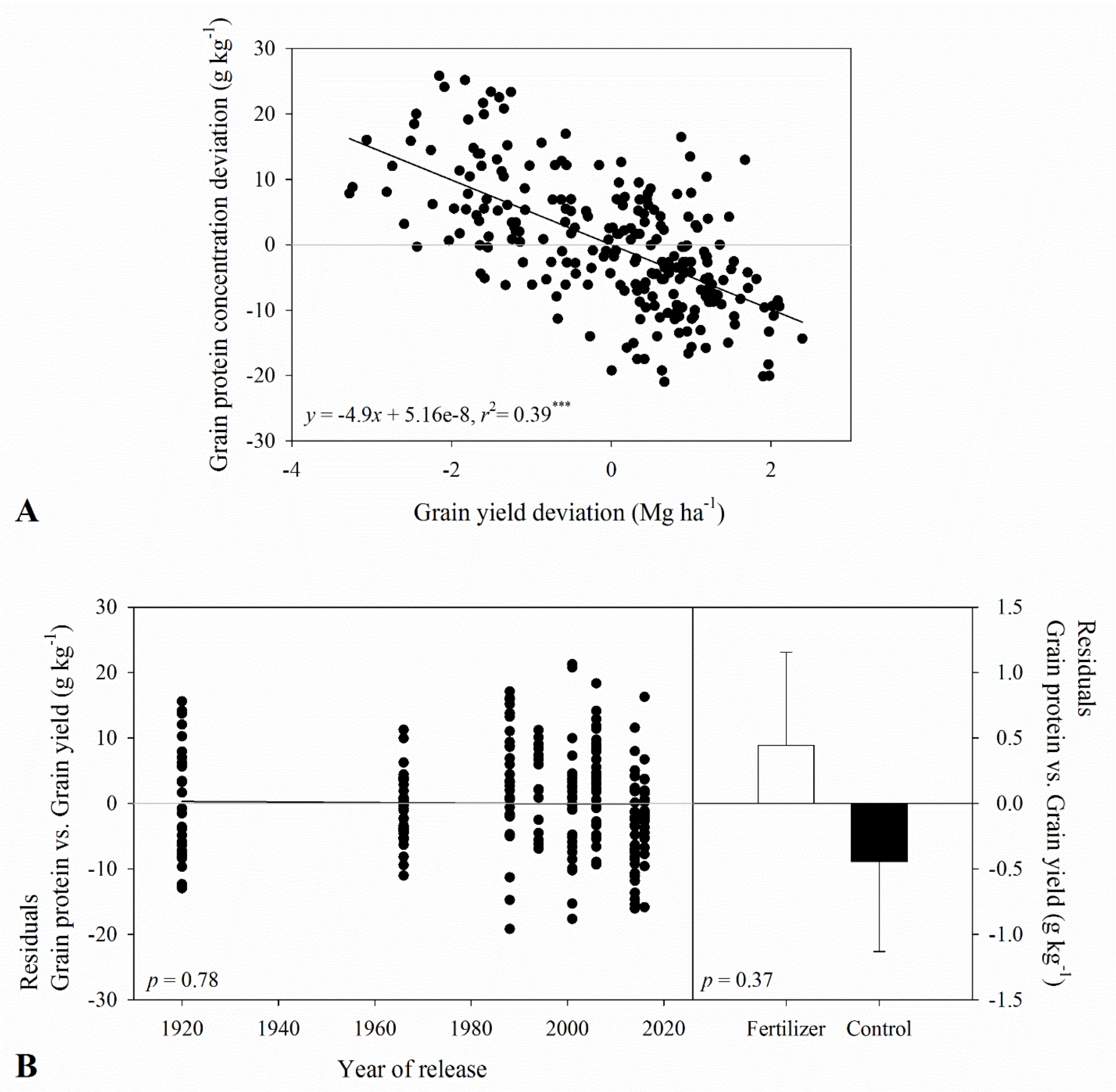


Figure 1.2 Relationship between grain protein concentration deviation and grain yield deviation for varieties released between 1920 and 2016 (A). Regression residuals as affected by year of variety release. Comparison of the regression residuals for in-furrow fertilizer treatment and no fertilizer (bars show mean and standard error (B). Values correspond to the data of four site-years during two growing seasons (2016-17 and 2017-18). * Significant ($P<0.05$); ** significant ($P<0.01$); * significant ($P<0.001$); ^{ns} non-significant ($P>0.05$).**

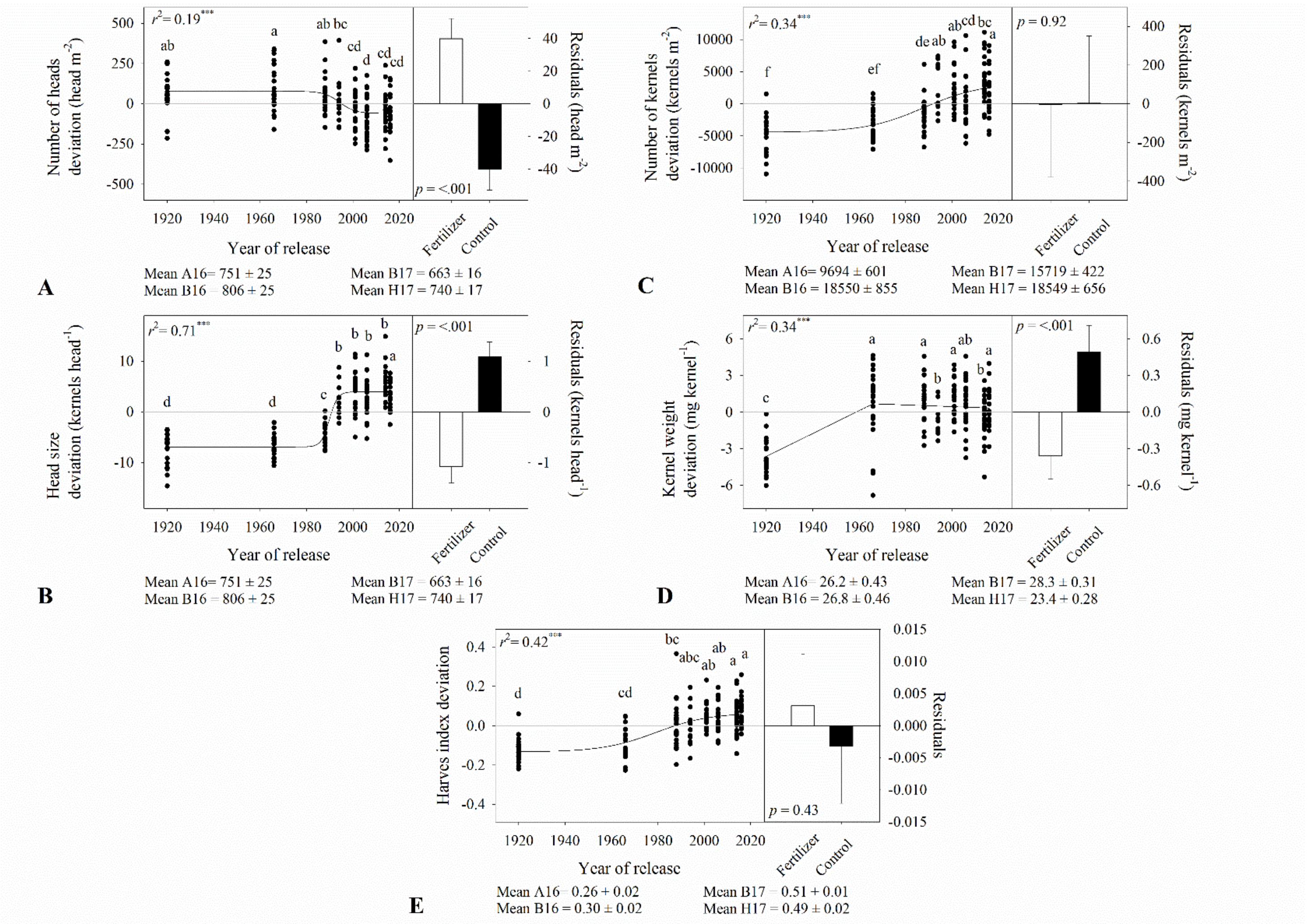


Figure 1.3 Relationship between year of release from wheat varieties released between 1920 and 2016 and yield components deviation. Comparison of the regression residuals for in-furrow fertilizer treatment and no fertilizer (mean and 1 standard error). Values correspond to the data of four site-years during two growing seasons (2016-17 and 2017-18). Mean for all varieties in each site and year. * Significant (P<0.05); ** significant (P<0.01); * significant (P<0.001); ns non-significant (P>0.05).**

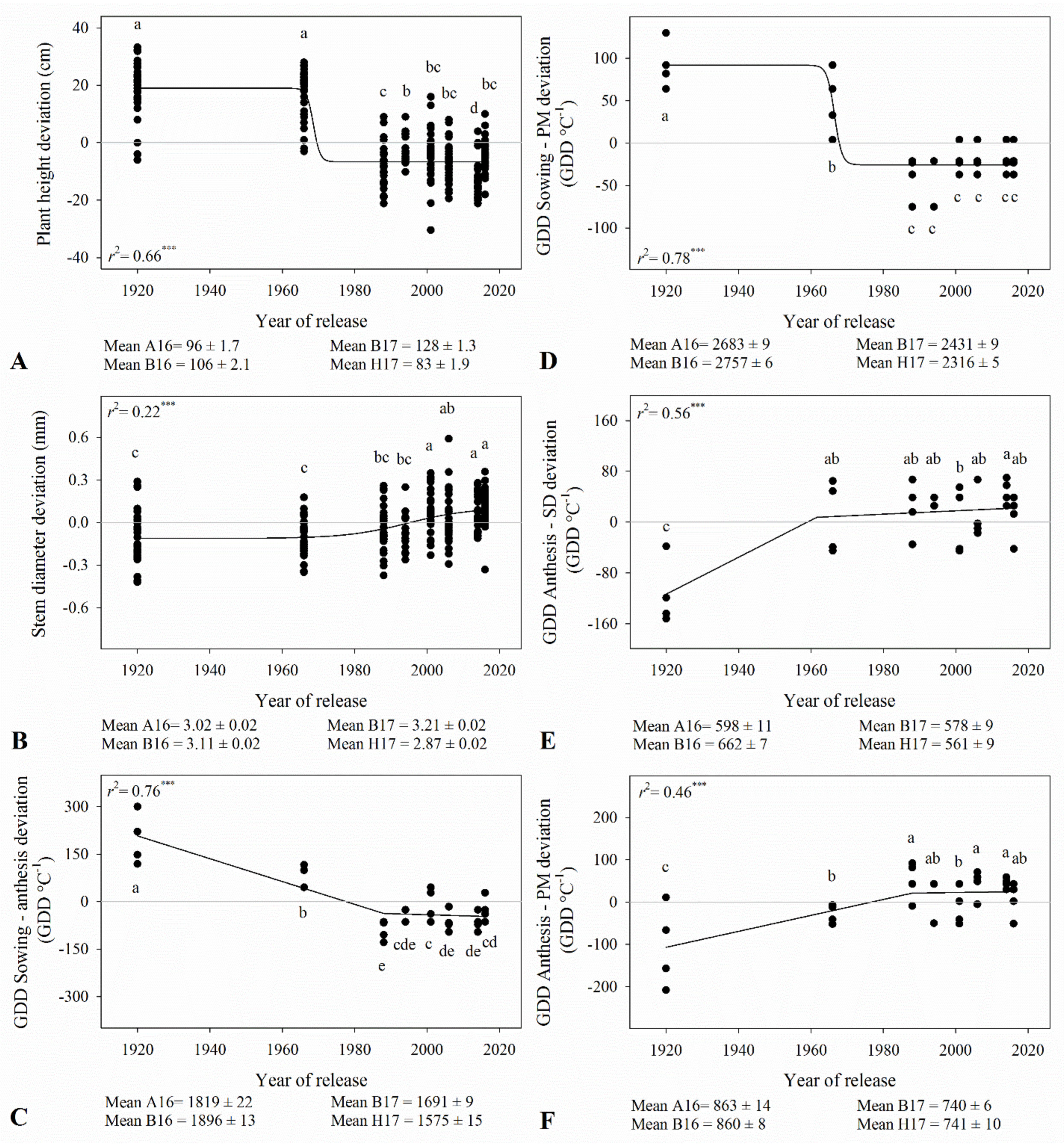


Figure 1.4 Relationship between year of release from wheat varieties released between 1920 and 2016 and: plant height (A), stem diameter (B), and thermal time development (C, D, E, F). Values correspond to the data of four site-years during two growing seasons (2016-17 and 2017-18). Mean for all varieties in each site and year. * Significant ($P<0.05$); ** significant ($P<0.01$); * significant ($P<0.001$); ^{ns} non-significant ($P>0.05$).**

