

Strategies for sustainable improvement of the wheat phenotype

by

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DOCTOR OF PHILOSOPHY

Department of Agronomy
College of Agriculture

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Abstract

This dissertation explores strategies for wheat yield and quality improvement in regional (United States Great Plains) and global scales. Throughout six individual chapters, I collaborate with experts from diverse backgrounds to explore multiple layers of biological organization - from genetic to social networks- aiming to understand drivers of wheat grain yield and quality.

In the first chapter we used quantitative literature synthesis methods to (i) assess the effect of N applications to wheat after flag leaf visible (GS 37) on grain yield and grain protein concentration; and to assess the variation in these responses with (ii) N fertiliser management, (iii) environmental factors, and (iv) physiological traits. Overall, late-season N fertilisation was neutral for grain yield and increased grain protein concentration with a pooled estimate of 3.96%.

The second chapter explored relations of wheat yield and grain protein concentration in response to N input and its physiological basis from the perspective of phenotypic plasticity. Grain yield plasticity was positively associated to yield in high-yielding environments without N limitations with no cost in low yielding environments, and associated to harvest index. Grain protein plasticity was a positively associated to protein in high protein environments without N limitations.

In the third chapter we proposed a Bayesian hierarchical framework to model the variance of grain yield response to plant density. We identify the plant density in each seed size, seed treatment and environment combination that maximizes the expected yield and minimizes yield variance.

In the fourth chapter we used data from variety trials conducted between 2000 and 2022 and cultivars released between 1967 and 2022, to explore time trends in phenotypic plasticity and heritability of yield. Breeding for yield and agronomic adaptation increased phenotypic

plasticity of yield at 0.5% year⁻¹; broad sense heritability of yield decreased from 0.23 in 1993 to 0.15 in 2017. Genome-wide-association analysis shows genomic regions associated with yield varied between high yielding and stressful environments and were partially independent of those associated with yield plasticity. Newer cultivars have a higher frequency of alleles associated with yield and its plasticity.

The fifth chapter aims to narrow winter wheat yield gaps in the US Great Plains, by understanding trade-offs and synergies between stripe rust resistance and yield phenotypic plasticity under varying management and environment. High yield stability and susceptibility to stripe rust comes at the expense of yield gaps regardless of environment yield potential and conditions conducive to stripe rust development.

In the last chapter, we propose a three-step process to advance food systems sustainability, using wheat as a case study. This process is informed by data collected during a two-day expert elicitation workshop involving 46 stakeholders from the wheat industry. First, we move toward an operational definition of sustainability grounded on wheat value chain stakeholders. Second, we propose a framework a framework to identify common and diverging priorities across sectors of the value chain. Third, we advance on collaboration strategies to advance on a unified sustainability stamp on a loaf of bread, that agrees with the conceptual definition of sustainability. We showed that (i) there is *a priori* consensus across the wheat industry on a definition of sustainability and, (ii) the ranking of sustainability priorities, was not associated to the level of agreement of a given sustainability indicator across the wheat industry, revealing each sector has its own unique sustainability goals.

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Table of Contents

List of Figures	xvi
List of Tables	xxxii
Acknowledgements	xxxiv
Dedication	xxxvi
Preface	xxxvii
Chapter 1 - Late-season nitrogen application increases grain protein concentration and is neutral for yield in wheat. A global meta-analysis	1
Abstract	1
1.1 Introduction	2
1.2 Method	4
1.2.1 Database construction	4
1.2.2 Nitrogen management	6
1.2.3 Environment	7
1.2.4 Physiological traits	8
1.2.5 Dough rheological properties	8
1.2.6 Data curation and quality control	8
1.2.7 Data analysis	9
1.2.8 Drivers of the response to late N	11
1.3 Results	12
1.3.1 Overview	12
1.3.2 Overall impact of late-season N on wheat grain yield and grain protein concentration	13

1.3.3 Fertiliser management affected GPC response	13
1.3.4 Environmental descriptors of GPC response to late-season N	14
1.3.5 Physiological drivers of the GPC response to late season N	14
1.3.6 Dough rheological properties response to GPC due to late-season N fertilisation.	14
1.4 Discussion	15
1.4.1 Late-season N application impact on wheat grain yield and protein concentration	15
1.4.2 Influence of late season N management on GPC response.....	16
1.4.3 Environmental effects on grain protein response to late season N	18
1.4.4 Physiological drivers of GPC response to late-season N.....	19
1.4.5 Impact of GPC response on dough rheological properties	20
1.5 Box 1	20
1.6 Conclusion	22
Chapter 2 - Cultivar-specific phenotypic plasticity of yield and grain protein concentration in response to nitrogen in winter wheat	34
Abstract	34
2.1 Introduction.....	35
2.2 Conceptual Framework.....	37
2.2.1 Phenotypic plasticity	37
2.2.2 Evaluation of yield and grain protein response to N for cultivars with contrasting plasticity	37
2.3 Method	39
2.3.1 Crop husbandry, plant material, and experimental design.....	39
2.3.2 Measurements	40

2.3.3 Phenotypic plasticity	41
2.3.4 Bayesian process models and statistical analysis	42
2.3.4.1 Phenotypic plasticity response models	43
2.3.4.2 Grain yield and protein concentration response to N supply models	43
2.3.4.3 Relationships between phenotypic plasticity, yield components and crop N traits	45
2.3.4.4 Model selection	47
2.4 Results.....	47
2.4.1 Environments, yield, and grain protein.....	47
2.4.2 Phenotypic plasticity of grain yield and grain protein concentration	48
2.4.3 Grain yield and protein concentration response to N for cultivars with contrasting plasticity for yield and grain protein concentration	49
2.4.4 Associations between phenotypic plasticity and crop traits	50
2.5 Discussion	51
2.6 Conclusion	54
Chapter 3 - A Bayesian framework to model variance of grain yield response to plant density..	66
Abstract	66
3.1 Background	68
3.2 Methods	70
3.3.1 Modeling grain yield response to plant density	70
3.3.2 Developing informative priors: Canadian Prairies data	72
3.3.3 Data analysis: Central Great Plains, Kansas US	74
3.3 Results.....	77

3.3.1 Informative priors: Canadian Prairies	77
3.3.2 Yield response to plant density under varying seed size, seed treatment and environment in Kansas.....	77
3.3.2.1 Seed treatment and size impacts expected yield and yield variance.....	78
3.3.2.2 Seed treatment and size effects on AOPD and minRPD.	78
3.3.2.3 Economic assessment of plant density recommendations	79
3.4 Discussion	79
3.4.1 Limitations	79
3.4.2 Modeling assumptions	80
3.4.3 Agronomic and economic implications behind minRPD	81
3.5 Conclusion	83
Chapter 4 - Genetic modulation of yield and phenotypic plasticity of yield in winter wheat	89
Abstract.....	89
4.1 Introduction.....	90
4.2 Method	92
4.2.1 Field experiments.....	92
4.2.2 Yield data	93
4.2.3 Environmental data	95
4.2.4 Genotypic data	96
4.3 Results.....	97
4.3.1 Rainfall and photothermal quotient associated with yield	97
4.3.2 Genotype-dependent phenotypic plasticity of yield is agronomically adaptive in the Central Plains	98

4.3.3 Phenotypic plasticity of yield increased and heritability of yield decreased over decades.....	98
4.3.4 Partial independence in the genetic modulation of yield phenotypes	99
4.4 Discussion	100
4.4.1 Agronomically adaptive changes on wheat yield phenotypes	100
4.4.2 Genetic modulation of yield phenotypes	102
4.5 Box 1	104
4.5.1 Genes associated with yield phenotypes	104
4.6 Conclusion	107
Chapter 5 - High yield stability and susceptibility to stripe rust associate with large yield gaps in rainfed winter wheat	116
Abstract	116
5.1 Introduction.....	117
5.2 Material and methods.....	121
5.2.1 Field experiments.....	121
5.2.2 Environment.....	123
5.2.3 Statistical analysis	123
5.2.3.1 Yield plasticity and yield gap	123
5.2.3.2 Stripe rust resistance and yield gap.....	125
5.2.3.3 Model fitting and validation.....	126
5.3 Results.....	126
5.3.1 Environments	126
5.3.2 Relationship between yield plasticity and yield gap	127