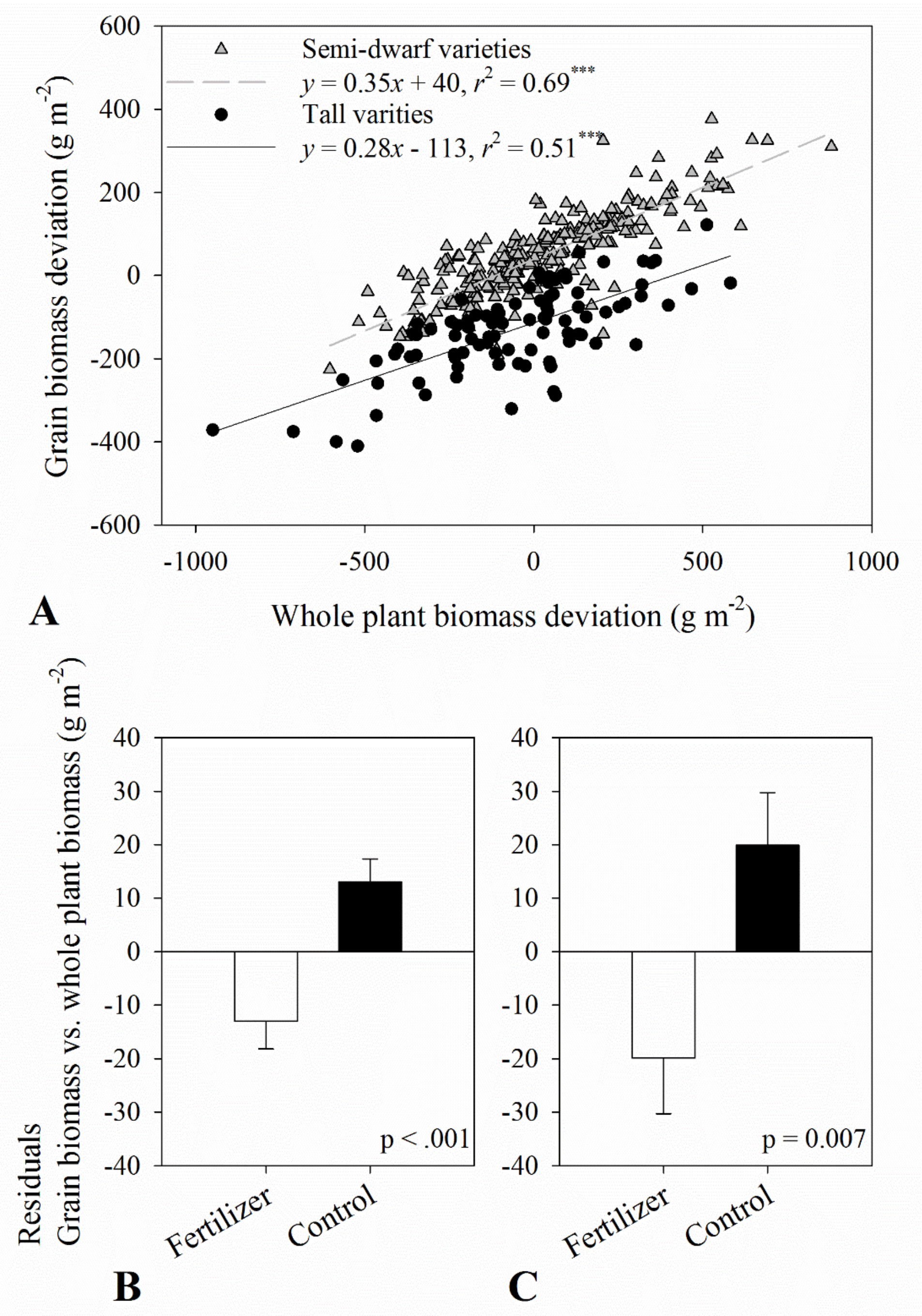
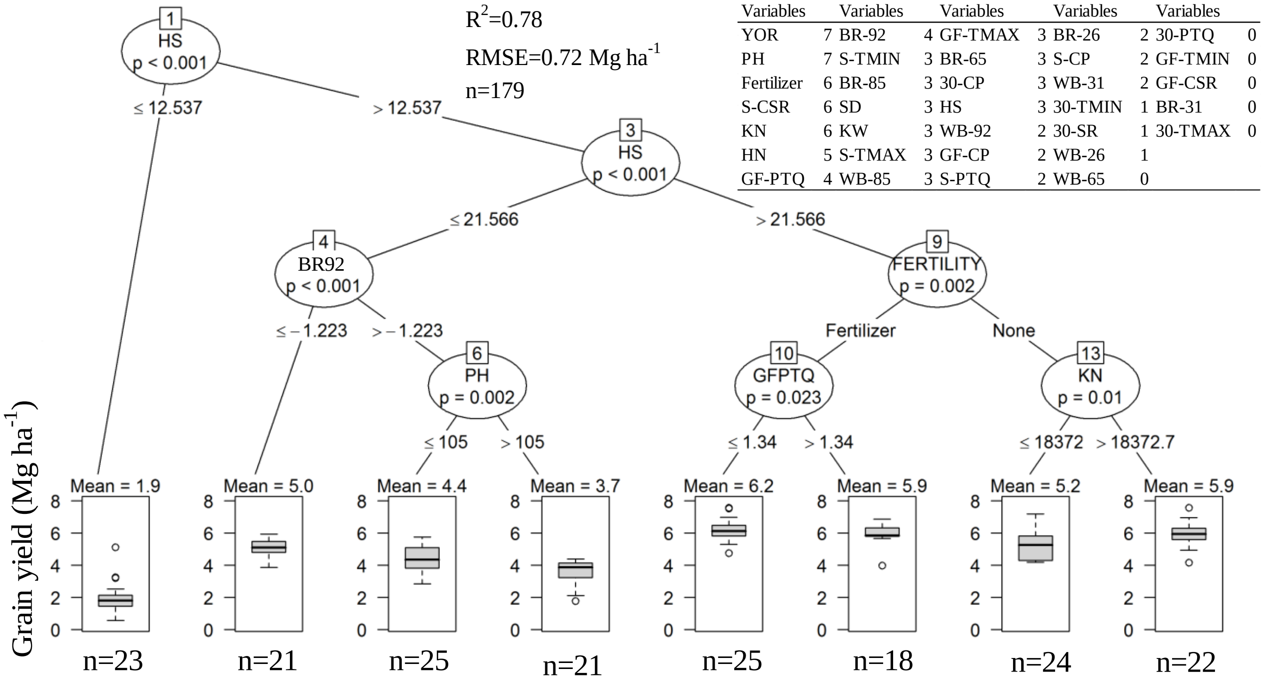


Figure 1.5 Relationship between grain biomass deviation and whole plant biomass deviation between GS 85 and 92, for the two groups: semi-dwarf varieties and tall varieties (A). Comparison of the regression residuals for in-furrow fertilizer treatment and no fertilizer (bars show mean and standard error) for semi-dwarf varieties (B). Comparison of the regression residuals for in-furrow fertilizer treatment and no fertilizer (bars show mean and standard error) for tall varieties (C). Values correspond to the data of four site-years during two growing seasons (2016-17 and 2017-18). * Significant ($P<0.05$); ** significant ($P<0.01$); * significant ($P<0.001$); ^{ns} non-significant ($P>0.05$).**



Variables		Variables		Variables		Variables		Variables	
YOR	7	BR-92	4	GF-TMAX	3	BR-26	2	30-PTQ	0
PH	7	S-TMIN	3	BR-65	3	S-CP	2	GF-TMIN	0
Fertilizer	6	BR-85	3	30-CP	3	WB-31	2	GF-CSR	0
S-CSR	6	SD	3	HS	3	30-TMIN	1	BR-31	0
KN	6	KW	3	WB-92	2	30-SR	1	30-TMAX	0
HN	5	S-TMAX	3	GF-CP	2	WB-26	1		
GF-PTQ	4	WB-85	3	S-PTQ	2	WB-65	0		

Figure 1.6 Conditional inference tree for the entire dataset. Boxplots shows spans of first to the third quartile with central rectangles, inside solid line are the means which are also shown above each boxplot. The lower and upper lines show the minimum and maximum values, respectively. Inset table shows a list of 33 candidate variables at influencing wheat grain yield and the number of statistical models in which each variable was significantly associated with grain yield, out of a total of seven models. Year of variety release (year of release), plant height (PH), kernel number (KN), head number (HN), stem diameter (SD), kernel weight (KW), head size (HS), maximum (TMAX) and minimum temperature (TMIN), cumulative solar radiation (CSR), cumulative precipitation (CP), photo thermal quotient (PTQ), whole plant biomass (WB), cropt biomass rate (BR). Letters left to each variable represent the period, growing season (S), thirty days before anthesis (30), grain filling (GF). Values right to each variable represent the growth stage, GS 26, 31, 65, 85, and 92 (26, 31, 65, 85, and 92).

Tables

Table 1.1 Similarity matrix for eight winter wheat varieties using genotyping by sequencing (GBS) single nucleotide polymorphisms (SNPs). A total of 9946 SNPs were used for the analysis to determine the percent similarity.

Varieties (Year of release)	Kharkoff (1920)	Scout66 (1966)	Karl92 (1988)	Jagger (1994)	Jagalene (2001)	Fuller (2006)	KanMark (2014)	Larry (2016)
Kharkoff (1920)		0.86	0.58	0.41	0.52	0.49	0.54	0.54
Scout66 (1966)			0.51	0.38	0.47	0.45	0.50	0.50
Karl92 (1988)				0.34	0.45	0.52	0.61	0.63
Jagger (1994)					0.78	0.75	0.37	0.51
Jagalene (2001)						0.63	0.51	0.52
Fuller (2006)							0.42	0.48
KanMark (2014)								0.52
Larry (2016)								

Table 1.2 Initial soil pH, extractable P, K, Ca, Mg, Na, SO_4-S, Zn, cation exchange capacity (CEC), organic matter (O.M.), and NO_3-N for the 0-15 and 15-60 cm soil layers at Ashland Bottoms, Belleville and Hutchinson, KS. Amount of inorganic N applied in each location during each growing season is also shown.

Year	Location	Depth (cm)	pH	P (mg kg^{-1})	K (mg kg^{-1})	Ca (mg kg^{-1})	Mg (mg kg^{-1})	Na (mg kg^{-1})	SO_4-S (mg kg^{-1})	Zn (mg kg^{-1})	CEC (Meq 100g^{-1})	O.M. (g kg^{-1})	NO_3-N (mg kg^{-1})	Applied N (kg ha^{-1})
2016-17	Ashland Bottoms	0 – 15	6.0	41	190	975	105	13	1.7	0.3	10	13	3.6	105
		15 – 60	6.9	11	90	1375	125	12	3.7	0.4	8	8	3.5	
	Belleville	0 – 15	5.9	42	474	1532	202	13	2.9	1.5	21	30	4.5	158
		15 – 60	5.9	12	224	2005	245	18	2.5	1.9	24	26	2.0	
2017-18	Hutchinson	0 – 15	6.0	77	218	1886	238	11	3.4	2.3	20	24	6.2	63
		15 – 60	6.8	55	214	2666	237	10	3.6	2.8	16	24	8.2	
	Belleville	0 – 15	5.6	42	400	1727	228	10	3.0	0.9	22	28	8.9	67
		15 – 60	5.9	35	342	2452	326	37	2.3	0.8	24	27	7.7	

Table 1.3 Cumulative precipitation (Precip.), average maximum (T_{max}) and minimum temperatures (T_{min}), cumulative solar radiation (R_s), and average photothermal quotient (PTQ) for each portion of growing season during 2016-17 and 2017-18 at Ashland Bottoms, Belleville and Hutchinson, KS. The 30-year mean of each variable for each location is also shown.

		Precip.			T_{min}/ T_{max}			R_s			PTQ		
Year	Location	Fall† (mm)	Winter‡ (mm)	Spring§ (mm)	Fall† (^{0}C)	Winter‡ (^{0}C)	Spring§ (^{0}C)	Fall† (MJ m^{-2})	Winter‡ (MJ m^{-2})	Spring§ (MJ m^{-2})	Fall† (MJ m^{-2} d^{-1} $^0C^{-1}$)	Winter‡ (MJ m^{-2} d^{-1} $^0C^{-1}$)	Spring§ (MJ m^{-2} d^{-1} $^0C^{-1}$)
2016-17	Ashland B.	99	146	227	2/16	-1/11	12/25	1027	1083	1909	0.79	0.77	1.82
	Belleville	91	74	262	-1/14	-3/10	10/24	876	996	1938	0.64	0.56	1.71
2017-18	Hutchinson	52	60	169	0/14	-5/10	11/26	874	1063	1567	0.62	0.55	1.33
	Belleville	37	36	217	-3/12	-8/6	10/24	861	1030	1811	0.54	0.30	1.33
30-year mean	Ashland B.	119	87	318	1/13	-4/9	12/25	792	941	1745	0.59	0.47	1.41
	Belleville	85	71	256	-1/12	-6/8	10/24	826	1002	1839	0.57	0.42	1.56
	Hutchinson	125	102	264	2/15	-3/9	10/23	764	786	1396	0.57	0.41	1.16

† Fall encompasses October, November, and December.

‡ Winter encompasses January, February, and March.

§ Spring encompasses the period between April 1st and harvest.

Table 1.4 Grain yield, head number, head size, kernel number, kernel weight, harvest index (HI), plant height (PH), stem diameter, grain protein concentration (GPC) and grain volume weight of wheat varieties released between 1920 and 2016, fertilizer treatment, and their interaction during the growing seasons 2016-17 and 2017-18. Variety and fertilizer means were averaged across locations within growing season.

Year	Variety (Year of release)	Fertilizer	Grain Yield (Mg ha^{-1})	Nitrogen removal (kg ha^{-1})	GPC (g kg^{-1})	Head number (heads m^2)	Head size (kernels $head^{-1}$)	Kernel number (kernels m^2)	Kernel weight (mg $kernel^{-1}$)	HI	PH (cm)	Stem Diameter (mm)	Volume weight (kg m^{-3})
2016-17	Kharkof (1920)‡		1.7e†	54d	135ab	813bc	11d	9383c	22.0b	0.13c	120a	2.88c	728e
	Scout 66 (1966)		2.4d	74c	133ab	931a	12d	10863c	26.7a	0.16c	123a	2.90c	751c
	Karl 92 (1988)		3.4c	103b	138a	854ab	14c	12221bc	26.8a	0.26b	93c	3.00b	744d
	Jagalene (2001)		5.2a	142a	122c	755bcd	23ab	17075a	27.2a	0.34a	95bc	3.17a	770a
	Fuller (2006)		4.5b	127a	131b	677d	23ab	15763a	27.9a	0.32ab	92c	3.16a	755bc
	KanMark (2014)		5.2a	138a	119c	712cd	24a	17904a	26.4a	0.37a	87d	3.18a	776a
	Larry (2016)		5.1ab	138a	121c	708cd	21b	15312ba	28.3a	0.36a	98b	3.18a	759b
		In-furrow	4.0A†	114A	129	825A	17B	13946	26.1B	0.28	102	3.06	754B
		Control	3.8B	108B	128	733B	20A	14203	26.9A	0.28	100	3.07	756A
2017-18	Kharkof (1920)		3.9d	116d	150a	767a	17e	12852c	22.9c	0.39c	125a	3.00	723ab
	Scout 66 (1966)		4.9c	137c	142b	766a	19de	14501bc	27.4a	0.44bc	119a	3.00	712bc
	Karl 92 (1988)		5.5b	148bc	137bcd	731ab	21d	15322bc	27.3a	0.54a	100bc	3.04	731a
	Jagger (1994)		5.9ab	155ab	139bcd	721ab	28bc	19982a	25.1b	0.50ab	104b	2.98	694de
	Jagalene (2001)		6.3a	163a	134cde	660bc	28abc	18443a	27.3a	0.56a	103b	3.07	721ab
	Fuller (2006)		5.5b	144bc	140bc	609c	26c	15657b	25.8b	0.52a	102b	3.02	681e
	KanMark (2014)		6.2a	152ab	129e	698ab	30a	21041a	24.9b	0.52a	94c	3.08	718b
	Larry (2016)		6.2a	166a	133de	666bc	29ab	19274a	26.2ab	0.55a	101bc	3.13	704cd
		In-furrow	5.8A	152Aa	137B	737A	24B	17237	25.4B	0.51	106	3.03	708B
		Control	5.4B	143Bb	139A	667B	26A	17031	26.3A	0.50	106	3.05	713A

† Values followed by the same letter within growing season and treatment are not statistically different at α = 0.05.

‡ Jagger was not included in the 2016-17 growing season analysis.

Table 1.5 Shoot biomass and crop growth rate in whole plant at Zadoks 26, 31, 65, 85 and 92 of wheat varieties released between 1920 and 2016, fertilizer treatment, and their interaction during the growing seasons 2016-17 and 2017-18. Variety and fertilizer means were averaged across locations within growing season.