5.3.3 Association between stripe rust resistance and yield gaps	128
5.3.4 Interactions between yield plasticity and stripe rust resistance	128
5.4 Discussion	129
5.4.1 Hypothesis 1: Yield plasticity related negatively with yield gap in high yielding environments	129
5.4.2 Hypothesis 2: Yield gaps are larger with cultivars susceptible to stripe rust in unprotected crops under conducive conditions for disease development	131
5.4.3 Hypothesis 3: Greater frequency of smaller yield gaps when combining high plasticity-resistant stripe rust phenotypes	133
5.5 Conclusion	134
Chapter 6 - From value chain to network – implications for sustainability.....	142
Abstract	142
6.1 Introduction.....	142
6.2 Methods	145
6.2.1 Study region	145
6.2.2 Expert elicitation.....	146
6.2.3 Definition of sustainability	147
6.2.4 Listing and ranking of sustainability indicators.....	147
6.2.5 Relevance and adoption of technologies to improve sustainability indicators	148
6.2.6 Industry network innovation strategies with “now-how-wow” structure	149
6.2.7 Data analysis	149
6.3 Results.....	152
6.3.1 A priori consensus across stakeholders on sustainability definitions	152

6.3.2 Relevant sustainability indicators are not necessarily common across sectors	152
6.3.3 Network collaboration to advance in a sustainability stamp on a loaf of bread	153
6.4 Discussion.....	155
6.4.1 Implications of a priori consensus on the definition of sustainability	155
6.4.2 Cooperation across sectors to advance on wheat industry sustainability.....	156
References.....	162
Appendix A - Chapter 1 Supplementary Material	195
Appendix B - Chapter 2 Supplementary Material	198
Appendix C - Chapter 3 Supplementary Material	209
Flat priors for the Canada dataset	209
Model Fitting	209
Supplementary Figures and Tables.....	212
Appendix D - Chapter 4 Supplementary Material	221
Variety testing network data from a sample of wheat producing regions.	221
Appendix E - Chapter 5 Supplementary Material.....	234
Appendix F - Chapter 6 Supplementary Material.....	243
Supplementary Figures	243
Guide for structured discussions during the two-day expert elicitation workshop.....	259
Day 1	259
What does sustainability mean to you?.....	259
Overview of the sessions and shared expectations (9 – 9.15).....	259
Small group introductions (9.15-9.30).....	259
Identify sustainability indicators for each domain (9:30 – 10:30).....	259

Continued. Identify sustainability indicators for each domain.	261
Rank indicators by importance (1:00 – 2:00)	262
Identify technologies and practices (2:00 – 2:30).....	262
Categorize technologies and practices according to degree of adoption (2:30-3:00)	263
Day 2	264
Introductions to new groups (8:00-8:15).	264
Value chain indicator voting (8:15-9:00).....	264
Collaborate across the supply chain (9:00-10:00).	264
Reconvene on collaboration (10:15-11:00).	265
Report out to the entire group (11:00-11:30).....	266
Wrap up and ticket out (11:30-12:00).....	266

List of Figures

Figure 1.1. Approach to screen articles from AJ (Agronomy Journal); CS (Crop Science); EJA (European Journal of Agronomy); and FCR (Field Crops Research).....	23
Figure 1.2. Distribution of field trials evaluating wheat response to late-season N application in the current meta-analysis.	24
Figure 1.3. (A) Comparisons of wheat grain yield (YLD), grain protein concentration (GPC), stover nitrogen uptake (NUP), stover biomass (SB) and stover nitrogen concentration (NCON) between basal N (red) and late N crops (blue). Basal N crops received N fertiliser before and late N after GS 37. Boxplots show the range, the median and inter-quantile range. (B) Grain yield-grain protein concentration relation across all studies and sources of variation; red symbols are basal N and blue are late N crops. The line is the SMA regression with its 95% bootstrapped confidence interval. Inset compares residuals for basal N (red) and late N (blue) (mean and s.e.).	25
Figure 1.4. Pooled effects for grain yield (green symbols) and grain protein concentration (red symbols). Symbols and their whiskers represent the mean effect and 95% bootstrapped CI for each of the studies in this analysis. The yellow symbols are the mean estimate and its 95% bootstrapped confidence interval. Opacity of whiskers is relative to the significance of each estimate, and size of the points is relative to the weight of each study. Studies are sorted according to the mean yield of the basal N treatment in each study in decreasing order from top to bottom. Abbreviations: confidence interval (CI), lower bound (LB), upper bound (UB), I² = I-squared statistic (%).	28
Figure 1.5. Impact of late nitrogen management practices on grain protein concentration response: (A) Grain protein concentration increased with the proportion of the late applied	

N (LNR) relative to the total N available (TN). Effect of different late N fertiliser timings of application (B), placement (C) and sources (D) on the residuals of the proportion of late N and GPC response to late N relationship (Panel A). Size of the individual datapoints is relative to the weight of each observation. In panels A and B: *p*-values represent the slope significance (mean and confidence interval (CI) of a resampling distribution); slope mean estimate and 95% bootstrapped CI are represented. **I²** = I-squared statistic. Ribbons around the fitted line indicate 95% bootstrapped CI for the slope of the meta-regression. In panels C and D: points represent the mean effect and whiskers correspond to the bootstrapped CI; grey whiskers indicate non-significant effects corresponding to the 97.5% quantile of the bootstrapped *p*-values. Key: AN (ammonium nitrate), AS, (ammonium sulphate), SRN (slow-release nitrogen), UAN (urea ammonium nitrate), UREA (granulated urea)..... 29

Figure 1.6. Environmental descriptors of the GPC response to late-season N fertilisation. (A) Bi-plot with first two dimensions of the principal component analysis, points represent studies and triangles the corresponding centroids for wheat type clusters; (B) individual contribution of the weather attributes in the first 4 dimensions, ‘Total Var’ represents the total variance explained by each of the dimensions; (C) effect of environmental descriptors on GPC response in the two clusters: HIGH (red) and LOW (blue) for the critical period (CP) and grain filling period (GF). In panel C whiskers represent the 95% bootstrapped CI. Significance of the means comparisons are provided in Appendix Table A.1. Variables evaluated were: mean temperature (Tmean), photothermal quotient (PQ), duration of the period (Duration), accumulated precipitation (PP). 30

Figure 1.7. Relationship between relative GPC response ratio and stover N uptake response ratio, stover nitrogen concentration response ratio and stover biomass response ratio. Colours

represent studies. <i>P</i> -values correspond to the 0.975 quantile of a resampling distribution.	
Grey area indicates 95% bootstrapped CI for the slope of the SMA regression. Mean slope and Pearsons <i>r</i> from a resampled distribution are represented.....	31
Figure 1.8. Grain protein concentration response ratio and its relation with the response in different dough traits: dough extensibility, dough tenacity, dough extensibility-tenacity ratio and alveogram index. <i>P</i> -values correspond to the 0.975 quantile of a resampling distribution. Grey area indicates 95% bootstrapped CI for the slope of the SMA regression. Mean slope and Pearsons <i>r</i> from a resampling distribution are represented.....	
	32
Figure 1.9 (A) Late N recovery efficiency for all studies included in the analysis. Studies are sorted according to the mean grain protein concentration of the basal N treatment in each study in decreasing order from top to bottom. (B) Effect of environmental descriptors on late N recovery efficiency in the two clusters: HIGH (red) and LOW (blue) for the critical period (CP) and grain filling period (GF). In panel B, whiskers represent the 95% bootstrapped CI and stars represent significant differences indicated by non-overlapping 95% bootstrapped CI. Abbreviations: grain N removal (N_G), late N fertiliser rate (N_F), mean temperature (T_{mean}), photothermal quotient (PQ), duration of the period (Duration), accumulated precipitation (PP).	
	33
Figure 2.1. Hypothetical relations between trait and trait plasticity for a phenotype with high (blue) and low (red) plasticity under conditions that favor high (circles) or low (triangles) traits. The higher plasticity of the blue phenotype arises from (A) responsiveness to favorable conditions, or (B) higher sensitivity to stressful conditions, or (C) high responsiveness to both favorable conditions and stress.	
	55

Figure 2.2. Conceptual model of grain yield (A; solid lines) and protein (B; dashed lines) in response to N supply for phenotypes with high (blue) and low (red) phenotypic plasticity. Vertical dashed lines are the boundaries of phases I, II, III in the response of yield and protein to N supply. In phase I, N supply limits both yield and grain protein; in phase II, N supply limits grain protein but not yield; and in phase III, N supply does not limit yield or grain protein concentration. 55

Figure 2.3. Frequency distribution of grain yield (A) and grain protein concentration (B) pooled for cultivars and location-season on the most contrasting N rates of 0 and 135 kg N ha⁻¹. The box represents the interquartile range and the line inside the box the median. Whiskers represent 1.5x the interquartile range. Cultivars are sorted in increasing order according to their phenotypic plasticity of yield (A) and protein (B); and location-seasons are sorted from left to right according to the mean grain yield in increasing order. Principal component analysis for grain yield, grain protein concentration and environmental variables: biplot (C) and variance contribution within dimension (D) in experiments carried out in Kansas in 2020 and 2021. In C and D, the color of the points represents the extreme N rates (0 kg N ha⁻¹ orange, 135 kg N ha⁻¹ green), while shapes represent cultivars. Abbreviations: Ashland Bottoms 2A2 field (AB), Ashland Bottoms M3 field (AM), Great Bend (GB), Hutchinson (HU), Manhattan (MA), Viola (VI), season 2019-2020 (20), season 2020-2021 (21), mean temperature (Tmean), vapor pressure deficit (VPD), photothermal quotient, (PQ), cumulative reference evapotranspiration (cumET0), critical period (CP) and grain filling period (GF)..... 59

Figure 2.4. Trait-plasticity relationships for grain yield (A) and protein (B), and relationship between plasticity of grain protein and yield (C). Colors highlight the least (red) and the

most plastic (blue) cultivars for each trait. Solid lines (posterior median) and ribbons (posterior 95% credible interval) are shown when the 95% credible interval of the slope of the relation is not overlapping zero. Inset text shows the slope posterior median and 95% credible interval..... 60

Figure 2.5. Wheat grain yield (A-D) and protein (E-F) response to N supply under conditions conducive to high (90th percentile, triangles) and low (10th percentile, circles) trait expression for cultivars with contrasting phenotypic plasticity. Red symbols are for cultivars with low plasticity for yield (LCS Chrome) and protein (WB4269), and blue is for cultivars with high plasticity for yield (Bentley) and protein concentration (Green Hammer). Linetype indicates the phases conceptualized in Figure 2: dashed (phase I), solid (phase II), dotted (phase III). Lines represent the posterior medians and ribbons the 95% estimation credible interval for model predictions. The size of the symbol shows protein concentration in the yield panels (A-D) and yield in the protein panels (E-H). 60

Figure 2.6. Association of yield and protein plasticity with grain yield (A, B, E, F) and protein (C, D, G, H, I, J) at the starting point of phases described in Figure 2 and Table 3 (phase I - N limits yield and protein; phase II, N limits for protein but not for yield; phase III – non-N limitation). In yield panels shapes represent high (triangles) and low (circles) yielding environments; in protein panels shapes represent high (triangles) and low (circles) protein environments. Lines shown only when the slope's credible interval not overlaps zero at different confidence levels (95% - solid lines; 90% - dashed lines). 61

Figure 2.7. Wheat grain yield (A-D) and N yield (E-H) response to N uptake across environments for cultivars with contrasting plasticity for yield (LCS Chrome, Bentley) and

protein (WB4269, Green Hammer). Solid lines represent the posterior medians and ribbons the 95% estimation credible interval for model predictions.	62
Figure 2.8. Association between yield and protein plasticity and yield at the critical N uptake, critical N uptake, N utilization efficiency (NUE) and N Yield for contrasting yield and protein plasticity cultivars pooled across environments. Lines shown only when the slope's credible interval does not overlap zero at 95% (solid line) and 90% (dashed lines). Inset slopes represent the median and credible interval.	63
Figure 2.9. Relations between grain yield phenotypic plasticity (A, C, F, H, J, L, N) and protein (B, D, G, I, K, M, O) phenotypic plasticity and crop traits (grain protein, grain yield, harvest index, shoot biomass, grain number m ⁻² , thousand kernel weight, head number m ⁻² , and grain number head ⁻¹) for crops grown in low (10 th percentile, circles) and high (90 th percentile, triangles) yield and protein environments. Points and lines shown only when the slope's credible interval does not overlap zero at 95% (solid lines), 90% (dashed lines) and; 80% (dotted lines). Inset slopes represent the median and credible interval.	64
Figure 2.10. Allometric relation between N harvest index (NHI) and harvest index (HI) for contrasting yield (A) and protein (B) plasticity cultivars; R ² = 0.34. Association between yield (C) and protein (D) plasticity and the linear term of the quadratic models presented above. Lines shown only when the slope's credible interval not overlaps zero at different confidence levels (95% - solid lines; 90% - dashed lines; 80% - dotted lines). Inset slopes represent the median and credible interval.	65
Figure 3.1. Posterior distributions of yield response to plant density model parameters (Eq. 2 and Eq. 3) pooling all 12 combinations of seed treatment, seed size and environment. Derived quantities from these distributions (e.g., the expected value, the standard deviation, and	

quantiles) were used to build informative priors described in Eq 6 – 10. Purple bars refer to parameters or quantities related to modelling the expected value (μ_{ij}) and yellow bars to parameters or quantities related to modelling the variance (σ_{ij2}) of grain yield.

Abbreviations: sample size (n), linear term of expected yield response to plant density (β_1), agronomic optimum plant density (AOPD), maximum variance plant density (maxVPD), minimum risk plant density (minRPD), linear term of variance of yield response to plant density (α_1). 84

Figure 3.2. Panel A shows expected grain yield (μ_{ij}) in response to plant density (s_{ij} , purple); panel B shows standard deviation of yield (derived from yield variance, σ_{ij2}) in response to plant density (yellow); panel C shows the posterior predictive distribution of grain yield (y_{ij}) response to plant density (brown) for the j th treatment $\times$ environment combination (in this example untreated, light seeds in low yield environment cluster). Solid black lines represent the median and ribbons the 95% credible interval. Purple refers to parameters or quantities related to modelling the expected value (μ_{ij}) and yellow to parameters or quantities related to modelling the variance (σ_{ij2}) of grain yield..... 85

Figure 3.3. Posterior distributions of expected grain yield response to seed management evaluated at the AOPD (Eq. 11); B) standard deviation of yield response to seed management evaluated at the minRPD (Eq. 11) in high (circles, opaque) and low (diamond, transparent) yielding environments. Contrasts represent heavy, treated seeds against light seed, untreated control treatment (Eq. 11). Points represent the median and whiskers are the 95% credible interval; p represents the posterior probability of $\Delta\mu_j$, $\Delta\sigma_j$ being greater than zero. Purple refers to parameters or quantities related to modelling the expected value (μ_{ij})

and yellow to parameters or quantities related to modelling the variance (σ_{ij}^2) of grain yield..... 85

Figure 3.4. Posterior distributions of AOPD (A) and minRPD (B) for contrasting seed management treatments (no treatment and light seeds, “None_Light”; treated and heavy seeds, “Treated_Heavy”) under high (circles, opaque) and low (diamond, transparent) yielding environments. Points represent the median and whiskers are the 95% credible interval. Purple refers to parameters or quantities related to modelling the expected value (μ_{ij}) and yellow to parameters or quantities related to modelling the variance (σ_{ij}^2) of grain yield. 86

Figure 3.5. Posterior distributions of AOPD (A) and minRPD (B) as affected by seed management treatments under high (circles, opaque) and low (diamond, transparent) yielding environments. Contrasts represent heavy, treated seeds against light, untreated (control) seeds. Points represent the median and whiskers are the 95% credible interval. Equation 11 describes the calculations used for contrasts between treatments. Purple refers to parameters or quantities related to modelling the expected value (μ_{ij}) and yellow to parameters or quantities related to modelling the variance (σ_{ij}^2) of grain yield. Abbreviations: agronomic optimum plant density (AOPD), minimum risk plant density (minRPD). 87

Figure 3.6. Posterior distribution of the difference in net income from plant density recommendations following minRPD compared to AOPD, under (A) low and (B) high yielding environments and varying seed chemical treatment and cleaning methods. Positive Δ Net Income values represent greater net income by following minRPD compared to AOPD (Eq. 12, 13). Points represent the mean and whiskers the 95% credible interval. 88

Figure 4.1. Association between genotype-dependent phenotypic plasticity of yield and actual yield in high (triangles, 95th yield percentile) and low (circles, 5th yield percentile) yielding environments in a sample of wheat producing regions. The genotypes with highest (blue) and lowest (red) plasticity are highlighted. Model used for quantile regression is in Equation 4. Data were obtained from variety testing networks in each region and reproduced with permission. Additional details on datasets used in this Figure can be found in Appendix Table D.1..... 108

Figure 4.2. (A) Frequency distribution of grain yield in three levels: high yielding environments (blue, 95th percentile), mean yield (white) and low yielding environments (red, 5th percentile). (B) Spatial distribution of experimental sites throughout the states of Colorado, Kansas, and Oklahoma. In (B), each point represents an experimental site, color of the point is relative to the average environmental index of a given location, and their size represents the standard deviation of environmental indexes within a site. (C) Associations between environmental index, **ej**, photothermal quotient and the cumulative precipitation from the start of the critical period (-300 °Cd from anthesis) and the end of the grain filling period (+600 °Cd from anthesis). Color of nodes/points is relative to the mean environmental yield. In B and C, environmental indexes are expressed as deviations from the overall intercept, **μ0** (mean: 3.4 Mg ha⁻¹, c.i.: 3.3 – 3.5 Mg ha⁻¹), both estimated following Equations 1 and 2. Estimation of levels of the grain yield distribution shown in A are described in Equations 1,2 and 4. Abbreviations: precipitation (PP), photothermal quotient (PQ), critical period (CP), grain filling period (GF). 109