Year	Variety (Year of release)	Fertilizer	GS 26 (g m^2 / g m^2 GDD ^{0}C^{-1})	GS 31 (g m^2 / g m^2 GDD ^{0}C^{-1})	GS 65 (g m^2 / g m^2 GDD ^{0}C^{-1})	GS 85 (g m^2 / g m^2 GDD ^{0}C^{-1})	GS 92 (g m^2 / g m^2 GDD ^{0}C^{-1})
2016-17	Kharkof (1920)‡		61a / 0.095a†	247 / 0.267	1108a / 1.250	1372c / 0.536b	1421 / 0.384ab
	Scout 66 (1966)		57a / 0.089a	285 / 0.328	1067ab / 1.388	1358c / 0.424b	1518 / 1.269a
	Karl 92 (1988)		59a / 0.092a	267 / 0.299	816c / 1.443	1537bc / 1.131a	1348 / -0.674bc
	Jagalene (2001)		54a / 0.085a	253 / 0.286	989b / 1.474	1889a / 1.419a	1530 / -1.814c
	Fuller (2006)		43b / 0.069b	248 / 0.294	858c / 1.468	1747ab / 1.424a	1446 / -1.065bc
	KanMark (2014)		43b / 0.069b	239 / 0.281	801c / 1.355	1604bc / 1.150 a	1447 / -0.668bc
	Larry (2016)		58a / 0.091a	252 / 0.278	976b / 1.452	1749ab / 1.254a	1441 / -1.487c
		In-furrow	64A / 0.099A†	290A / 0.326A	1005A / 1.451A	1722A / 1.128	1492 / -0.923
		Control	43B / 0.069B	221B / 0.255B	885B / 1.358B	1494B / 0.968	1408 / -0.236
2017-18	Kharkof (1920)		36 / 0.061	157 / 0.178	841a / 1.212	1103 / 0.592	1033 / -0.263
	Scout 66 (1966)		30 / 0.052	199 / 0.249	880a / 1.371	1193 / 0.591	1133 / -0.358
	Karl 92 (1988)		39 / 0.067	167 / 0.190	621b / 1.350	1091 / 0.759	1011 / -0.559
	Jagger (1994)		35 / 0.61	170 / 0.200	651b / 1.319	1168 / 0.858	1174 / -0.367
	Jagalene (2001)		36 / 0.062	165 / 0.190	679b / 1.292	1128 / 0.792	1116 / -0.098
	Fuller (2006)		32 / 0.055	151 / 0.175	624b / 1.338	1086 / 0.777	1030 / -0.304
	KanMark (2014)		34 / 0.059	169 / 0.200	716b / 1.493	1174 / 0.761	1179 / 0.024
	Larry (2016)		34 / 0.058	138 / 0.153	657b / 1.428	1164 / 0.843	1136 / -0.181
		In-furrow	42A / 0.071A	200A / 0.234A	773A / 1.422A	1233A / 0.806	1134A / -0.669B
		Control	27B / 0.047B	129B / 0.150B	644B / 1.279B	1044B / 0.688	1069B / 0.142A

† Values followed by the same letter within growing season and treatment are not statistically different at $\alpha = 0.05$.

‡ Jagger was not included in the 2016-17 growing season analysis.

Table 1.6 Shoot biomass in different plant components (leaves, stem, chaff, grain) at Zadoks 26, 31, 65, 85 and 92 of wheat varieties released between 1920 and 2016, fertilizer treatment, and their interaction during the growing seasons 2016-17 and 2017-18. Variety and fertilizer means were averaged across locations within growing season.

			GS 26	GS 31		GS 65			GS 85				GS 92			
Year	Variety (Year of release)	Fertilizer	Leaves $(g\ m^2)$	Leaves $(g\ m^2)$	Stem $(g\ m^2)$	Leaves $(g\ m^2)$	Stem $(g\ m^2)$	Chaff $(g\ m^2)$	Leaves $(g\ m^2)$	Stem $(g\ m^2)$	Chaff $(g\ m^2)$	Grain $(g\ m^2)$	Leaves $(g\ m^2)$	Stem $(g\ m^2)$	Chaff $(g\ m^2)$	Grain $(g\ m^2)$
2016-17	Kharkof (1920)[‡]		60.8a[†]	158.3	88.3c	243.1a	749.9a	103.2c	190.1	798.3a	148.0c	185.7c	159.5a	797.2a	154.7c	209.1c
	Scout 66 (1966)		56.7a	156.3	128.9ab	224.0ab	707.2a	131.8b	171.4	757.1a	169.5c	227.3c	144.6ab	808.9a	196.2ab	285.5bc
	Karl 92 (1988)		58.6a	131.8	134.9a	184.2b	493.0d	134.5b	151.3	730.8a	238.5ab	365.6b	103.2d	589.5b	227.5a	331.2b
	Jagalene (2001)		54.0a	150.5	102.6bc	221.1ab	603.5b	154.6a	192.3	804.7a	247.7a	582.6a	132.7abcd	611.0b	210.5ab	464.6a
	Fuller (2006)		43.1b	134.8	113.3abc	190.7b	525.5cd	133.4b	164.9	805.9a	238.7ab	492.6a	109.2cd	581.8b	202.5ab	439.3a
	KanMark (2014)		43.4b	138.3	100.9c	185.1b	458.5d	143.5ab	168.9	600.9b	247.9a	538.8a	125.9bcd	512.8b	221.9ab	474.3a
	Larry (2016)		57.9a	154.7	96.9c	221.4ab	585.6bc	144.9ab	212.8	759.5a	216.1b	514.8a	133.7abc	587.1b	189.8bc	425.6a
		In-furrow	63.5A[†]	163.9A	126.5A	228.2A	626.5A	140.3A	198.8A	807.6A	227.0A	443.9	140.9A	674.4A	204.5	365.0
		Control	43.4B	128.9B	92.3B	191.7B	551.6B	130.0B	158.9B	694.4B	203.4B	396.8	118.8B	607.9B	196.3	386.3
2017-18	Kharkof (1920)		36.0	102.1	55.0bc	150.4	466.7a	201.1a	112.9	471.7a	181.3	308.2d	93.6	441.5a	184.3	292.3c
	Scout 66 (1966)		30.0	118.6	80.5a	187.5	498.9a	196.5ab	103.1	451.2a	188.5	408.6c	91.1	417.2a	201.0	397.8b
	Karl 92 (1988)		38.8	97.6	69.6ab	140.1	335.7b	149.3cd	84.9	327.7b	194.1	436.1bc	72.4	299.0bc	190.1	415.3b
	Jagger (1994)		35.2	103.5	66.7ab	171.7	340.0b	142.3d	98.3	355.1b	188.6	478.6ab	94.9	351.4b	196.9	491.4a
	Jagalene (2001)		36.4	104.8	60.2b	171.0	381.0b	162.3bcd	91.0	332.5b	172.9	488.9ab	84.3	312.3bc	187.4	495.2a
	Fuller (2006)		31.9	89.4	61.5b	158.6	327.5b	144.5cd	98.3	333.3b	189.7	433.6bc	85.9	306.8bc	199.7	406.0b
	KanMark (2014)		34.1	107.0	62.2b	192.8	330.4b	178.3abc	110.9	305.4b	209.0	511.8a	100.9	297.0c	210.5	519.9a
	Larry (2016)		33.8	95.7	42.3c	199.0	349.9b	173.6abcd	99.0	343.0b	186.9	494.4ab	90.5	325.4bc	189.5	496.9a
		In-furrow	41.5A	120.5A	79.3A	193.6A	416.9A	181.8A	112.8A	405.2A	203.3A	471.2A	97.5A	365.3A	201.2A	434.8
		Control	27.4B	84.2B	45.2B	149.2B	340.6B	155.2B	86.8B	324.8B	174.5B	418.8B	80.9B	322.4B	188.7B	443.9

[†] Values followed by the same letter within growing season and treatment are not statistically different at α = 0.05.

[‡] Jagger was not included in the 2016-17 growing season analysis.

Chapter 2 - Changes in Winter Wheat Phenotype in Response to Breeding for Yield and In-Furrow Fertilizer.II. Macronutrients

Introduction

Global wheat yield increased from 1.1 Mg ha^{-1} in 1960 to 3.4 Mg ha^{-1} in 2016 (FAOSTAT, 2018b) partially due to increased crop yield potential and to better agronomic practices (Bell et al., 1995). The partial contribution of breeding or agronomy to wheat yield increments range from 28% in Mexico to 79% in the US central Great Plains, and yield gains from improved agronomics range from 21% in Kansas to 48% in Mexico (Bell et al., 1995; Nalley et al., 2008). From a physiological perspective, these yield gains are often associated with improvements in harvest index, kernels m^2, kernels spike^{-1}, reduced plant height, increased shoot biomass, and improved kernel weight (Brancourt-Humel et al., 2003; Zhou et al., 2007a; Fischer and Edmeades, 2010; Sadras and Lawson, 2011; Sanchez-Garcia et al., 2013; Beche et al., 2014; Wu et al., 2014; Aisawi et al., 2015; Lo Valvo et al., 2017). Although extensive literature is available on the physiological components partially responsible for the observed yield increase, limited research exists on nutrient uptake and partitioning among plant components as affected by changes in varieties over decades.

Most of the available literature evaluating the interaction between genetic progress in wheat and fertilizer rates has focused on N (Brancourt-Humel et al., 2003; De Vita et al., 2007; Tian et al., 2011; Gizzi and Gambin, 2016; Wang et al., 2017), and results mostly suggest that modern varieties were higher yielding under greater N rates (Brancourt-Humel et al., 2003; Tian et al., 2011; Wang et al., 2017). Previous research with tall and semi-dwarf varieties suggests that about 83% of the total N uptake occurred prior to anthesis, from which 68% was remobilized to the grain, with only about 10% of the total N uptake occurring during grain fill

(Austin et al., 1977). The tall varieties showed higher N concentration in the dry matter of the whole plant during the fall, declining towards physiological maturity (Knowles and Watkin, 1931; Miller, 1939). Nitrogen uptake in tall varieties ceased about three weeks before maturity (Knowles and Watkin, 1931). While some literature has evaluated the dynamics of N uptake and partitioning within the wheat plant, limited information is available about N uptake dynamics for modern wheat genotypes, and contrasting results exist in the current literature. In some cases, N uptake is positively correlated with year of variety release (Giunta et al., 2007; Sadras and Lawson, 2013) and negatively correlated in others (Daniel F Calderini et al., 1995; Gustavo A Slafer et al., 1990).

Equally important to N, the dynamics of uptake and partitioning of other essential macronutrients such as P, K, S, have received limited attention in modern wheat genotypes. Karlen and Whitney (1980) reported that P and K concentration in dry matter of whole wheat plant reduced slightly during tillering and a greater reduction occurred in later growth stages. Clarke et al. (1990) reported that 64 to 100% of P at maturity was taken up prior to anthesis and around 81% was remobilized to the grain. Rengel and Damon (2008) suggested that modern wheat varieties were more efficient in K utilization and uptake. Similar to N and P, K was most absorbed by the plants prior to anthesis, however, only 17% of the total K was remobilized to the grain (Waldren and Flowerday, 1979). Regarding S, about 82% of its total uptake occurs prior to anthesis, and leaves remobilize more than stems to the grain (Hocking, 1994). Balanced nutrition improves wheat productivity, and understanding the dynamics of these different macronutrients within the wheat plant and identifying how these are affected by genetics, management, and their interaction, will benefit future advancements in grain yield from both an agronomic and a breeding perspective.

The primary objective of this study was to determine whether historical and modern winter wheat varieties differ in response to in-furrow fertilization in their dynamics of N, P, K, and S uptake and partitioning to plant components during the growing season. A second objective was to evaluate macronutrient balances and ratios on the entire shoot biomass, as well as at different plant components.

Materials and Methods

Experimental design, treatment structure, and crop management practices are concisely described in this manuscript. For full details, please refer to chapter 1, which explored the effects of variety and fertilizer on wheat yield and yield components.

Sites, treatment structure, and experimental design

Fields experiments were conducted in four Kansas environments. During 2016-17, experiments were established at the Kansas State University (KSU) Research Farm in Ashland Bottoms, KS and at the KSU North Central Experiment Field in Belleville, KS. In 2017-18, experiments were conducted at the South Central Kansas Experiment Field near Hutchinson, KS and in Belleville on the same location as in the previous year. A two-way factorial treatment structure was established in split-plot design with four replications. Plots were eight varieties released in different historical eras arranged as randomized complete block design, and subplots were two different fertilization treatments completely randomized within whole plots. The eight varieties evaluated in the main plots were released between 1920 and 2016: ‘Kharkof’, released in 1920; ‘Scout 66’ (1966); ‘Karl 92’ (1992); ‘Jagger’ (1994); ‘Jagalene’ (2001); ‘Fuller’ (2006); ‘KanMark’ (2014); and ‘Larry’ (2016). The varieties Kharkof and Scout 66, are hereafter referred to as tall varieties. The varieties Karl 92, Jagger, Jagalene, Fuller, KanMark, and Larry, are hereafter referred to as semi-dwarf varieties. The subplots consisted of two fertilization treatments, namely i) control and ii) 112 kg ha^{-1} in-furrow fertilizer (12-40-00-10-1). In-furrow fertilizer was applied at each individual subplot at sowing through the drill with the seed. Selected soil chemical and physical characteristics can be found in chapter 1.

Nutrient uptake and partitioning

A complete description of aboveground biomass dynamics was presented in chapter 1. Briefly, aboveground biomass was collected five times in the growing season from Zadoks GS 26 (tillering) to GS 92 (physiological maturity) (Zadoks et al., 1974). For each specific growth stage the plants were separated into leaves, stem, chaff, and grain. After partitioning, all plant material was placed in a forced-air oven at 65^{0}C for at least 24 hours before grinding. Grain was ground by using the WonderMill Electric Grain Mill, and the other components were ground by laboratory mill Thomas-Wiley Mill (model 4) equipped with a 2.0 mm screen size. The total ground material was homogenized and around 20 g were sent to Kansas State Soil Testing Laboratory for tissue analysis. Nitrogen content was analyzed through the procedure of dry combustion (TruSpec CN, LECO Corporation, St. Joseph, MI, 2005) and the other nutrients were analyzed through the procedure of nitric perchloric digestion (Gieseking et al., 1935). Total N, P, K and S uptake (g m^{-2}) in each plant component were calculated by multiplying the nutrient concentration by the biomass of each corresponding plant component. Nutrient content (g m^{-2}) in this manuscript is presented on a dry basis.

Calculations

Whole plant nutrient concentration for N, P, K, and S were calculated by growth stage as the sum of each plant component uptake divided by the whole plant biomass for the same period, and expressed in (g kg^{-1}).

Equation 2.1

*Whole plant nutrient concentration (g kg^{-1}) = (whole plant uptake (g m^{-2})/ whole plant biomass (g m^{-2})) * 10*

Nutrient harvest indices (NHI, PHI, KHI, and SHI) were calculated as the quotient from grain uptake and whole plant uptake at maturity, similar to previous literature (Wang et al., 2017a). Although, at soft dough typically occurs the maximum nutrient uptake (i.e. at maturity would be overestimating), comparisons between both stage showed high slope (c.a. 0.88) and high coefficient of determination (c.a. 0.72) (Fig. A - 1)

Whole plant uptake rate was calculated for the grain filling period as the difference between the whole plant uptake measured at soft dough and that measured at anthesis, divided by the difference from the accumulated GDD during the period, and expressed in (g m^{-2} GDD ^{o}C).

Equation 2.2

Whole plant uptake rate (g m^{-2} GDD^{o}C) = (whole plant uptake (g m^{-2})$_{\text{soft dough}}$ – whole plant uptake (g m^{-2})$_{\text{anthesis}}$)/ thermal time for the period (GDD^{o}C)

Head allocation rate was calculated as the difference between grain plus chaff uptake measured in GS 85 and chaff uptake measured in GS 65, divided by the difference in accumulated GDD between both stages, and expressed in (g m^{-2} GDD ^{o}C).

Equation 2.3

Head allocation rate (g m^{-2} GDD^{o}C) = ((grain uptake (g m^{-2})$_{\text{soft dough}}$ + chaff uptake (g m^{-2})$_{\text{soft dough}}$) – chaff uptake (g m^{-2})$_{\text{anthesis}}$)/ thermal time for the period (GDD^{o}C)

Data analysis

As described in chapter 1, to evaluate whether site-years could be combined, we analyzed the residuals from a combined ANOVA that allowed us to combine sites within years. Thus, all analysis presented in this manuscript are across locations within year of the study. Analyses of variance (ANOVA) were performed using PROC GLIMMIX in SAS version 9.4 (SAS Institute, Cary, NC) to determine significant difference in nutrient uptake among plant components as affected by wheat genotype, fertility, and their interaction in each growth stage. This analysis considered replication, sites, and replication nested within sites as random effects. We used the LINES statement for pairwise comparisons when the interaction variety × fertilization was not significant.

Historical trends in N, P, K, and S total were performed by testing different regression models against year of release, as detailed in chapter 1 for grain yield and biomass. Investigation of allometric relationships between whole plant nutrient concentration and whole plant biomass was performed using an exponential decay regression model. Nutrient partitioning to head was investigated as the relationship between nutrient allocation rate to the head and whole plant uptake rate (Ciampitti et al., 2013). We evaluated the residuals of these relationships to determine the effects of fertilizer practice and year of variety release (Sadras and Moran, 2012). All regression analyses and graphics were built using SigmaPlot version 13.0 (Systat Software, San Jose, CA). Lastly, we performed a comprehensive analysis to identify the relationships among the HI of different nutrients, and the whole plant uptake of the different nutrients using PROC CORR in SAS version 9.4 (SAS Institute, Cary, NC).

Results

Nitrogen uptake and partitioning

With very few exceptions, the analysis of variance for N uptake in the different plant components showed significant variety and fertility effects, but no significant interaction (Table 2 - 1). Early in the season (i.e. tillering and jointing), N uptake dynamics showed no identifiable pattern among varieties and followed similar results to leaves and stem biomass (Chapter 1). From anthesis onwards, N stored in the stem was typically greater in tall varieties, accounting for as much as 54% of the total N uptake. Meanwhile, N content in the stem of semi-dwarf varieties only accounted for 36 to 45%. Instead, N content in the grain was greater in semi-dwarf varieties (Table 2 - 1). Interestingly, approximately 100% of the total N uptake during the growing season occurred by anthesis in tall varieties, and 84% in semi-dwarf varieties; suggesting that post-anthesis nutrient uptake increased over time. At GS 85, grain N content ranged from 50 to 70% for semi-dwarf varieties and only from 30 to 58% in tall varieties; consequently, total N uptake by semi-dwarf varieties was significantly greater (c.a. 13 *versus* 6 g m^{-2} in 2016-17, and 12.5 *versus* 10 g m^{-2} in 2017-18). Grain N content increased slightly from soft dough to maturity and accounted for as much as 71% of total N uptake in semi-dwarf varieties, and less than 60% in tall varieties (Table 2 - 1). Maximum N content was observed at anthesis for leaf and stem (Table 2 - 1). Irrespective of growth stage and plant component, in-furrow fertilizer showed greater N uptake than control treatment (Table 2 - 1).

Phosphorus uptake and partitioning

The main effects variety and fertility were usually significant on P uptake on the different plant fractions, but there were no consistent significant interactions. During the vegetative measurements, P uptake was similar from tall to semi-dwarf varieties in the leaves and stem (Table 2 - 2). At GS 65, leaf P content was greater in semi-dwarf varieties in the 2017-18 growing season, but no clear pattern was observed subsequently regardless of growing season (Table 2 - 2). Phosphorus uptake at anthesis on the stem ranged from 50 to 57% of the total in tall varieties and was around 47% in semi-dwarf varieties, showing a substantial decrease by soft dough. About 80% of the total P uptake during the growing season occurred by anthesis in semi-dwarf varieties, and 99% in tall varieties. Phosphorus content on the grain at GS 85 was greater in semi-dwarf varieties relative to tall varieties in both growing seasons (c.a. 1.9 *versus* 0.9 g m^{-2}

in 2016-17, and 1.5 *versus* 1.2 g m^{-2} in 2017-18, corresponding to 64 to 87% of the total plant P for semi-dwarf varieties and 41 to 79% for tall varieties) (Table 2 - 2). At maturity, P uptake was greater in semi-dwarf varieties relative to tall varieties in both growing seasons, with an estimated linear increase as high as 0.009 g m^{-2} yr^{-1} (data not shown). Irrespective of year of release, P allocation to the leaves and stem ceased at GS65, while chaff and grain showed different patterns depending on growing season (Table 2 - 2). In-furrow fertilizer treatment increased P uptake relative to no fertilizer.

Potassium uptake and partitioning

Potassium uptake showed different patterns than N and P early in the season, as tall varieties stored more K than semi-dwarf varieties in the leaves and stem (Table 2 - 3). At anthesis, tall varieties allocated from 9.6 to 14.8 g K m^{-2} in the stem while semi-dwarf varieties allocated from 7 to 11.2 g m^{-2}. There were no discernible patterns in K allocation afterwards. Semi-dwarf varieties had greater K accumulation at the chaff relative to tall varieties (Table 2 - 3), although K allocation to the chaff only ranged from 5-14% of the total. Total K uptake during the growing season occurred by anthesis for both tall and semi-dwarf varieties. At soft dough and at maturity, semi-dwarf varieties showed greater amount of K stored in the grains than tall varieties (Table 2 - 3). For instance, tall varieties stored from 0.87 to 1.21 g K m^{-2} in the grain at GS 85 (c.a., 5 and 9% of whole plant K uptake). Meanwhile, semi-dwarf varieties accumulated c.a. 1.96 and 1.58 g K m^{-2} in the grain (c.a., 12 and 13% of total uptake) (Table 2 - 3). Regardless of year of release, the maximum amount of K in the leaves and chaff occurred at anthesis and decreased until maturity. In-furrow fertilizer increased K uptake relative to the control treatment irrespective of growth stage and plant component (Table 2 - 3).

Sulfur uptake and partitioning

Sulphur uptake showed similar uptake patterns to N and P early in the season, with slightly greater leaf uptake by tall varieties in GS 26, and lower stem uptake by tall varieties at GS31 (Table 2 - 4). From anthesis onwards, there were significant differences among varieties and different patterns across growing seasons. For instance, semi-dwarf varieties showed greater allocation of S to the leaves at anthesis relative to tall varieties during the 2017-18 season (43 *versus* 32%) (Table 2 - 4). The S uptake by anthesis corresponded to about 100% for tall and 85% of total S uptake for semi-dwarf varieties. At GS 85 and 92, tall varieties showed greater S uptake at the chaff (c.a. 14 *versus* 12%) and stem (45-76% versus 38-68% of the total S uptake) (Table 2 - 4). Grain S uptake was greater in semi-dwarf varieties relative to tall varieties during both growing seasons. At soft dough, grain S uptake ranged from 0.28 to 0.57 g m^{-2} for tall varieties and 0.59 to 0.73 g m^{-2} for semi-dwarf varieties, with similar levels measured at maturity (Table 2 - 4). Tall varieties allocated no more than 45% of the total S to the grain, while semi-dwarf varieties allocated as much as 55% (Table 2 - 4). Besides variety effect, in-furrow fertilizer increased S uptake for all growth stages and plant components (Table 2 - 4).

Whole plant nutrient concentration

Whole plant nutrient concentration was greater for N (c.a., 12 to 52 g kg^{-1}), followed by K (c.a., 7 to 40 g kg^{-1}), P (c.a., 1 to 6 g kg^{-1}), and S (c.a., 0.5 to 4.5 g kg^{-1}) (Fig. 2 - 1). Concentrations of all studied macronutrients decreased with increases in whole plant aboveground biomass both studied seasons, although growing season 2017-18 showed overall greater nutrient concentration than growing season 2016-17 (Fig. 2 - 1). The residuals of these relationships suggested that N, P and S concentration in the whole plant increased over decades, while K concentration decreased. Irrespective of nutrient, in-furrow fertilizer showed significantly greater nutrient concentration than the control treatment.

Nutrient harvest index

There were significant relationships between the HI of N, P, K and S and year of variety release (Fig. 2 - 2). The best-fit model differed depending the growing season within nutrient (non-linear or bi-linear), but despite small differences in the best model, the trends were consistent: The HI of all nutrients typically increased after 1960s, showing lower gains after 2000s. The increase in nutrient HI from tall to modern varieties was as much as 1.6, 1.4, 1.7, and 1.5 fold for N, P, K, and S. The 2017-18 growing season had greater HI relative to 2016-17 regardless of nutrient, mostly due to differences in total biomass, as reported in chapter 1. The residuals of these regressions suggested that in-furrow fertilizer decreased the HI of N, P, K and S relative to no fertilizer, likely due to greater biomass allocation to the vegetative tissues.

Nutrient partitioning from plant to head during grain filling

Overall, nutrient partitioning from plant to head during the grain filling period followed a positive non-linear relationship for N, P, K, and S (Fig. 2 - 3). Although the shapes of the non-linear models were not precisely identical across growing seasons, there was a clear pattern of low nutrient allocation rate to the head at low plant uptake rates, with steep increases in allocation to the head at higher plant uptake rates. Nitrogen and P showed different thresholds of whole plant uptake rate necessary to start the allocation to the head depending on the growing season. There was typically no minimum requirement during 2016-17, while a positive whole plant uptake rate was needed for the onset of nutrient allocation to the head during 2017-18. For instance, the rate of N allocation to the head was constant (c.a. 0.15 g m^{-2} GDD$^{o}C^{-1}$) until whole plant uptake rate reached ~0.005 g m^{-2} GDD$^{o}C^{-1}$, showing a steep increase afterwards (Fig. 2 -

3A). Similar ratio was observed for P and S, while K showed less steep increases in allocation to the head. In-furrow fertilizer increased allocation rate to the head relative to the control treatment for P in both growing seasons, and N, K, and S during the 2017-18 growing season, with no variety x fertility interaction (Fig. 2 - 3). The allocation rate from whole plant to the head typically increased for N, K, and S over decades, but there was no apparent effect on P.

Grain nutrient uptake

There was a significant positive linear relationship for both tall and semi-dwarf varieties for N, P, K, and S grain uptake and whole plant nutrient uptake during soft dough and maturity both growing seasons (Fig. 2 - 4). This analysis showed that: i) semi-dwarf varieties were able to partition more N, P, K, and S into the grain than tall varieties at identical whole plant uptake; ii) higher slopes in all nutrients for semi-dwarf varieties relative to tall varieties points to an increase in partitioning of N, P, K, and S to the grain over decades; iii) semi-dwarf varieties partitioned more than 0.5 g of N m^{-2} to the grain, up to 0.82 g of P m^{-2}, around 0.1 g of K m^{-2}, and from 0.36 to 0.5 g of S m^{-2} for every increase in 1 g m^{-2} of the respective nutrient in the whole plant; iv) in-furrow fertilizer decreased the grain N uptake and grain S uptake in semi-dwarf varieties during 2016-17.

Associations among nutrient harvest indices and whole plant uptake of nutrients

Interesting outcomes for the analysis of the association among nutrient harvest indices were: i) N harvest index was strongly and positively associated with P, K, and S harvest indices during both growing seasons, and a linear relationship was observed between the nutrients (Fig. 2 - 5 A, C, E); ii) P and S harvest indices were more strongly correlated with N harvest index ($r^2 = 0.9^{***}$) than K harvest index ($r^2 = 0.63$ to 0.73); iii) the increase in P harvest index for each unit increase in N harvest index was the greatest (from 0.84 to 1.09), followed by S and K; iv) as grain yield increased (larger bubbles on Fig. 2 - 5), nutrient harvest indices increased for all macronutrients; v) besides the association with N, the harvest indices of other nutrients were correlated (Pearson's *r* = 0.75 between P and K; *r* = 0.85 between P and S, and *r* = 0.81 between K and S, data now shown); vi) the residuals of the relationship between N harvest index and P, K, and S harvest indices as affected by year of variety release showed that for the same N harvest index level, the HI of P and S decreased and of K increased over time (Fig. 2 - 5 B, D, F); vii) the residuals of the relationship between N harvest index and P, K, and S harvest index as affected by fertilizer treatment were not significant.

Major findings for the association between whole plant N uptake and whole plant P, K, and S uptake were: i) whole plant N uptake was strongly and linear-positive associated with whole plant P, K, and S uptake during both growing seasons (i.e. r^2 ranging from 0.79 to 0.95) (Fig. 2 - 6 A, C, E); ii) K showed the greatest increase per unit increase in N uptake (c.a. 0.72 to 0.78 g of K m^{-2}), followed by P (c.a., 0.09 to 0.1 g of P m^{-2}) and S (c.a. 0.05 to 0.08 g of S m^{-2}); iii) the relationships between total nutrient uptake among P, K, and S were also significant (*r* = 0.82 between K and P, *r* = 0.81 between K and S, and *r* = 0.83 between P and S, data now shown); iv) the ratios for whole plant N:P, N:K, and N:S were 9.2, 1.1, and 15.4; v) for the same N uptake levels, year of variety release significantly increased whole plant S uptake and decreased whole plant K uptake (Fig. 2 - 6 B, D, F); vi) in-furrow fertilizer increased the whole plant uptake of P and S at the same levels of N uptake.

Discussion

Nitrogen uptake

The primary objective of wheat breeders is to increase grain yield while meeting minimum standards for quality parameters for a given wheat class. We hypothesized that this selection for yield *per se* may have caused, as a hidden consequence, a change in the dynamics of nutrient uptake and partitioning during the season. However, we found no significant variety × fertility interactions. Our results showed that N uptake and partitioning early in the season was similar for tall and semi-dwarf varieties, but during reproductive stages the shifts in N uptake and partitioning were more evident, with an increase over decades especially in the allocation of N to the grain. In agreement with our study, Giunta et al. (2007) showed that modern wheat varieties in Italy increased N uptake relative to historical wheat varieties, and allocated more N in the grains and less in the stem. Likewise, there were also positive correlations between N uptake at maturity and year of variety release in Australia (Sadras and Lawson, 2013) and China (Tian et al., 2016).

Our results suggest that the changes in N allocation might result from the differences among varieties regarding biomass allocation to plant components (reported in chapter 1). This is consistent with Austin et al. (1977) in which a strong and positive correlation between N and biomass accumulation was found in a large set of 47 historic winter wheat varieties. Other studies reported no changes over decades in N uptake (Wang et al., 2017a), concomitant to no differences in biomass (Wang et al., 2017b). Besides wheat, other crops also presented a correlation between N uptake and biomass, such as maize (Ciampitti and Vyn, 2011) and soybean (Gaspar et al., 2017). The greater amount of N in the grain of semi-dwarf varieties can be explained by larger grains, longer grain filling period (Chapter 1), and greater post-anthesis N uptake.

In-furrow fertilizer increased N uptake, but decreased nutrient harvest index, likely because in-furrow fertilizer increased vegetative biomass production more than reproductive biomass production (Chapter 1). Previous studies reported N uptake as affected by fertilizer treatment solely at anthesis and/or at maturity, also suggesting that N uptake was greater under high yielding environments, which are supported by in-furrow fertilizer (Barraclough et al., 2010; Gaju et al., 2011; Giunta et al., 2007; Sadras and Lawson, 2013).

Phosphorus uptake

Our results suggest that winter wheat varieties improved their ability to uptake P rather than their capacity to remobilize P from vegetative tissues, as tall varieties usually showed greater P uptake in the stem. Different patterns of P partitioning were reported by Clarke et al. (1990) (i.e., no changes in P partitioning across varieties). The literature also suggests that these results would be dependent on region and perhaps breeding program. For instance, Calderini et al. (1995) and Wang et al. (2017a) found no relationship between whole plant P accumulation at maturity and year of variety release in Argentina and China. Meanwhile, Egle et al. (1999) described a positive relationship between P uptake and year of variety release in Mexico.