Figure 4.3. Reaction norms relating genotype-dependent yield and environmental index and (B) association of yield and yield plasticity for 234 cultivars grown in at least 25 environments

in Central Great Plains. In (A) color lines and symbols are for cultivars with the highest (blue) and lowest (red) yield plasticity, and black lines are the population as a bundle of reaction norms (sensu Van Noordwijk (1989); dashed line is $y = x$. In (B) triangles are high (95th percentile), squares are average, and circles are low (5th percentile) yielding environments. Model used for quantile regression is described in Equation 5. Environmental index is estimated from the sum of μ_0 and e_j (Equation 2). Yield phenotypic plasticity was estimated as $1 + \beta_i$ (Equation 2), i.e., the slope of the reaction norm in panel A. 110

Figure 4.4. Time trends for (A) phenotypic plasticity of yield, (B) root mean squared error (RMSE) from yield-yield environment reaction norm, (C) broad sense heritability of yield and (D) expected value of variance components from broad sense heritability estimation. In A and B, colors show the cultivar with the highest (blue) and lowest (red) yield plasticity. Heritability of yield was estimated using a sliding window of 10 years starting in 1989 until 2022, x-coordinate of open points represents the average heritability for the window sampled. Jitter was added to black points on x, which represent the uncertainty in the estimation of y. Data from cultivars released between 1967-1989, were excluded as only three cultivars were representative of the entire population in that period. 111

Figure 4.5. Relationship between first two principal components from PCA conducted on the genotypic matrix. Closed symbols represent presence and open symbols represent absence of 2N^vS translocation on chromosome 2A. Jagger is the canonical for the 2N^vS translocation in North American hard winter wheat. (B) Increasing frequency of the 2N^vS translocation with cultivar year of release. Allelic frequency in the population was calculated using a sliding window of 10 years starting in 1989 until 2022; data prior 1989 were scarce, and therefore were excluded. (C-F) Distribution of yield phenotypes for cultivars with presence

and absence of the 2N^VS translocation, circles represent the median and whiskers the 95% credible interval of the posterior predictive distribution of yield phenotypes, while open points represent the observed yield phenotypes. (G-J) Posterior distribution of the difference between presence and absence of the 2N^VS translocation, showing magnitude of effect sizes for each yield phenotype, points represent the mean and whiskers the 95% credible interval. 95% credible interval does not overlap with zero in all four comparisons shown in panels F-I. 112

Figure 4.6. Associations of 15,224 SNPs and four yield phenotypes: (A) phenotypic plasticity of yield, (B) yield in high yielding environments (95th yield percentile), (C) mean yield, and (D) yield in low yielding environments (5th yield percentile). Black dashed line is the exploratory threshold of $-\log_{10}(P) = 3.0$, and shaded areas show the position of SNPs above the exploratory threshold. 113

Figure 4.7. (A-D) Variation in the frequency of the favorable alleles associated with four yield phenotypes with cultivar year of release. Allelic frequency in the population was calculated using a sliding window of 10 years starting in 1989 until 2022; data prior 1989 were scarce, and therefore were excluded. Opacity of the allelic frequency lines is relative effect of the favorable allele in each SNP, being the darker colors the SNPs with major effects on traits. (E-H) Distribution of allelic effects for yield traits. Yield plasticity is unitless in E, and units are Mg ha⁻¹ for yield phenotypes in F, G and H. Relative effects represent the effect size of a given SNP relative to the maximum effect size for a given trait. 114

Figure 5.1. Conceptual framework and working hypotheses. (A) Hypothesis 1: Relationship between yield and yield plasticity in environments with high (Y_{w1}) and low (Y_{w2}) water-limited yield potential (dashed lines). We hypothesize that high yield stability (low

plasticity) correlates with larger yield gaps in high yielding environments. Solid lines are the actual yield for high (blue) and low (red) yield plasticity cultivars. (B) Hypothesis 2: resistant (+R) phenotypes have smaller yield gaps under conditions favoring stripe rust development and larger gaps under absence of disease conditions than susceptible (−R) phenotypes. (C) Hypothesis 3: Distributions of the slope of yield versus yield plasticity (see panel A) and the yield difference between resistant (+R) and susceptible (−R) phenotypes to stripe rust (also shown in panel B), with (green) and without (blue) fungicide application. In C, stripe rust-resistant phenotypes will have smaller yield gap compared to susceptible counterparts when unprotected (blue) and *vice versa* when protected (green) with foliar fungicide. 135

Figure 5.2. Spatial distribution of the factorial trials combining 20-55 winter wheat cultivars and two management intensities. Experiments were replicated in 21 location-seasons with some locations hosting trials during more than one season; location-season codes are explained in Appendix Table E.1. Color codes indicate soil series..... 136

Figure 5.3. Principal component analysis for environmental variables: biplot (A) and variance contribution within dimension (B) in experiments carried out in the Great Plains between 2014 and 2021. Abbreviations: Mean temperature (Tmean), vapor pressure deficit (VPD), photothermal quotient (PQ), incident solar radiation (SR), plant available water at sowing (PAWS), total seasonal water supply including seasonal rainfall and PAWS (WATER), precipitation (PP), number of days with temperatures between 7 and 12 °C between GS 25 and GS 31 (DT712_GS_25_31), number of days with rainfall between GS 25 and GS 31 (DWRF_GS_25_31), accumulated rainfall between GS 25 and GS 31

(PRECIP_GS_25_31), critical period (CP) and grain filling period (GF). Prefix “s”

indicates seasonal averages of environmental variables. 137

Figure 5.4. Relationship between grain yield and yield phenotypic plasticity (unitless) for winter wheat grown in 20 location-seasons in the Great Plains under intensive (yellow) and standard (purple) management intensity. Dashed line represents the water-limited yield potential Y_{wj} (Eq. 4) in each location-year. Solid lines represent the mean and ribbons the 95% credible interval of the posterior predictive distribution of grain yield, presented in Equations 2 and 3. The slope of the relationship between yield-yield plasticity represents parameter β_{1jk} in Eq. 3.6. Panels are ordered from top left to bottom right according to Y_w 138

Figure 5.5. (A) Relationship between water-limited yield potential and actual yield for cultivars with high (solid lines; cultivar: `WB4303`; plasticity = 1.45) and low (dashed lines; cultivar: `Double Stop CL+`; plasticity = 0.42) yield phenotypic plasticity under intensive (yellow lines, circles) and standard (purple lines, squares) management. (B) Relationship between the probability of an improved plasticity x management combination yielding more than the baseline (low plasticity, standard management). In B, dashed line is the threshold of 0.9 probability of greater yield with improved plasticity x management combination, while arrows indicate the Y_w at the intersection with posterior probability = 0.9. (C) Comparison of water-limited yield potential (Y_w , grey bars expressed in $Mg\ ha^{-1}$) and actual yield for cultivars with contrasting yield plasticity (cultivars are `WB4303`, high plasticity and `Double Stop CL+`, low plasticity) and management. In A, lines represent the mean of the actual yield; points are a 10-draw sample of $\mu_{ijk|y}$; inset legend show the mean and the 95% credible interval of the slope of the relationship between Y_{wj} and $\mu_{ijk|y}$; solid black

line represents the 1:1 line. In B, Y_w is expressed in $Mg\ ha^{-1}$ and labels in shaded areas are the expected yield gap for a given G x E x M management combination, whiskers are the 95% credible intervals around the mean. Abbreviations: water-limited yield potential (Y_w), management intensity (M), standard (Std) and intensive management (Int)..... 139

Figure 5.6. Contributions of management intensification and stripe rust resistance to yield gap under responsive (left) and unresponsive (right) environments to stripe rust resistance. Colored bars represent the mean and whiskers the standard deviations for each combination of environment, management and stripe rust resistance. Grey bars are the mean Y_w , while whiskers are the standard deviations of Y_w . The numbers on top of the bars shows the average yield gap, expressed in percentage units. Abbreviations: management (M), intensive (Int), standard (Std), stripe rust resistance (Yr), resistant phenotype (RES), susceptible phenotype (SUS). 140

Figure 5.7. (A) Comparison of observed yield response to stripe rust resistance and response predicted with model. Model assumes that the yield response to stripe rust resistance (i.e., yield difference between resistant and susceptible cultivars) is associated with management and environmental factors described in Equation 8. Contour plots show the probability of greater yields with resistant (RES) vs susceptible (SUS) phenotypes under varying rainfall days and days with daily mean temperatures between 7°C and 12°C between GS 25 and GS 31 under intensive (B) and standard (C) management intensity. Dashed lines in B and C represent the iso-probability lines. 140

Figure 5.8. Relationship between the slope of yield versus yield plasticity and yield difference between resistant and susceptible phenotypes to stripe rust. Each point represents the expected value for an E x M combination and whiskers are the 95% credible interval.