Besides variety effect, we observed significant year and fertility effects. Less P uptake during 2017-18 as compared to 2016-17 irrespective of growth stage and plant component was likely a consequence of the reduced water available (Clarke et al., 1990), as described in chapter 1. Meanwhile, in-furrow fertilizer increased P uptake relative to no fertilizer treatment, with greater increases in vegetative tissues compared to in the grain. Similar findings were reported for the maturity growth stage by Egle et al. (1999), who suggested that the main factor affecting P content was P uptake rate under fertilization.

Potassium and sulfur uptake

There are limited literature allowing for comparison for K and S uptake and partitioning during the season into plant components. Potassium accumulation differed from the other nutrients as it was mostly partitioned to the stems. Although K was found in lower amounts in the grain, semi-dwarf varieties accumulated a greater fraction of grain K than tall varieties (13% vs. 8% of total K) likely due to a greater K uptake. Interestingly, there was no K uptake from anthesis to maturity, suggesting grain K was mostly remobilized from vegetative tissues to the grain rather. Available literature agrees that less than 20% of total K at maturity is allocated in the grain (Hocking, 1994; Waldren and Flowerday, 1979), although we are not aware of other studies comparing varieties released in different eras. In-furrow fertilizer increased total K accumulation despite having zero K in its composition, suggesting that the increase in biomass led by the fertilizer was the main driver for K accumulation. In agreement, Baker and Tucker (1973) showed that P application increased K uptake and the lack of P decreased K uptake.

Sulfur uptake was greater in the stem and chaff in tall varieties, and in the grain and leaves of semi-dwarf varieties, following a more similar pattern to N and P. Sulfur accumulation in the grain accounted for c.a. 38% in tall varieties and c.a. 51% in semi-dwarf varieties, in a similar range to the 42% reported by Hocking (1994). We observed that tall varieties had greater S uptake in the stem then semi-dwarf varieties at maturity, suggesting that modern wheat varieties remobilized more S from stem into the grain relative to historical ones. The greater amount of S in the grain in semi-dwarf varieties is important and interesting as S can contribute to modifications in grain protein composition and consequently enhance the baking quality (Steinfurth et al., 2012). The lack of studies in comparison of S uptake and partitioning as affected by year of variety release warrants further investigation. Besides variety effect, S uptake was greater under in-furrow fertilizer treatment, perhaps as a result of the S present in the fertilizer composition and the greater biomass induced by the fertilizer. Previous studies showed that S application increased S uptake relative to no S treatment (Cui and Wang, 2005; Rasmussen et al., 2010); and also that the application of other nutrients such as N (Rasmussen et al., 2010) and Zn (Cui and Wang, 2005) in combination with S can also increase S uptake.

Whole plant nutrient concentration

The decrease in N, P, K, and S concentration as affected by biomass has been previously shown for wheat and other crops (Ciampitti et al., 2013; Copeland and Crookston, 2010; Karlen and Whitney, 1980; Riedell, 2010). However, we showed that whole plant nutrient concentration increased over decades for N, P, and S, and decreased for K. The increase in N, P, and S were likely resulting from i) greater grain biomass in modern varieties as a large fraction of these nutrients at maturity were allocated in the grain, and ii) greater increases in nutrient uptake rate as opposed to biomass accumulation rate over decades. On chapter 1 we showed that biomass accumulation did not change among varieties, while partitioning to the grain increased. Other research showed that grain N concentration (Tian et al., 2016; Wang et al., 2017a) and grain P concentration (Wang et al., 2017a) at maturity decreased in modern wheat varieties, similar to our findings. The decrease in whole plant K concentration might actually result from greater percentage of stem in tall varieties, as the majority of the K was allocated in the stem. In-furrow fertilizer increased the concentration of all nutrients, as well as biomass of all components (Chapter 1). The increase in nutrient concentration despite increases in biomass suggests that increases in plant nutrient uptake were greater than increases in biomass.

Nutrient harvest index

The harvest index for N, P, K and S increased non-linearly over decades, with substantial increases after 1960s. These changes coincided with the introduction of dwarfing genes, suggesting that selection for reduced plant height and increased grain yield improved nutrient partitioning to the grain of semi-dwarf varieties. Calderini et al. (1995) and Gaju et al. (2011)

also reported a positive relationship between N harvest index and year of variety release in Argentina, the United Kingdom, and France. Wang et al. (2017a), however, suggested that N harvest index did not increase over time in China despite significant increases in P harvest index. The divergence in results might be due to the different range of year of varieties studied, as the authors included varieties released from 1970 to 2005. In our study, the HI of N averaged 0.58, of P averaged 0.72, of K averaged 0.12, and of S averaged 0.48. Hocking (1994) reported harvest indices of 0.74, 0.76, 0.19, and 0.44 respectively. Similar to our results, Calderini et al. (1995) documented N harvest index ranging from 0.5 to 0.7 and P harvest index from 0.4 to 0.65. Recently, Chuan et al. (2013) reported values slightly greater (HI of 0.74 for N, 0.78 for P, and 0.21 for K), probably because the authors evaluated solely modern wheat varieties. In-furrow fertilizer decreased the HI of N, P, K, and S, likely due to the greater nutrient accumulation in the vegetative tissues as opposed to the grain.

Head nutrient allocation rate and nutrient uptake

Positive non-linear models adequately described the relationship between nutrient allocation rate to the head and whole plant nutrient uptake rate for all nutrients. Ciampitti and Vyn (2013) and Ciampitti et al. (2013) also reported positive relationships for macro and micro-nutrients allocation rate to the head and plant nutrient uptake rate, although the shape of the relationship seems to differ between maize and wheat. For wheat, the allocation rate to the head was either low or steady at low whole plant uptake rates, required a minimum whole plant uptake rate to start, and increased substantially at higher or positive plant uptake rates. For maize, nutrient allocation rate to the ear had no minimum requirement, tended to increase at a faster rate at low whole plant uptake levels, and slowly decreased at higher whole plant nutrient uptake levels (Ciampitti et al., 2013). These differences might result from the discrepancy in sink strength between wheat and maize, as wheat is typically sink-limited and maize, source-limited (Borrás et al., 2004). The requirement of a minimum whole plant uptake rate to increase head nutrient allocation rate suggests that sink was the main regulator of the relationship for wheat: at low whole plant uptake rate, the sink strength was weak; and as the whole plant uptake rate increased, the sink strength intensified.

At the same level of whole plant uptake rate, N, K, and S allocation rate to the head increased over time while P allocation to the head was independent of year of release. Thus, increases in grain-N, K, and S are physiologically explained by i) a longer grain filling (Chapter 1) and ii) a greater relative rate of allocation to the head. Meanwhile, increases in grain-P over time at maturity resulted solely from a longer grain filling period of semi-dwarf varieties. In-furrow fertilizer increased N, P, K, and S allocation rate to the head despite decreasing nutrient HI. This likely occurred because the increment of these nutrients into the head was lower than the increase into the leaf and stem.

The grain N, P, K, and S uptake and whole plant nutrient uptake showed a positive significant linear relationship for all nutrients, variety group (tall and semi-dwarf), and growing seasons. This suggests that: i) breeding programs selecting for grain yield indirectly changed the dynamics of N, P, K, and S uptake and partitioning at maturity over time; ii) there is scope for improvement in K grain uptake as its slope is well below that of other nutrients; and iii) in-furrow fertilizer increased nutrient allocation to vegetative tissues more than to grains.

Association among harvest indices and among uptake of different nutrients

We observed that N harvest index and P, K, and S harvest indices were all positively related during both growing seasons, and for the same level of N harvest index (i.e. residuals), P and S harvest index decreased, while K increased over decades. Likewise, greater grain yield levels were related with higher nutrient harvest index, similar to that suggested for maize (Ciampitti and Vyn, 2013). Furthermore, our results showed significant positive linear relationship between whole plant N uptake and whole plant P, K, and S uptake for both growing seasons. The high correlation among nutrients harvest index and whole plant nutrient uptake shows the challenge for breeding programs to focus exclusively on the increase of one nutrient. For instance, programs aiming to increase S uptake and S harvest index focused on wheat baking quality might as consequence increase P uptake and P harvest index to levels on the grain that could have a negative effect on human and animal nutrition (Raboy, 2009; Wang et al., 2017a).

The correlation among the aforementioned nutrients allowed us to calculate N:P, N:K, and N:S ratios and their changes over time. The ratio between N and other nutrients could be used as a tool to identify nutrient deficiency in natural conditions (Salvagiotti et al., 2012). Previous studies reported N:P ratio between 4 and 6 for maximum grain yield in cereals (Sadras, 2006), and a value around 5.2 for 60 to 70% yield potential in wheat (Chuan et al., 2013). For rice, optimum N:P ratio was reported as 5.6 (Wit et al., 1999). In our study, the N:P ratio was greater and averaged 9.2, perhaps suggesting an excessive N consumption when both N and P are available in non-limiting conditions. Interestingly, the ratio decreased at higher N and P uptake levels, suggesting an asynchrony between uptake of N and P depending on uptake levels. For the N:K relationship, a ratio of 1.19 was suggested for 60 to 70% of the yield potential in wheat (Chuan et al., 2013), and a ratio of ~1 for rice (Wit et al., 1999). Our results showed that N:K ratio was around 1.1, suggesting room for more N uptake for every unit K uptake to theoretically increase grain yield. Optimum N:S ratio for maximum grain yield in wheat was suggested as 15-17 (Byers and Bolton, 1979; Randall et al., 1981), with greater values suggesting

S deficiency. The N:S ratio of c.a. 15 in our study suggests that the optimum N:S ratio was achieved.

Figures

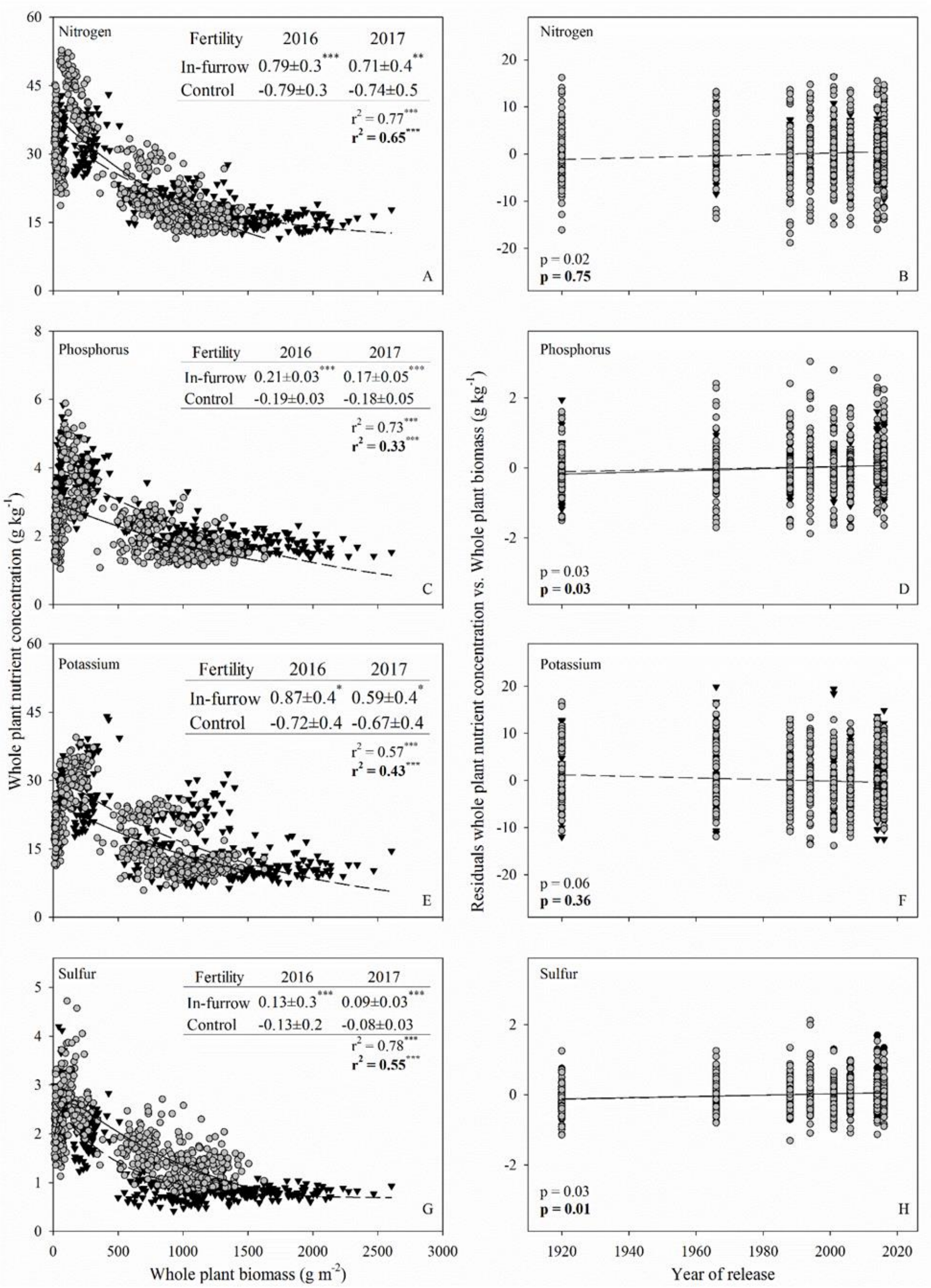


Figure 2.1 Relationship between whole plant nutrient concentration and whole plant aboveground biomass from tillering to physiological maturity (A, C, E, G). Residuals of these relationships were plotted against year of variety release (B, D, F, H), and comparison of the regression residuals for in-furrow fertilizer treatment and no fertilizer (mean and 1 standard error) are shown as inset table. Black symbols, un-bold text and dashed line correspond to the 2016-17 growing season, and grey symbols, bold text and solid line correspond to the 2017-18 growing season. * Significant ($P<0.05$); ** significant ($P<0.01$); * significant ($P<0.001$); ^{ns} non-significant ($P>0.05$).**

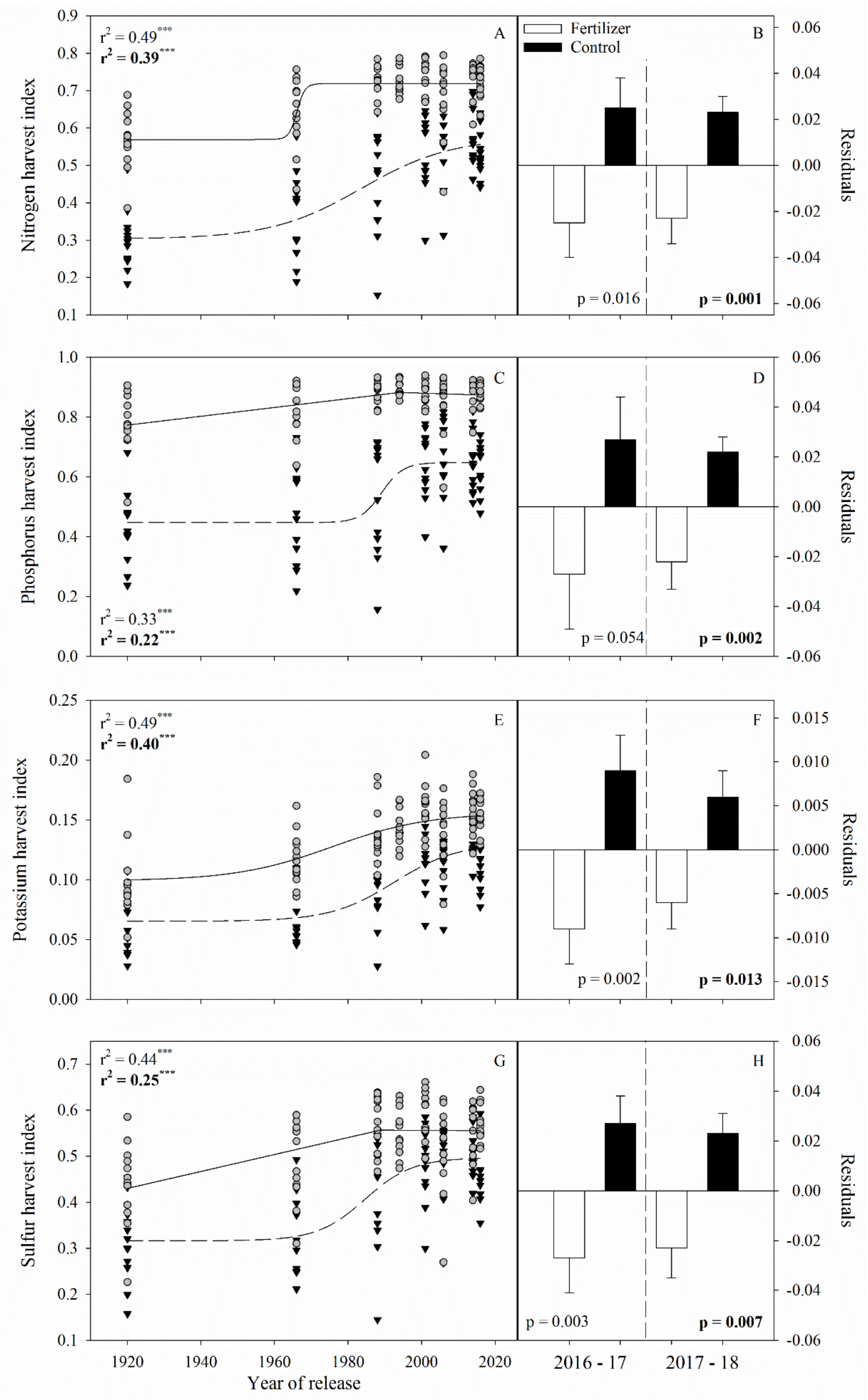


Figure 2.2 Relationship between nutrient harvest index and year of variety release (A, C, E, G). Residuals of these relationships were plotted against fertility treatment for each growing season (B, D, F, H). Black symbols, un-bold text and dashed line correspond to the 2016-17 growing season, and grey symbols, bold text and solid line correspond to the 2017-18 growing season. * Significant (P<0.05); ** significant (P<0.01); * significant (P<0.001); ^{ns} non-significant (P>0.05).**

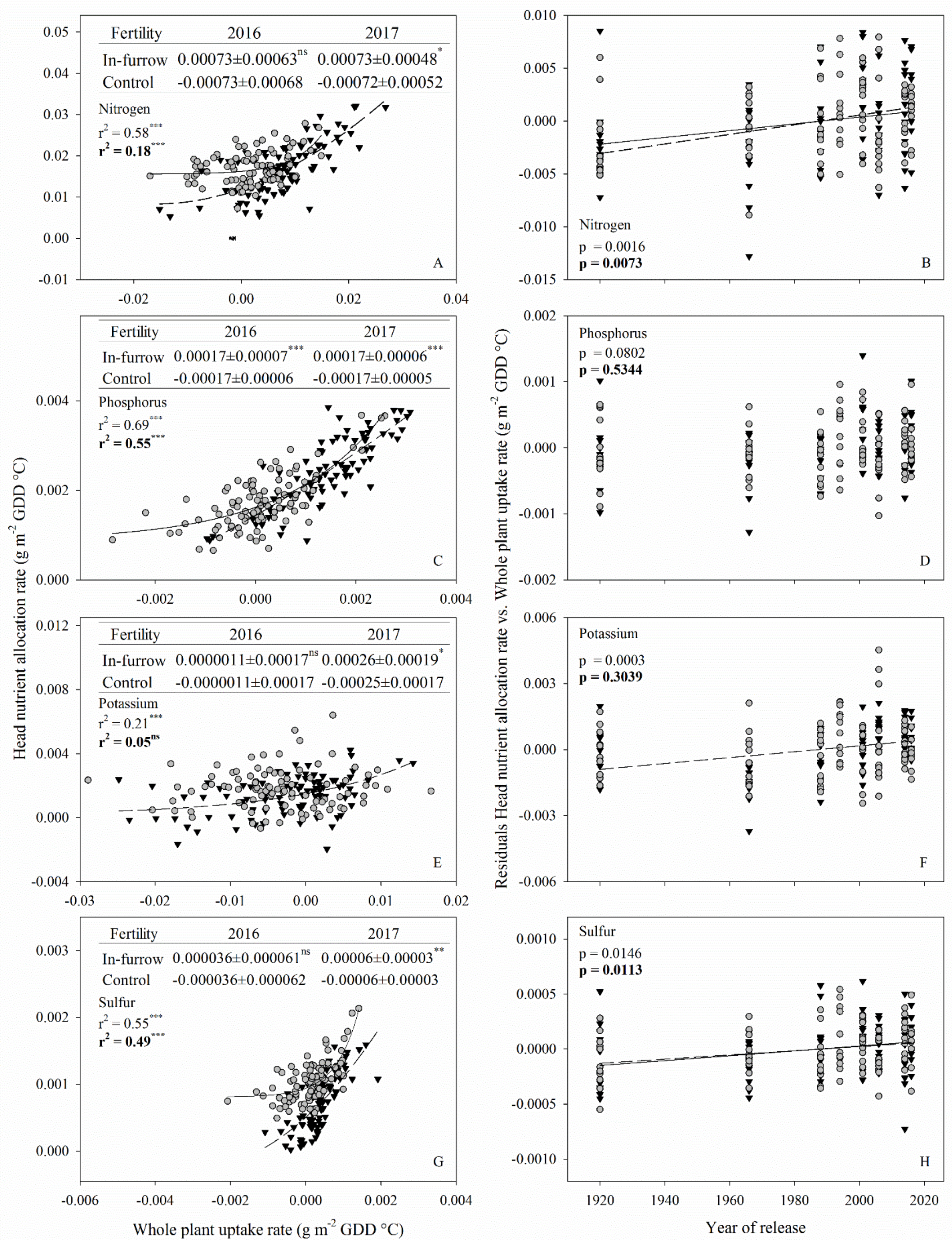


Figure 2.3 Nutrient allocation rate from the whole plant to the head during the grain filling period (Anthesis – Soft dough) (A, C, E, G). Residuals of these relationships were plotted against year of variety release (B, D, F, H), and comparison of the regression residuals for in-furrow fertilizer treatment and no fertilizer (mean and 1 standard error) are shown as inset table. Black symbols, un-bold text and dashed line correspond to the 2016-17 growing season, and grey symbols, bold text and solid line correspond to the 2017-18 growing season. * Significant ($P<0.05$); ** significant ($P<0.01$); * significant ($P<0.001$); ^{ns} non-significant ($P>0.05$).**

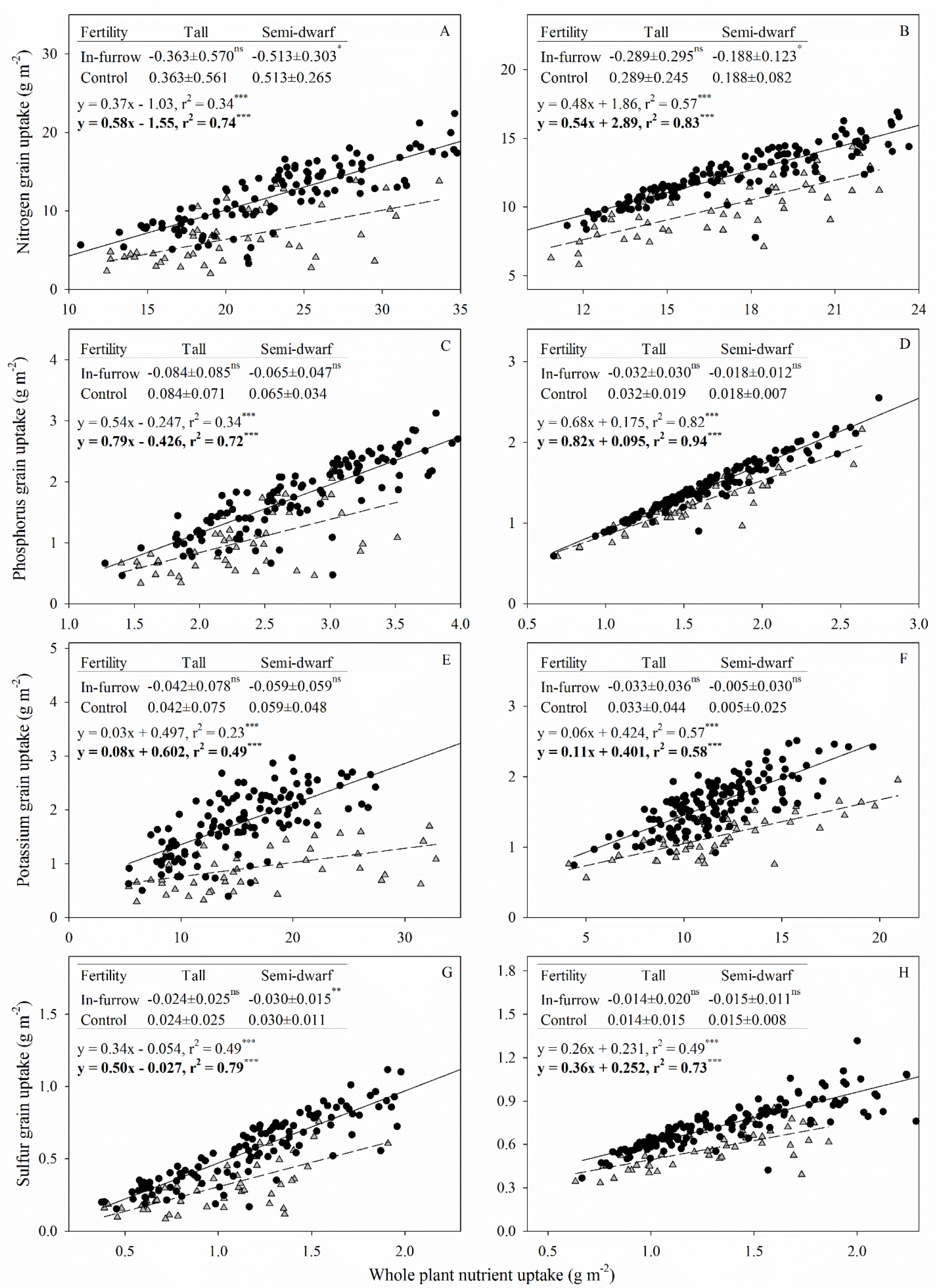


Figure 2.4 Relationship between grain nutrient uptake and whole plant nutrient uptake from soft dough to physiological maturity, plotted by variety group (tall and semi-dwarf varieties), during the 2016-17 growing season (A, C, E, G), and 2017-18 growing season (B, D, F, H). Comparison of the regression residuals for in-furrow fertilizer treatment and no fertilizer (mean and 1 standard error) are shown as inset table. Grey symbols, un-bold text and dashed line correspond to tall varieties, and black symbols, bold text and solid line correspond to semi-dwarf varieties. * Significant ($P<0.05$); ** significant ($P<0.01$); * significant ($P<0.001$); ^{ns} non-significant ($P>0.05$).**

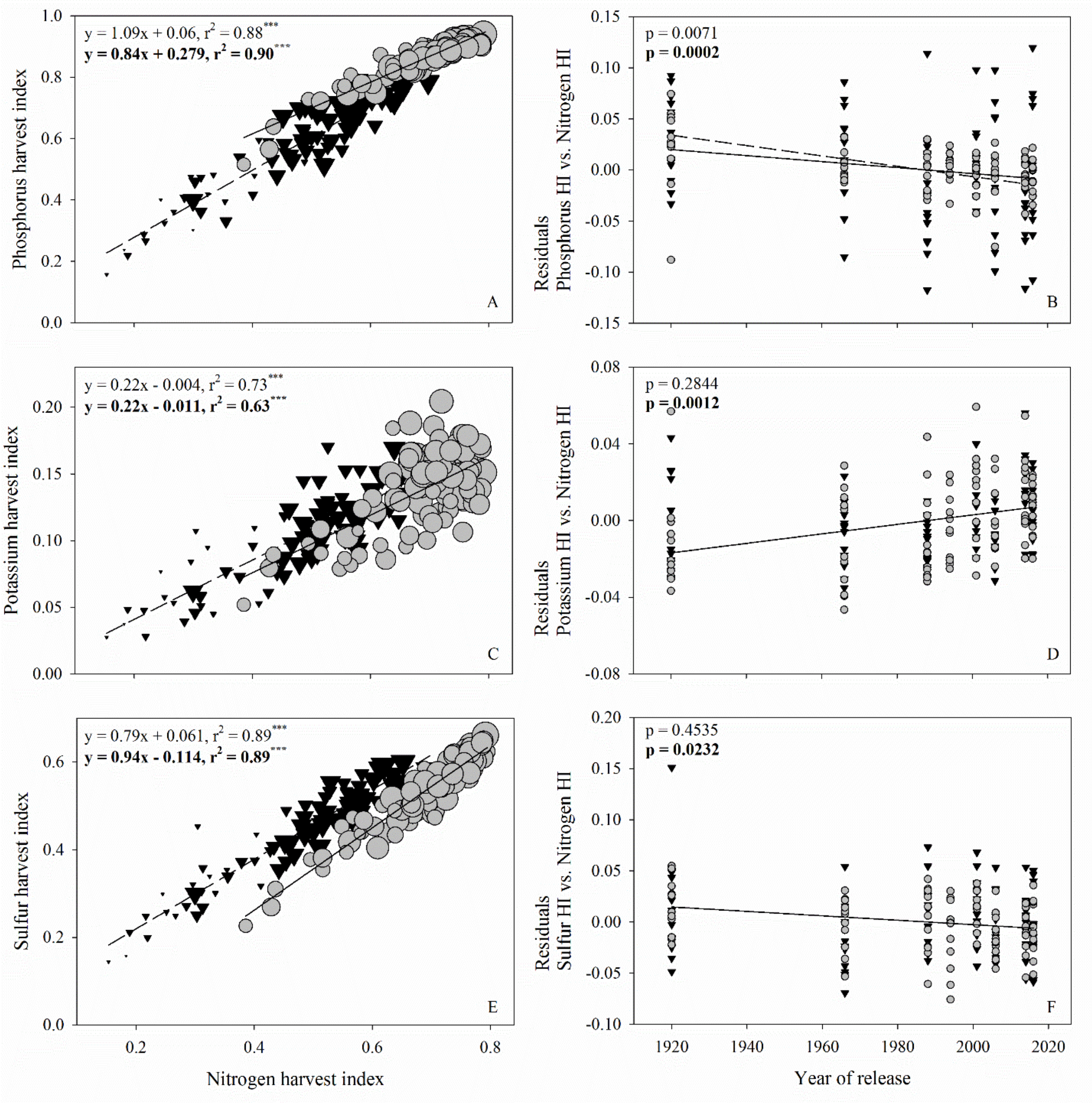


Figure 2.5 Relationship between N and P, K, and S harvest indices as related to the grain yield (A, C, E). Residuals of these relationships were plotted against year of variety release (B, D, F). Black symbols, un-bold text and dashed line correspond to the 2016-17 growing season, and grey symbols, bold text and solid line correspond to the 2017-18 growing season. * Significant (P<0.05); ** significant (P<0.01); * significant (P<0.001); ^{ns} non-significant (P>0.05).**