Management combinations were a grower standard practice (purple) and intensive management (brown) adding of N and fungicide. Bold labels in each quadrant indicates the combination of yield plasticity x stripe rust resistance that produced the highest yield in each E x M combination. Side boxplots show the distribution of the responses to plasticity (top), and to stripe rust resistance (right). 141

Figure 6.1. Hypothetical relations across sectors on the wheat industry. Top panel A is business as usual, where limited information flow across sectors exists. Bottom panel B is the scenario under enhanced collaboration towards common sustainability goals across sectors. 157

Figure 6.2. A) Network reflecting common and unique elements in the definitions of sustainability across stakeholders in the wheat network industry. Node sizes are relative to the number of times a concept appeared while tie weights are relative to the number of times two concepts appeared together in a definition. Colors indicate the number of sector where the same concept appeared, a sector was counted if at least one participant included the concept within the definition. Agreement across sectors (yellow) was assumed when the concept was included in at least five or six industry sectors. Sectors are: i) wheat breeding, ii) wheat agronomy, iii) input supply, iv) wheat growers, v) milling and baking industries and vi) retail and consumers. B) Association between tie weights and number of concepts conforms to a power law. Open symbols represent the association resulting from analysis of the unbiased answers, written by participants before they interact in table discussions, upon arrival at expert elicitation. Closed symbols represent the association resulting from biased answers written at the end of the two-day expert elicitation. P-value represents the significance of the comparison of the exponential slope of biased and unbiased sustainability definitions. 158

Figure 6.3. Sustainability assessment framework resulting from surveying a group of 46 wheat industry network experts. Sustainability indicators were filtered to the top five from the raking exercise on paired comparisons in each sector x dimension combination. Checkmark indicates that a specific sector within the network selected the indicator as relevant. Points represent percent votes of that given indicator compared to others indicators within each sector x dimension combination.	159
Figure 6.4. Distribution of rankings of sustainability indicators for sector agreement clusters. Colors indicate the number of sector where an indicator appeared. When an indicator was raised by five or six sectors it was classified as “all sectors”. Sectors are: i) wheat breeding, ii) wheat agronomy, iii) input supply, iv) wheat growers, v) milling and baking industries and vi) retail and consumers.	160
Figure 6.5. A) Current challenges in the wheat industry network limiting development of sustainable brand bread. B) Network of associations among wheat industry stakeholders under implementation of strategies for bread with sustainability stamp.	161

List of Tables

Table 1.1. Comparison of mean yield ($\pm$ s.d.) and mean grain protein concentration GPC ($\pm$ s.d.) of wheat in basal N and late N crops. PWC is the number of pairwise comparisons; Env. is the number of environments; wheat type is D (durum wheat), W (winter bread wheat), S (spring bread wheat). Studies are arranged according to the mean yield of the basal N treatment in each study. n.a.: data not available.	26
Table 2.1. Year, location, soil type, geolocation, crop husbandry, and mineral soil N (0-0.6 m) at sowing in eight location-seasons. Fungicide was applied at GS65. Abbreviation: DAS, days after sowing.....	56
Table 2.2. Characteristics of the 14 winter wheat commercial cultivars included in the study: year of release, average protein deviation, maturity, plant height, drought tolerance and standability. Phenotypic plasticity (unitless), calculated as variance ratio (Eq. 1), is shown for yield, its components, grain protein concentration, and crop N traits. Abbreviations: year of release (YOR), grain protein deviation from the grain yield ~ grain protein regression line (GPD), maturity (MAT, 1 = early; 5 = medium; 9 = late), plant height (PH), drought tolerance (DT, 1 = excellent; 5 = good; 9 = poor straw strength: 1 = excellent; 5 = good; 9 = poor), standability (Sta), harvest index (HI), N uptake (Nup), N harvest index (NHI), N utilization efficiency (NUtE). *sources: https://bookstore.ksre.ksu.edu/pubs/mf991.pdf ; http://www.ramwheatdb.com/database.php	57
Table 2.3. Analytical solutions implemented for identifying the starting point of the phases described in Figure 2 and fitted in Figure 5. In phase III, only those cultivars that reached maximum protein were compared. Abbreviations: N supply (N_s).....	58

Table 4.1. Genes associated with yield phenotypes in a 20kb window centered on each SNP

above the $-\log_{10}(P) = 3.0$ threshold. Genes were described using the Chinese Spring (CS)

reference genome RefSeq v2.1 (Zhu et al., 2021). Abbreviations: chromosome (Chr.), base

pairs (bp). 115

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Dedication

—To those who believed in me since my very first steps in crop science.

—To my grandfather, Bocha.

Preface

Within the list of cultivated crops in the Neolithic some 10,500 years ago lies two ancestors (emmer wheat - *Triticum dicoccum* L., einkorn wheat - *Triticum monococcum* L.) of wheat (*Triticum aestivum* L., Abbo et al., 2022). Since the onset of domestication of plants in the northern Levant (N Syria, SE Turkey) the area cultivated to wheat spanned enormously, ranging from 67° N in Scandinavia and Russia to 45° S in Argentina (Shewry, 2009). At present times, wheat covers 9.1 % (244 M ha) of the area planted to crops on Earth across 200 countries (FAO, 2024) providing 20% of calories to worldwide population and 20% of proteins in the human diet in underdeveloped countries (Shewry and Hey, 2015) becoming crucial to food security.

Trends indicate wheat production is increasing 1.1% *per annum* or stagnated in some regions, running behind the projected 1.7% *per annum* wheat demand increase for 2050 (Agcaoili and Rosegrant, 1995). There is strong agreement throughout the scientific community that matching increasing food demand must come from crop yield increases without further expansion of current cropland area (Cassman and Grassini, 2020). Further points of consensus highlight that, crop yield, its nutritional value and environmental performance metrics are key to long-term success (Cassman and Grassini, 2020).

The prevailing framework determines phenotypic variance in grain yield and quality as a result of a combined set of interactions among the genotype, the environment, agronomic management and some “residual error” (Messina et al., 2009). Sadras and Hayman (2025) advance on a developmental perspective suggesting, that the causal unidirectional arrow from genotype, environment and management interactions driving the phenotype overlooks the effects of the phenotype on the genotype, the environment and management. Strategies for wheat yield and quality improvement must come from research questions and hypotheses formulated within

the notion of the existent quadruple interaction of the phenotype, genotype, environment and management.

This dissertation explores avenues for wheat yield and quality improvement in regional (Great Plains, United States) and global scales. Throughout five individual chapters I collaborate with experts from diverse backgrounds to formulate questions and hypotheses that fall within the ‘Pasteur’s quadrant’ (Stokes, 1997). Implications and benefits from our findings are (i) discussed from the perspective of adjoining levels of the biological organizational scale surrounding the wheat crop phenotype (N, N-1, N+1 in Passioura, 1979) and, (ii) are of interest to a wide range of actors across the wheat industry and society.

Chapter 1 - Late-season nitrogen application increases grain protein concentration and is neutral for yield in wheat. A global meta-analysis

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Abstract

Late-season nitrogen (N) application has been proposed to boost grain yield and grain protein concentration (GPC) in cereals; however, its effects on bread and durum wheat have been inconsistent in field experiments. We performed a meta-analysis to (i) assess the effect of N applications to wheat after flag leaf visible (GS 37) on grain yield and GPC; and to assess the variation in these responses with (ii) N fertiliser management, (iii) environmental factors, and (iv) physiological traits. We searched ‘*Agronomy Journal*’, ‘*Crop Science*’, ‘*European Journal of Agronomy*’, and ‘*Field Crops Research*’ for articles published between 1980 and 2021 that allowed for a direct comparison of wheat yield and GPC between N application after GS 37 to an otherwise equally managed crop that received basal N fertilisation. We also collected other traits such as stover biomass and N uptake at plant maturity, and dough rheological properties, when available. The search resulted in 38 articles that, in addition to one unpublished trial from our group, evaluated 542 pairwise comparisons in 127 environments. Across studies, grain yield ranged from 1.15 to 10.63 Mg ha⁻¹ and showed a negative relation with GPC, which ranged from 65 to 189 g kg⁻¹. Late-season N fertilisation was neutral for grain yield (I^2 , proportion of the overall variance due to variation in real effects rather than chance, 26.2%) and increased GPC

with a pooled estimate of 3.96%. The response of GPC was heterogeneous ($I^2 = 84\%$), suggesting the need for exploration of potential moderators of the response. Meta-regression suggested that increasing the proportion of late N relative to the total available N positively associated to increases in GPC, and the residuals of this analysis suggested that later applications increased GPC response, with no effect of N fertiliser source or placement. Environments with low temperature, high photothermal quotient, and long duration of the critical period associated with greater GPC response to late-season N applications. The relative response of GPC to late fertilisation correlated with the relative response of both stover N uptake and nitrogen concentration in stover at maturity, but not with stover biomass at maturity. Alveogram index and dough extensibility increased when late-season N increased GPC. Enhancing GPC through late N applications should consider associations between management, environmental, and physiological factors. Future research should focus on forecasting GPC response to late N, based on GPC response drivers identified in the current research.

Abbreviations: grain protein concentration (GPC), nitrogen (N), growth stage (GS), late-season applied nitrogen (late N), ammonium nitrate (AN), ammonium sulphate (AS), slow release urea (SRN), urea ammonium nitrate (UAN), critical period (CP), grain filling period (GF).

1.1 Introduction

Nitrogen supply is critical for wheat (*Triticum aestivum* L., *T. durum*) yield and grain end-use quality (Hawkesford, 2014; Blandino et al., 2015; Zörb et al., 2018). Matching N supply with crop N demand can reduce the risk of both release of reactive nitrogen onto the environment and soil mining (Alvarez et al., 2014; Angus et al., 2017). Late N fertilisation, hereafter referring to N applications after flag leaf visible (GS 37; Zadoks et al., 1974), can provide N when crop yield, a major driver of N requirement, could be more accurately predicted (Raun and Johnson,

1999), N deficient zones within fields could be detected allowing for variable N rate (Raun et al., 2005), and the root system is fully developed thus promoting higher N uptake and N recovery efficiency (Foulkes et al., 2009). Therefore, it is crucial to assess the effect of late N application on grain yield and grain protein content (GPC), and the influence of management, physiological, and environmental factors on this effect.

Late N application can increase N availability and crop N uptake after flowering, and thus relax the negative relation between grain yield and GPC (Monaghan et al., 2001b; Kichey et al., 2007; Bogard et al., 2010). A wheat crop at anthesis (GS 61; Zadoks et al., 1974) can typically accumulate 70-90% of the seasonal N uptake (Salvagiotti et al., 2009; Kong et al., 2013); however, this amount can range from 100% to less than 50% (Slafer et al., 1990; Abreu et al., 1993; Lollato et al., 2021), suggesting a need to identify opportunities in which late N application would be more likely to enhance post-anthesis N uptake and improve grain yield and quality.

Most of the literature reports little to no yield response to N fertilisation around anthesis (Altman et al., 1983; Woolfolk et al., 2002; Blandino et al., 2015; Lollato et al., 2021), but there are exceptions. For example, Rossmann et al. (2019) reported yield increases with N fertilisation at anthesis in two out of six genotype $\times$ N rate combinations. Wuest and Cassman (1992) documented significant wheat yield response to soil-injected N at anthesis under irrigation. While these yield increases may relate to post-anthesis weather conditions modulating N uptake (*e.g.*, Lollato et al., 2021), the conditions for yield response to late-season N have not yet been characterised. Late-season N fertilisation generally increases wheat GPC and quality (Blandino et al., 2015; Cruppe et al., 2017; Lollato et al., 2021); however, GPC response to late-season N depends on management practices (Finney et al., 1957; Woolfolk et al., 2002; Bly and Woodard,

2003; Cruppe et al., 2017), plant N status at anthesis (Varinderpal-Singh et al., 2012), and to a greater extent, the environmental conditions after anthesis (Triboi, 2003; Bogard et al., 2010).

Meta-analyses provide robust inference of effect sizes on a broad range of environments and agronomic practices (Fernandez et al., 2020; Quinn et al., 2020). Previous meta-analyses focused on the effects of late-season N applications on maize (*Zea mays* L.) yield (Fernandez et al., 2020), and splitting N doses across the crop cycle of wheat (Hu et al., 2021). Because late-season N applications can increase N use efficiency and minimize net N losses (Hawkesford, 2014), quantifying its global impact can contribute towards more sustainable wheat production. Therefore, our aim was to perform a meta-analysis of the effect of N applications after GS 37 to wheat grain yield and GPC, and to assess the variation in this effect with N fertiliser management, environmental factors, and physiological traits.

1.2 Method

1.2.1 Database construction

We searched the literature that assessed the effects of late-season N application in wheat after the Green Revolution (between 1980 and February 2021, both inclusive). We screened for articles published in *Agronomy Journal*, *Crop Science*, *European Journal of Agronomy*, and *Field Crops Research*. Additionally, data from one unpublished trial from our research group was added to the database as it met all criteria (see below). We note that using unpublished data can help avoid publication bias (McLeod and Weisz, 2004).

The literature search was performed in February 2022 introducing the following search query (Eq. 1) in Scopus database:

$$\begin{aligned} &SOURCE - ID(78796 OR 59988 OR 38753 OR 15639) AND \\ &TITLE - ABS - KEY((wheat OR nitrogen)AND(yield OR protein)) AND \end{aligned} \quad (1)$$

PUBYEAR > 1980,

where SOURCE-ID contains a list of numeric codes that uniquely identify the four target journals, TITLE-ABS-KEY section would return documents where the words ‘wheat’, ‘nitrogen’, ‘protein’ or ‘yield’ appear in the title, abstract or keywords; and PUBEAR term filtered data for articles published after 1980. Along the search query, boolean operators (“AND”, “OR”) and parenthesis were used for transparency and replicability. The search resulted in 5,734 publications. We used the *revtools* package available in R Studio software (Westgate, 2019) for logging and archiving collected articles as we applied specific criteria for manuscript inclusion, summarised in Figure 1.1.

Criteria for manuscript inclusion in the final database were:

- (i) Studies evaluating N applications before and after GS 37 that allowed for a direct comparison of the late-season N application *versus* a *ceteris paribus* treatment (we excluded observations that did not generate a pairwise comparison);
- (ii) Grain yield and/or GPC were measured from a minimum area of 0.2 m² and either directly reported or reported in a manner that allowed trait calculation;
- (iii) Data were from field studies without manipulation of atmospheric CO₂ concentration, radiation, or ambient temperature;
- (iv) The timing of N application was clearly defined using well-known cereal developmental scales e.g., Zadoks or Feekes (Large, 1954);
- (v) Experiments were conducted under appropriate agronomic practices (e.g., pest and weed incidence were not limiting factors).

Our screening criteria returned 38 articles that, together with our unpublished dataset, comprised 542 pairwise comparisons for grain yield and 496 for GPC. The unpublished data

only accounted for 5% of yield and 6% of GPC in the final database. Studies were mostly conducted in North America ($n = 18$) and Europe ($n = 13$), with fewer in Oceania ($n = 3$) and Asia ($n = 3$), and a single study in South America (Figure 1.2).

We classified grain yield and GPC observations according to the timing of N application: under the category ‘basal N’ for treatments in which N was applied before GS 37 and ‘late N’ when the basal N treatments was complemented with an application at or after GS 37. Using the same criteria, we collected data on N fertiliser management (Section 2.2), environmental variables (Section 2.3), and physiological traits (Section 2.4) to further examine the impacts of late N on these variables and their associations with yield and GPC. When available, we also collected data on dough rheological properties (Section 2.5) to explore their responses to late N fertilisation.

1.2.2 Nitrogen management

We considered three N sources to calculate total N available for the crop (TN): late N rate (LNR), early N rate (ENR), and N – NO₃ available in the soil profile at sowing:

$$TN(\text{kg N ha}^{-1}) = N - \text{NO}_3(\text{kg N ha}^{-1}) + \text{ENR}(\text{kg N ha}^{-1}) + \text{LNR}(\text{kg N ha}^{-1}). \quad (2)$$

This approach does not consider N mineralised from organic matter during the season. The quotient between LNR and TN was calculated and used hereafter as ‘proportion of late N’. We categorised the main aspects of N fertiliser management, such as placement, source, and timing of application. Nitrogen fertiliser sources reported in the articles were ammonium nitrate (AN), ammonium sulphate (AS), granulated urea, manure, slow-release urea (SRN), urea-ammonium nitrate (UAN) or other (specific commercial mixes and non-reported late N sources). Timing of application was evaluated using the Zadoks scale, and placement was either foliar

(sprayed with broadcast flat fan nozzles) or soil-applied (broadcast solid fertilisers, liquid fertilisers applied with streamer bars, or injected).