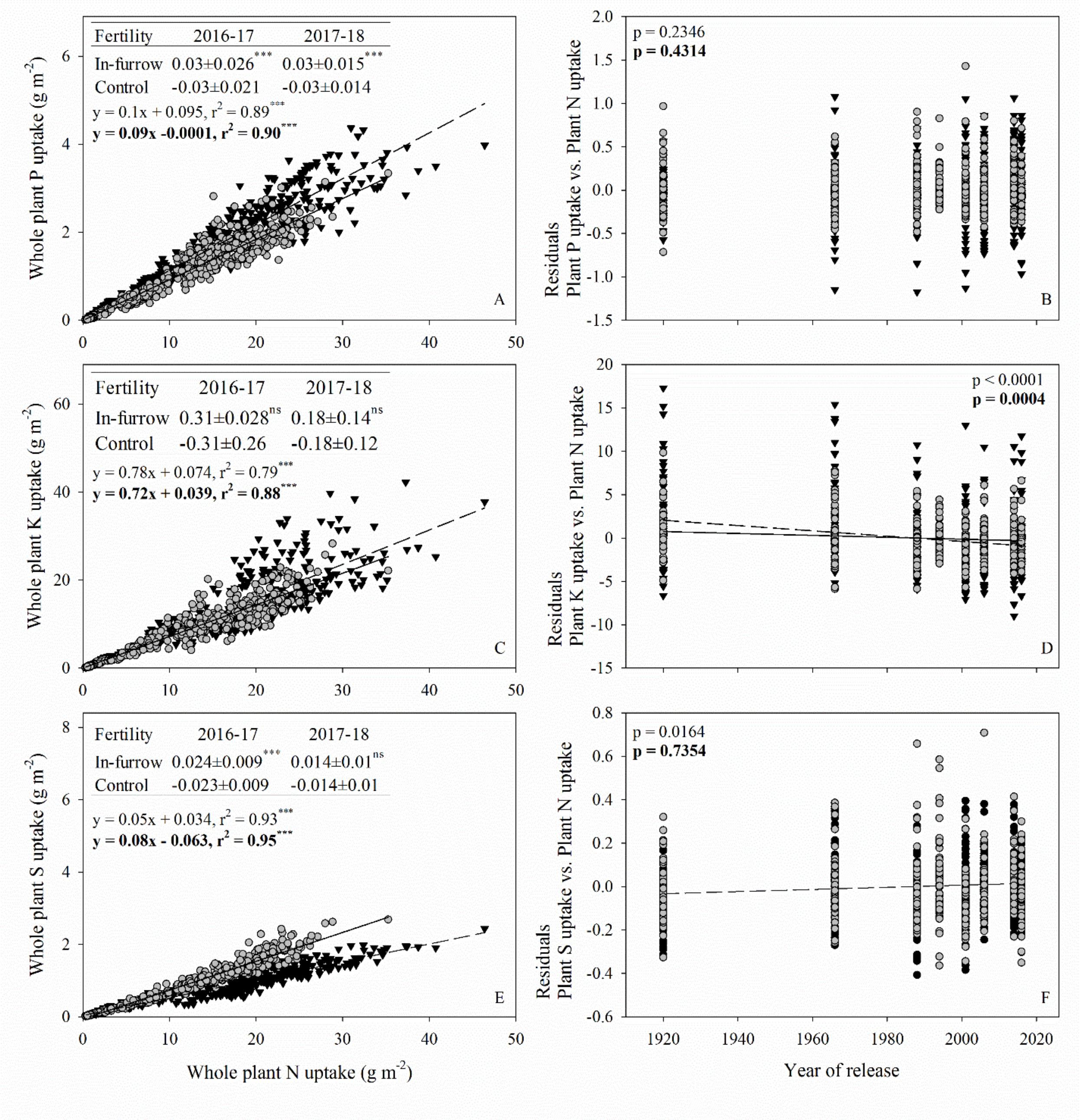


Figure 2.6 Relationship between N and P, K, and S whole plant uptake (A, C, E). Residuals of these relationships were plotted against year of variety release (B, D, F), and comparison of the regression residuals for in-furrow fertilizer treatment and no fertilizer (mean and 1 standard error) are shown as inset table. Black symbols, un-bold text and dashed line correspond to the 2016-17 growing season, and grey symbols, bold text and solid line correspond to the 2017-18 growing season. * Significant ($P<0.05$); ** significant ($P<0.01$); * significant ($P<0.001$); ^{ns} non-significant ($P>0.05$).**

Table 2.1 Nitrogen uptake in different plant components (leaves, stem, chaff, grain) at Zadoks 26, 31, 65, 85 and 92 of wheat varieties released between 1920 and 2016, fertilizer treatment and their interaction during the growing seasons 2016-17 and 2017-18. Variety and fertilizer means were averaged across locations within growing season.

	Variety (Year of release)	Fertilizer	GS 26	GS 31		GS 65			GS 85				GS 92			
Year			Leaves ($\mathrm{g\ m^{-2}}$)	Leaves ($\mathrm{g\ m^{-2}}$)	Stem ($\mathrm{g\ m^{-2}}$)	Leaves ($\mathrm{g\ m^{-2}}$)	Stem ($\mathrm{g\ m^{-2}}$)	Chaff ($\mathrm{g\ m^{-2}}$)	Leaves ($\mathrm{g\ m^{-2}}$)	Stem ($\mathrm{g\ m^{-2}}$)	Chaff ($\mathrm{g\ m^{-2}}$)	Grain ($\mathrm{g\ m^{-2}}$)	Leaves ($\mathrm{g\ m^{-2}}$)	Stem ($\mathrm{g\ m^{-2}}$)	Chaff ($\mathrm{g\ m^{-2}}$)	Grain ($\mathrm{g\ m^{-2}}$)
2016-17	Kharkof (1920)‡		1.93a[†]	5.92	2.25	6.39	10.91a	2.36c	3.34	8.03	3.01	5.42c	2.71	8.12a	3.00	6.15d
	Scout 66 (1966)		1.83ab	6.07	3.09	6.38	10.09ab	3.07b	3.04	7.40	3.32	6.56c	2.54	8.22a	3.48	8.51c
	Karl 92 (1988)		1.97a	5.47	3.33	6.72	8.50cd	2.95b	2.77	6.92	3.01	9.88b	1.97	5.96b	3.13	9.65bc
	Jagalene (2001)		1.80ab	6.22	2.60	8.13	9.92abc	3.71a	3.67	7.35	3.11	14.87a	2.64	5.55bc	3.01	12.63a
	Fuller (2006)		1.49c	5.57	2.66	7.03	8.27de	2.89b	3.14	7.24	3.02	12.95a	1.97	5.02bc	2.77	12.38a
	KanMark (2014)		1.55bc	5.51	2.27	6.75	6.96e	3.12b	2.77	4.71	2.91	13.77a	2.07	4.32c	2.75	12.78a
	Larry (2016)		1.93a	6.06	2.48	7.84	8.83bcd	3.22b	4.01	6.13	2.37	13.05a	2.63	5.18bc	2.47	11.51ab
		In-furrow	2.19A[†]	6.62A	3.09A	7.61A	9.89A	3.23A	3.62A	7.28A	3.10A	11.37	2.62A	6.50A	3.16A	10.17
		Control	1.39B	5.04B	2.24B	6.45B	8.25B	2.86B	2.88B	6.37B	2.83B	10.49	2.10B	5.61B	2.73B	10.85
2017-18	Kharkof (1920)		1.07	4.85	1.77bc	4.24d	6.75b	5.02a	1.39	3.72a	2.73a	9.03c	1.17ab	3.32a	2.35a	8.70d
	Scout 66 (1966)		0.92	5.53	2.42a	6.61bc	8.08a	4.77ab	1.54	3.32a	1.83b	11.26b	1.42a	2.98a	1.97ab	11.06c
	Karl 92 (1988)		1.06	4.71	2.13ab	5.33cd	6.11bc	3.56cd	1.05	2.20b	1.51bc	12.24ab	0.93b	2.06b	1.48c	11.62bc
	Jagger (1994)		1.05	5.04	2.09ab	7.22ab	5.99bc	3.33d	1.26	2.52b	1.60bc	12.69ab	1.22a	2.46b	1.60bc	13.41a
	Jagalene (2001)		1.05	5.09	1.90b	7.17ab	6.35bc	3.88cd	1.28	2.59b	1.53bc	12.93a	1.20ab	2.27b	1.50c	13.05ab
	Fuller (2006)		0.94	4.30	1.81b	6.22bc	5.74bc	3.46cd	1.32	2.44b	1.73bc	11.41b	1.18ab	2.32b	1.75bc	10.85c
	KanMark (2014)		0.96	5.13	1.87b	7.77ab	5.37c	3.94bcd	1.56	2.11b	1.69bc	12.72ab	1.43a	2.17b	1.64bc	13.09ab
	Larry (2016)		0.97	4.62	1.30c	8.50a	6.10bc	4.30abc	1.38	2.59b	1.42c	13.12a	1.22a	2.47b	1.47c	13.32ab
		In-furrow	1.24A	5.73A	2.36A	7.40A	6.93A	4.40A	1.55A	2.98A	1.90A	12.50A	1.38A	2.74A	1.85A	11.66
		Control	0.77B	4.08B	1.46B	5.86B	5.69B	3.66B	1.15B	2.39B	1.61B	11.35B	1.06B	2.27B	1.59B	12.10

† Values followed by the same letter within growing season and treatment are not statistically different at $\alpha = 0.05$.

‡ Jagger was not included in the 2016-17 growing season analysis.

Table 2.2 Phosphorus uptake in different plant components (leaves, stem, chaff, grain) at Zadoks 26, 31, 65, 85 and 92 of wheat varieties released between 1920 and 2016, fertilizer treatment and their interaction during the growing seasons 2016-17 and 2017-18. Variety and fertilizer means were averaged across locations within growing season.

Year	Variety (Year of release)	Fertilizer	GS 26	GS 31		GS 65			GS 85				GS 92			
			Leaves (g m^{-2})	Leaves (g m^{-2})	Stem (g m^{-2})	Leaves (g m^{-2})	Stem (g m^{-2})	Chaff (g m^{-2})	Leaves (g m^{-2})	Stem (g m^{-2})	Chaff (g m^{-2})	Grain (g m^{-2})	Leaves (g m^{-2})	Stem (g m^{-2})	Chaff (g m^{-2})	Grain (g m^{-2})
2016-17	Kharkof (1920)‡		0.25a†	0.57	0.33	0.45	1.17a	0.34c	0.24	0.73	0.40ab	0.87d	0.18	0.65a	0.45	0.96d
	Scout 66 (1966)		0.23ab	0.57	0.42	0.45	1.08ab	0.45b	0.22	0.59	0.49a	1.02d	0.17	0.60ab	0.51	1.22cd
	Karl 92 (1988)		0.24a	0.53	0.45	0.49	0.81bc	0.44b	0.20	0.54	0.40ab	1.45c	0.15	0.45bc	0.53	1.32bc
	Jagalene (2001)		0.20bc	0.59	0.38	0.55	0.97abc	0.56a	0.24	0.53	0.34b	2.19a	0.18	0.34c	0.40	1.75a
	Fuller (2006)		0.17d	0.54	0.38	0.45	0.84bc	0.44b	0.19	0.55	0.32b	1.86b	0.12	0.35c	0.38	1.68a
	KanMark (2014)		0.18cd	0.53	0.34	0.50	0.70c	0.48b	0.24	0.39	0.32b	2.10ab	0.19	0.37c	0.39	1.88a
	Larry (2016)		0.23ab	0.57	0.34	0.55	0.88bc	0.50ab	0.31	0.44	0.29b	1.96ab	0.18	0.32c	0.36	1.61ab
		In-furrow	0.28A†	0.67A	0.46A	0.55A	1.06A	0.48A	0.26A	0.58A	0.39A	1.70	0.18A	0.49A	0.47A	1.44
		Control	0.15B	0.44B	0.30B	0.44B	0.79B	0.43B	0.21B	0.49B	0.34B	1.57	0.15B	0.39B	0.39B	1.53
2017-18	Kharkof (1920)		0.08	0.34	0.19bc	0.20d	0.76	0.57	0.06ab	0.16a	0.18a	1.14	0.05ab	0.11a	0.18a	1.13d
	Scout 66 (1966)		0.06	0.44	0.27a	0.29bcd	0.85	0.58	0.05ab	0.10b	0.11b	1.31	0.05ab	0.10ab	0.15ab	1.31bcd
	Karl 92 (1988)		0.09	0.35	0.24ab	0.25cd	0.68	0.44	0.04c	0.07b	0.08b	1.51	0.03c	0.05c	0.09c	1.24cd
	Jagger (1994)		0.08	0.41	0.24ab	0.39a	0.74	0.45	0.04bc	0.09b	0.10b	1.57	0.04bc	0.06c	0.09c	1.56ab
	Jagalene (2001)		0.08	0.37	0.23ab	0.35ab	0.88	0.50	0.04bc	0.09b	0.08b	1.42	0.04bc	0.06c	0.10c	1.54ab
	Fuller (2006)		0.06	0.32	0.21abc	0.29bc	0.69	0.45	0.04bc	0.08b	0.09b	1.30	0.04bc	0.07bc	0.13bc	1.26cd
	KanMark (2014)		0.08	0.44	0.24ab	0.41a	0.73	0.52	0.06a	0.08b	0.09b	1.51	0.06a	0.07bc	0.10c	1.58a
	Larry (2016)		0.07	0.33	0.15c	0.42a	0.78	0.55	0.05bc	0.08b	0.08b	1.42	0.04bc	0.06c	0.09c	1.45abc
		In-furrow	0.10A	0.46A	0.29A	0.38A	0.87A	0.56A	0.06A	0.11A	0.12A	1.50A	0.05A	0.09A	0.13A	1.39
		Control	0.05B	0.29B	0.15B	0.27B	0.66B	0.46B	0.03B	0.07B	0.08B	1.29B	0.03B	0.05B	0.09B	1.37

† Values followed by the same letter within growing season and treatment are not statistically different at α = 0.05.

‡ Jagger was not included in the 2016-17 growing season analysis.

Table 2.3 Potassium uptake in different plant components (leaves, stem, chaff, grain) at Zadoks 26, 31, 65, 85 and 92 of wheat varieties released between 1920 and 2016, fertilizer treatment and their interaction during the growing seasons 2016-17 and 2017-18. Variety and fertilizer means were averaged across locations within growing season.