1.2.3 Environment

Weather data were collected from studies that reported the geocoordinates of the field experiment, application dates, and GPC for each environment evaluated. From the subset of studies meeting the criteria for analysing the influence of environmental indicators ($n = 13$ studies), 248 GPC pairwise comparisons were retrieved from 54 environments. Weather patterns were characterised for (i) the period between -300°Cd to $+100^{\circ}\text{Cd}$ ($^{\circ}\text{Cd}$, degree days) centred on late N application date using a base temperature of 4.5°C (Fischer, 1985; Cossani and Sadras, 2021), as a surrogate for the critical period for yield determination, and (ii) the period from $+100^{\circ}\text{Cd}$ to $+600^{\circ}\text{Cd}$ after late N application using a base temperature of 0°C , as a surrogate for the grain filling period as N accumulation typically stagnates after approximately 600°Cd after anthesis (Dupont et al., 2006). These analyses were centred on application dates rather than anthesis dates because applications were performed usually near anthesis (Appendix Figure A.1) and anthesis dates were not always available. Weather data were retrieved from NASAPOWER (Sparks, 2018), and summarised for each period using the *agromet* code in R (Correndo et al., 2021a). A single weather data source across experimental sites worldwide since 1981 avoids bias from multiple sources. While individual NASAPOWER daily data for precipitation may differ from ground weather stations, pooling the data over longer periods result in acceptable representations of the ground proof data (Van Wart et al., 2013). Daily weather data retrieved included solar radiation, minimum and maximum temperature, and precipitation. From these, we calculated mean temperature, photothermal quotient, cumulative precipitation, and period duration (days) for both periods.

1.2.4 Physiological traits

A subset of the original data allowed for comparisons of maturity N uptake and stover biomass ($n = 149$ and 117 pairwise comparisons), from which we derived stover N uptake ($\%N_{UP}$, *Eq 3*), stover N concentration ($\%N_S$, *Eq 4*), and stover biomass (S_B , *Eq 5*) as:

$$N_{UP} = WP_{Nup} - (N_f \times YLD), \quad (3)$$

$$\%N_S = \frac{N_{UP}}{WP_B - YLD}, \quad (4)$$

$$S_B = WP_B - YLD, \quad (5)$$

where WP_{Nup} is the whole plant N uptake, N_f is the fraction of N in the grain, YLD is grain yield, and WP_B is the whole plant biomass; all on a dry basis. Grain N was obtained from GPC, assuming 5.7 units of protein per unit N (Sosulski and Imafidon, 1990).

1.2.5 Dough rheological properties

A subset of studies ($n = 5$, 59 pairwise comparisons) allowed for assessing the effects of late N fertilisation and GPC on dough quality, including data of dough extensibility (L), tenacity (P), dough extensibility-tenacity ratio (P/L), and alveogram index (W).

1.2.6 Data curation and quality control

When data were not reported in tables, we either retrieved them from figures using ‘Web Plot Digitizer’ (<https://apps.automeris.io/wpd>), or directly from the study authors. We then implemented formulas to convert reported data into effect size and measures of variance that could be handled by meta-analytic models. Finally, we used multiple imputation techniques (Ellington et al., 2015) to estimate missing standard deviation (SD) values when none of the previous steps succeeded. Briefly, this multiple imputation technique selects the missing values to be imputed from a distribution derived from the relationship between variables without

missing data. Across the database, 38% of the SD data were missing, and consequently imputed using the *mi* package in R. This process generated 1,000 imputed datasets and selected their average (Ellington et al., 2015; Nakagawa and Freckleton, 2011).

To assess data quality and consistency, we searched for influential studies using Cook's Distance procedures (Viechtbauer and Cheung, 2010). A study was considered a strong influencer in the fitted model when its Cook's D was three times greater than the average (Stephanie, 2016). This leave-one-study-out diagnosis suggested that no studies in our database exerted a strong influence in our pooled effects model, highlighting the robustness of our data. However, when we modelled the relation of GPC response and the proportion of late N, two studies (Hooper et al., 2015; Corassa et al., 2018) strongly influenced the model, so we set their weight to zero.

1.2.7 Data analysis

The response to late N was summarised in effect sizes and calculated as the natural logarithm of the response ratio between treatments that received late N and the corresponding basal N treatment that received otherwise the exact same agronomic management (Eq. 6). The natural logarithm linearizes the metric of the response ratio, and treat both groups equally so that deviations in the basal N group are equivalent to those in the late N group rendering the observed outcome independent of and unaffected by the metric of the observed values (Hedges et al., 1999). For easiness of interpretation, when possible, we calculated the proportional effect in the late N group relative to the basal N group as in Eq. 7.

$$\ln RR_i = \ln \left\{ \frac{\bar{X}_{\text{Late N}}}{\bar{X}_{\text{Basal N}}} \right\}, \quad (6)$$

$$\text{Late N Effect (\%)} = \left\{ \frac{\bar{X}_{\text{Late N}}}{\bar{X}_{\text{Basal N}}} - 1 \right\} * 100, \quad (7)$$

where $\bar{X}$ is the trait of interest, including grain yield, GPC, stover N uptake, stover N concentration, stover biomass, dough extensibility, dough tenacity, dough extensibility-tenacity ratio and alveogram index. Effect sizes were weighed according to w_i (Eq 8), which is the inverse of the pooled sampling variance v_i (Eq 9) between the two groups, as follows:

$$w_i = v_i^{-1}, \quad (8)$$

$$v_i = \frac{SD_{LN}^2}{n_{LN}\bar{X}_{LN}} + \frac{SD_{BN}^2}{n_{BN}\bar{X}_{BN}}, \quad (9)$$

where $\bar{X}$ represents the mean, SD the standard deviation and n the sample size for the late N (LN) or basal N (BN) group. Model parameters, confidence intervals, and p -values were obtained with bootstrapping techniques and selecting the 2.5 and 97.5% quantiles from a resample distribution of 10,000 iterations (Adams et al., 1997). Significance of model coefficients was determined from a resample distribution of omnibus tests p -values.

The overall associations between late N, yield, and GPC, were assessed by fitting an intercept-only model representing the overall effect of late N across multiple environmental and management conditions (Eq. 10). This model accounted for genotype $\times$ environment $\times$ management interactions and variation between studies. Thus, the variance component was divided in three sources: (i) between studies, (ii) between environments, and (iii) genotype $\times$ management combination. The model was then expressed as:

$$\widehat{\theta}_{ijk} = \beta_0 + \zeta(1)i + \zeta(2)ij + \zeta(3)ijk + \epsilon_{ijk}, \quad (10)$$

where $\widehat{\theta}_{ijk}$ is the estimated effect on the k^{th} genotype $\times$ management combination nested within the j^{th} environment, in the i^{th} study. β_0 is the intercept representing the overall population effect. The parameters $\zeta(1)i, \zeta(2)ij, \zeta(3)ijk$ represent the between studies, environments, and genotype $\times$ management variance components, and ϵ_{ijk} accounts for the residual variation. These models

deal with interdependency of effect sizes, as sometimes the basal N treatment was shared among different effect size observations (Assink and Wibbelink, 2016).

1.2.8 Drivers of the response to late N

Test for residual heterogeneity determined whether there was significant variance between effect sizes for potential drivers of the response to late N. Heterogeneity reveals the level of inconsistency between studies, environments, and management combinations, and can be represented through the I^2 statistic (Higgins and Thompson, 2002). The I^2 represents the proportion of the overall variance that is due to variation in real effects rather than chance (Borenstein et al., 2017). Higgins (2003) quantified heterogeneity as low, moderate, or high, when the I^2 is 25%, 50% or 75%, respectively. For high I^2 , we tested potential moderators improving the predictability of the response in multiple univariate models (to avoid multicollinearity). Moderators included the effects of N fertiliser management (Section 3.3), environmental variables (Section 3.4), and physiological traits (Section 3.5) associated with the responses to late-season N. Analysis of residuals was used for testing the late N management practices independently of the proportion of late N. Thus, residuals were calculated as the difference between the fitted line and the actual GPC response from the proportion of late N and GPC response meta-regression model.

We used principal component analysis (PCA) to identify weather variables that explained most of the response to late N fertilisation. Weather variables were introduced into K-means clustering algorithm, which separated each weather variable into two groups “Low” and “High” depending on their mean in each respective cluster. Clusters were defined by ensuring that the within group variance was minimised and the between group variance was maximised, ensuring the balance between groups. Finally, we tested the effect of each cluster in a multi-level meta-

analytic model (Borja Reis et al., 2021), with between studies variance as the only variable in the random component. For assessing the effects of N uptake and related physiological traits, and dough rheological properties, we implemented standard major axis (SMA) regression models to account for errors in x and y variables (Warton et al., 2006).

1.3 Results

1.3.1 Overview

The final database spanned from the 1979-80 to the 2019-2020 cropping season. About 87% of the studies evaluated bread wheat (85% winter wheat and 15% spring wheat) and 13% evaluated durum wheat (Table 1.1). The studies evaluated a broad diversity of late N management scenarios: Timing of late N application ranged from GS 37 to GS 71; urea and UAN fertilisers accounted for 53% of the studies while the remaining 47% was equally split into sources such as AN, AS, SRN, manure and others. Fertilisers were applied either as foliar- (66%) or soil-applied (44%). Late N fertiliser rates ranged from 0.45 to 100 kg N ha⁻¹, averaging 33 kg N ha⁻¹.