	Variety (Year of release)	Fertilizer	GS 26	GS 31		GS 65			GS 85				GS 92			
Year			Leaves (g m^{-2})	Leaves (g m^{-2})	Stem (g m^{-2})	Leaves (g m^{-2})	Stem (g m^{-2})	Chaff (g m^{-2})	Leaves (g m^{-2})	Stem (g m^{-2})	Chaff (g m^{-2})	Grain (g m^{-2})	Leaves (g m^{-2})	Stem (g m^{-2})	Chaff (g m^{-2})	Grain (g m^{-2})
2016-17	Kharkof (1920)[‡]		1.75a[†]	4.90	2.76	4.46	14.96a	1.28c	2.89	12.58	1.00b	0.86c	1.81	12.41	0.84	0.90c
	Scout 66 (1966)		1.56ab	5.12	3.81	5.42	14.61ab	2.04ab	2.58	12.66	0.85b	0.88c	1.46	13.34	0.79	1.10bc
	Karl 92 (1988)		1.63a	4.07	3.62	4.86	11.11c	1.72bc	2.76	10.46	1.03b	1.39b	1.39	9.93	0.76	1.18b
	Jagalene (2001)		1.36bc	4.66	2.70	5.33	11.84bc	2.47a	3.11	12.65	1.14ab	2.26a	1.67	10.75	0.65	1.68a
	Fuller (2006)		1.10d	4.19	2.79	4.25	11.00c	1.58bc	2.37	12.09	1.15ab	1.98a	1.39	10.28	0.70	1.54a
	KanMark (2014)		1.22cd	3.94	2.56	4.28	9.74c	1.88b	2.91	8.67	1.39a	2.11a	1.96	8.57	0.89	1.80a
	Larry (2016)		1.58ab	4.37	2.75	5.12	12.41abc	1.90b	3.11	11.10	0.91b	2.07a	1.81	10.04	0.61	1.59a
		In-furrow	1.76A[†]	5.15A	3.50A	5.26A	13.40A	1.97A	3.07A	12.51A	1.11	1.72	1.77A	11.59A	0.76	1.36
		Control	1.15B	3.78B	2.49B	4.37B	11.07B	1.71B	2.56B	10.41B	1.03	1.58	1.51B	9.93B	0.73	1.43
2017-18	Kharkof (1920)		0.73	3.32ab	1.79bc	3.64	8.61b	2.08	1.44	9.07	1.66a	1.14c	0.40e	8.15	0.86e	0.96c
	Scout 66 (1966)		0.56	3.87a	2.68a	4.84	10.66a	2.19	0.95	8.66	1.60abc	1.28bc	0.65de	7.89	1.42abc	1.28b
	Karl 92 (1988)		0.72	3.07bc	2.17ab	3.93	7.04b	1.82	1.23	7.41	1.29bcd	1.31bc	0.77cd	6.55	1.07de	1.30b
	Jagger (1994)		0.61	3.19bc	1.99b	4.35	7.13b	1.72	1.61	8.11	1.60abc	1.69a	1.19ab	8.34	1.56a	1.85a
	Jagalene (2001)		0.62	3.15bc	1.78bc	4.34	7.12b	1.89	1.38	7.25	1.22d	1.62a	1.09bc	6.89	1.22bcd	1.76a
	Fuller (2006)		0.56	2.59c	1.72bc	3.87	6.87b	1.86	1.49	6.57	1.59abc	1.54ab	1.08bc	6.69	1.38abcd	1.44b
	KanMark (2014)		0.69	3.53ab	1.92bc	5.01	6.91b	2.15	1.84	6.84	1.64ab	1.71a	1.54a	6.99	1.56ab	1.85a
	Larry (2016)		0.62	2.99bc	1.35c	5.23	7.08b	2.16	1.57	7.95	1.26cd	1.62a	1.13b	7.60	1.17cde	1.76a
		In-furrow	0.79A	3.75A	2.45A	5.00A	8.46A	2.12a	1.55A	8.48A	1.60A	1.59A	1.01	7.83A	1.31	1.53
		Control	0.48B	2.67B	1.40B	3.79B	6.89B	1.85B	1.33B	6.99B	1.36B	1.38B	0.94	6.95B	1.24	1.52

[†] Values followed by the same letter within growing season and treatment are not statistically different at α = 0.05.

[‡] Jagger was not included in the 2016-17 growing season analysis.

Table 2.4 Sulfur uptake in different plant components (leaves, stem, chaff, grain) at Zadoks 26, 31, 65, 85 and 92 of wheat varieties released between 1920 and 2016, fertilizer treatment and their interaction during the growing seasons 2016-17 and 2017-18. Variety and fertilizer means were averaged across locations within growing season.

			GS 26	GS 31		GS 65			GS 85				GS 92			
Year	Variety (Year of release)	Fertilizer	Leaves (g m^{-2})	Leaves (g m^{-2})	Stem (g m^{-2})	Leaves (g m^{-2})	Stem (g m^{-2})	Chaff (g m^{-2})	Leaves (g m^{-2})	Stem (g m^{-2})	Chaff (g m^{-2})	Grain (g m^{-2})	Leaves (g m^{-2})	Stem (g m^{-2})	Chaff (g m^{-2})	Grain (g m^{-2})
2016-17	Kharkof (1920)‡		0.14ab[†]	0.34	0.14	0.26	0.56	0.14d	0.20	0.34	0.12	0.24c	0.16	0.37ab	0.13	0.29d
	Scout 66 (1966)		0.13b	0.37	0.19	0.27	0.51	0.21b	0.20	0.35	0.16	0.31c	0.17	0.44a	0.17	0.40c
	Karl 92 (1988)		0.14ab	0.34	0.21	0.26	0.43	0.18bcd	0.16	0.24	0.16	0.46b	0.12	0.28bc	0.17	0.44bc
	Jagalene (2001)		0.12bc	0.38	0.16	0.37	0.48	0.26a	0.24	0.34	0.17	0.69a	0.18	0.30bc	0.15	0.60a
	Fuller (2006)		0.11c	0.36	0.18	0.28	0.41	0.17cd	0.20	0.33	0.17	0.60a	0.15	0.30bc	0.14	0.58a
	KanMark (2014)		0.13b	0.34	0.16	0.26	0.37	0.20bc	0.22	0.24	0.17	0.61a	0.15	0.25c	0.14	0.58a
	Larry (2016)		0.16a	0.37	0.16	0.34	0.49	0.21bc	0.26	0.29	0.14	0.58ab	0.18	0.29bc	0.12	0.52ab
		In-furrow	0.17A[†]	0.42A	0.21A	0.33A	0.52A	0.21A	0.24A	0.34A	0.17A	0.52	0.18A	0.34A	0.16A	0.47
		Control	0.09B	0.29B	0.14B	0.26B	0.41B	0.18B	0.18B	0.27B	0.14B	0.48	0.14B	0.29B	0.13B	0.50
2017-18	Kharkof (1920)		0.06	0.29	0.10bc	0.35c	0.57ab	0.31ab	0.16	0.39a	0.19a	0.50b	0.11c	0.39a	0.18a	0.48d
	Scout 66 (1966)		0.06	0.38	0.15a	0.55ab	0.68a	0.34a	0.16	0.38ab	0.17abc	0.64ab	0.14abc	0.38a	0.17ab	0.63c
	Karl 92 (1988)		0.08	0.32	0.13ab	0.42bc	0.46bc	0.23c	0.16	0.30bc	0.15bcd	0.77a	0.11c	0.27c	0.14c	0.67bc
	Jagger (1994)		0.07	0.36	0.13ab	0.60a	0.48bc	0.22c	0.21	0.32abc	0.16abcd	0.74a	0.18ab	0.34ab	0.15abc	0.78ab
	Jagalene (2001)		0.07	0.32	0.11abc	0.50abc	0.51bc	0.25bc	0.16	0.28c	0.13d	0.73a	0.14bc	0.28b	0.14c	0.76ab
	Fuller (2006)		0.06	0.29	0.11abc	0.52abc	0.44c	0.22c	0.20	0.29c	0.16abcd	0.65a	0.15ab	0.29b	0.17abc	0.61c
	KanMark (2014)		0.07	0.38	0.13ab	0.59a	0.45bc	0.26bc	0.21	0.27c	0.18ab	0.76a	0.18a	0.30b	0.18a	0.77ab
	Larry (2016)		0.07	0.30	0.08c	0.61a	0.46bc	0.27abc	0.19	0.29c	0.15cd	0.74a	0.16ab	0.31ab	0.15bc	0.78a
		In-furrow	0.09A	0.39A	0.15A	0.60A	0.57A	0.28A	0.21A	0.36A	0.17A	0.73A	0.16A	0.35A	0.17A	0.67
		Control	0.05B	0.27B	0.09B	0.43B	0.44B	0.24B	0.15B	0.27B	0.14B	0.66B	0.13B	0.29B	0.15B	0.69

† Values followed by the same letter within growing season and treatment are not statistically different at $\alpha = 0.05$.

‡ Jagger was not included in the 2016-17 growing season analysis.

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Appendix A - Supporting Figure

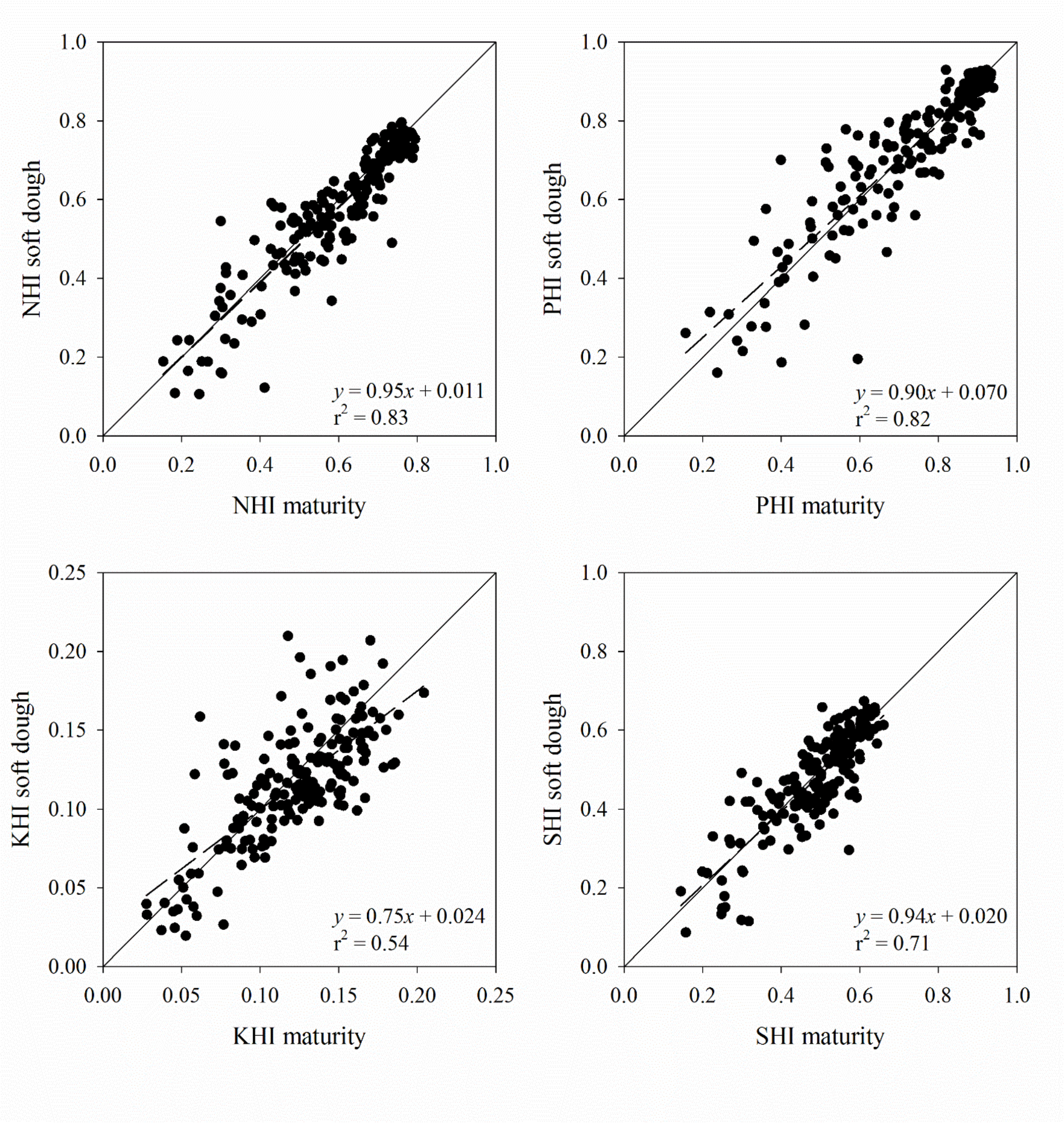

Figure A - 1 N, P, K, and S harvest indices at soft dough stage relationship with N, P, K, and S harvest indices at maturity. Dashed lines correspond to linear regression from the relationship. Solid line corresponds to the 1:1 line. Values correspond to the data of four site-years during growing seasons (2016-17 and 2017-18).

Appendix B - Table with significances

Table B - 1 Significance of variety, fertility treatment, and variety x fertility interactions for grain yield, grain-N removal, grain protein concentration (GPC), head number (HN), head size (HS), kernel number (KN), kernel weigh (KW), harvest index (HI), plant height (PH), stem diameter (SD), volume weight, biomass and crop growth rate at GS 26, 31, 65, 85, and 92, biomass by plant component at GS 26, 31, 65, 85, and 92 for leaves (L), stem (S), chaff (C), and grains (G).

	2016-17			2017-18		
Variables	Variety	Fertility	Variety x Fertility	Variety	Fertility	Variety x Fertility
Grain yield	<.001	0.033	0.069	<.001	<.001	0.776
Grain-N removal	<.001	0.091	0.189	<.001	0.007	0.823
GPC	<.001	0.151	0.026	<.001	0.034	0.302
HN	0.001	0.003	0.569	0.009	0.002	0.859
HS	<.001	0.002	0.938	<.001	0.001	0.845
KN	<.001	0.761	0.878	<.001	0.685	0.999
KW	<.001	0.023	0.521	<.001	0.001	0.117
HI	<.001	0.881	0.532	0.009	0.597	0.981
PH	<.001	0.069	0.511	<.001	0.859	0.761
SD	<.001	0.597	0.917	0.252	0.499	0.101
Volume weight	<.001	0.033	0.395	<.001	0.003	0.128
GS 26	0.002 / 0.002	<.001 / <.001	0.607 / 0.495	0.502 / 0.434	<.001 / <.001	0.667 / 0.638
GS 31	0.727 / 0.791	<.001 / <.001	0.697 / 0.679	0.106 / 0.074	<.001 / <.001	0.831 / 0.808
GS 65	<.001 / 0.276	<.001 / 0.040	0.044 / 0.163	<.001 / 0.369	<.001 / 0.007	0.842 / 0.645
GS 85	0.001 / <.001	0.001 / 0.067	0.431 / 0.778	0.846 / 0.347	<.001 / 0.059	0.372 / 0.479
GS 92	0.731 / 0.002	0.169 / 0.071	0.818 / 0.799	0.180 / 0.978	0.039 / 0.005	0.988 / 0.925
GS 26 - L	0.002	<.001	0.607	0.502	<.001	0.667
GS 31 -L	0.398	<.001	0.725	0.306	<.001	0.987
GS 31 - S	0.016	<.001	0.531	0.007	<.001	0.285
GS 65 - L	0.049	<.001	0.481	0.055	<.001	0.723
GS 65 - S	<.001	<.001	0.02	<.001	<.001	0.418
GS 65 - C	0.003	0.005	0.034	0.004	0.001	0.582
GS 85 - L	0.105	<.001	0.069	0.182	<.001	0.359
GS 85 - S	0.005	0.002	0.579	<.001	<.001	0.055
GS 85 -C	<.001	0.001	0.225	0.32	<.001	0.577
GS 85 - G	<.001	0.068	0.463	<.001	0.009	0.815
GS 92 -L	0.009	<.001	0.642	0.054	0.002	0.948
GS 92 -S	<.001	0.007	0.568	<.001	0.004	0.62
GS 92 -C	0.009	0.344	0.854	0.582	0.048	0.908
GS 92 - G	<.001	0.334	0.926	<.001	0.459	0.998