Yield varied from 1.23 to 10.63 Mg ha⁻¹ (mean = 4.38 Mg ha⁻¹) in crops receiving basal N fertilisation, and from 1.15 to 10.63 Mg ha⁻¹ (mean = 4.43 Mg ha⁻¹) in late N fertilised crops (Figure 1.3A). Grain protein concentration ranged between 65 and 176 g kg⁻¹ (mean = 126 g kg⁻¹) in basal N group and from 78 to 189 g kg⁻¹ (mean = 133 g kg⁻¹) in late-fertilised crops (Figure 1.3A). Across all sources of variation, GPC decreased with increasing yield at the same rate for basal N and late N crops (Figure 1.3B); analysis of residuals showed late N fertilisation increased GPC by 7 g kg⁻¹ at a given yield (inset Figure 1.3B).

1.3.2 Overall impact of late-season N on wheat grain yield and grain protein concentration

Across all sources of variation, late N fertilisation did not affect grain yield (Figure 1.4). Pooled estimated effect on yield averaged 1.58% and ranged from -0.21 % to 3.53 %. The analysis of residual heterogeneity showed that inconsistencies from real effects accounted for 26% of the unaccounted variability by the model, resulting in a low I^2 . Due to the low level of inconsistency, there were low probabilities of finding factors that could potentially further explain yield response to late N.

Late N fertilisation increased GPC ($p < 0.001$), with a pooled effect of 3.96% ranging from 1.21% to 6.63% (Figure 1.4). Grain protein concentration response to late N tended to be higher at greater yield levels ($p = 0.15$, $r = 0.19$) (Figure 1.4, Appendix Table A.2), and was negatively correlated with GPC environment (defined by the GPC of the basal N crop; $p = 0.06$, $r = -0.43$) (Appendix Table A.2). However, there was substantial heterogeneity in the response ($I^2 = 84\%$), indicating a high inconsistency across studies, environments and genotype $\times$ management combinations ($p < 0.01$), warranting further exploration of the factors driving GPC response to late N fertiliser.

1.3.3 Fertiliser management affected GPC response

Grain protein concentration increased linearly with the proportion of late N (Figure 1.5A). Residuals of this analysis indicated that the GPC response was positively associated with the timing of N application (97.5% quantile of the distribution of bootstrapped p -values = 0.09) when independent of the proportion of late N (Figure 1.5B). Likewise, analysis of residuals indicated that GPC response to late N was independent of fertiliser placement (Figure 1.5C).

Grain protein concentration response to late N did not vary with the source of fertiliser (Figure 1.5D).

1.3.4 Environmental descriptors of GPC response to late-season N

The first dimension of the PCA explained 54% of the total variation and was mainly characterised by variations in Tmean, PQ, and period duration (days) (Figure 1.6A, Figure 1.6B). Precipitation in both critical and grain filling period were the greater contributors to total variance in the second dimension (21%). Higher GPC response to late-season N was more common in environments where the critical period had low temperature, high PQ, and long duration (Figure 1.6C). Significance of the means comparisons are provided in Appendix Table A.1. There were no clear trends for the environment during grain filling period modulating GPC response to late-season N (Figure 1.6C). Cumulative precipitation did not show clear patterns in any period.

1.3.5 Physiological drivers of the GPC response to late season N

The relative response of GPC to late N fertilisation (Eq. 6) correlated with the relative response of both stover N uptake and stover N concentration at maturity, but not with stover biomass at maturity (Figure 1.7).

1.3.6 Dough rheological properties response to GPC due to late-season N fertilisation.

Dough extensibility and alveogram index correlated positively with GPC response to late N, and dough tenacity and dough extensibility-tenacity ratio were unrelated to the response of GPC (Figure 1.8).

1.4 Discussion

1.4.1 Late-season N application impact on wheat grain yield and protein concentration

Our analysis highlighted that late N application was neutral for grain yield in wheat, as reported with few exceptions in individual studies (Altman et al., 1983; Bly and Woodard, 2003; Dick et al., 2016; Cruppe et al., 2017). The lack of yield response in wheat could relate to the high proportion of seasonal N uptake by anthesis (Palta and Fillery, 1995; Martre et al., 2006; De Oliveira Silva et al., 2021; Lollato et al., 2021). In contrast, yield response to late fertilisation seems more likely in maize (Fernandez et al., 2020) that only absorbs 45-65% of the total seasonal N during vegetative stages (Rajcan and Tollenaar, 1999; Gallais and Coque, 2005; Gastal et al., 2015b). Under the experimental conditions of Blandino and Reyneri (2009), late N applied in combination with a foliar fungicide at anthesis increased both yield and GPC in wheat. Brown and Petrie (2006) reported that delayed N application increased yield of irrigated wheat only when low rates of N were applied before sowing, in two out of three years. One commonality among the studies reporting yield response to late N application was enhanced kernel weight (Brown and Petrie, 2006; Blandino and Reyneri, 2009a), reinforcing the limited potential of this practice to consistently improve yield as kernel weight is usually not a strong determinant of wheat yield as compared to kernel number (Slafer et al., 2014, 2022). Additionally, because late-season N is often applied with a foliar fungicide, which is shown to increase kernel weight (Jaenisch et al., 2019; Cruppe et al., 2021a; Jaenisch et al., 2022), factorial experiments are needed to separate the effect of late N, fungicide, and their interaction.

We showed that GPC is usually responsive to late fertilisation, but benefits are subject to complex environment $\times$ management interactions. In common with many studies, we found a

negative relationship between GPC and yield (Figure 1.3) (Calderini et al., 1995; Triboi et al., 2006; Jaenisch et al., 2019; Lollato et al., 2019a). Contrary to our initial expectation, late-season N fertilisation did not modify the slope of the relationship; instead, increased GPC by 7 g kg⁻¹ at a given yield. However, the degree of GPC response to late N depended upon both yielding and GPC environment. From the positive association between yield environment and GPC response to late N (Appendix Table A.2), we could have expected a flatter relation between GPC and yield in late-fertilised crops. The negative association between GPC response and GPC environment can account for unexplained variation in the relation among GPC response and yield environment. We acknowledge that, even though the GPC response and GPC environment are not fully independent variables, basal N and late N crops resulted in similar coefficients of variation (cv = 18 and 16%). Additionally, as GPC response is expressed in a log scale, there is a low risk of spurious relations (Brett, 2004).

1.4.2 Influence of late season N management on GPC response

The proportion of late N applied after GS 37 over the total N available for the crop in the season reflects variation in both early season N supply (i.e., the soil N-NO₃ availability plus the basal N fertilisation) and late-season N rate. Different early-season N fertilisation regimes can trigger a wide variety of plant N status at the time of late N applications. Triboi and Triboi-Blondel (2002) demonstrated that N-deficient plants at anthesis had a greater N demand and thus, greater post-anthesis N uptake. Barneix (2007) proposed that the concentration of phloem free amino acids works as an indicator of plant N status, having a negative feedback regulation on activity of NO₃⁻ transporters, and thus reducing N absorption. However, N-status and consequent N uptake does not necessarily correlate with GPC to delayed N applications, which can be observed in the wide dispersion of our data (Figure 1.5A). This was highlighted by

Arregui et al. (2006) who identified a N-status threshold at GS 45 to predict GPC, and a poor correlation between GPC and chlorophyll meter readings after pollination when environmental influences dominated. Both the duration of grain filling and post-anthesis N uptake influence GPC (Bogard et al., 2010), as both processes are highly responsive to water deficit and heat stresses (Triboi, 2003), which are typical in many wheat growing regions (Sadras et al., 2006, 2022; Chenu et al., 2011; Lollato et al., 2020; Couëdel et al., 2021).

Our study indicated that GPC response was greater when N was applied later in the crop cycle within the GS 37 to 71 window (Figure 1.5B), in comparison to individual studies showing variable responses. For instance, Bly and Woodard (2003) found that fertilisation after anthesis increased GPC in comparison to fertilisation at booting in three out of six environments. Finney et al. (1957) found that applications right after anthesis showed greater GPC response than applications before anthesis in a two site-year study. On the other hand, Woolfolk et al. (2002) concluded from a six site-year study that grain N was equally increased when N was applied either before or after flowering. Our review provides evidence from combined studies ($n = 39$) and environments ($n = 121$) to support higher GPC response with later application between GS 37 and GS 71, irrespective of the proportion of late N.

Foliar fertilisation improved GPC more consistently than soil fertilisers but results were heterogeneous. Nitrogen uptake from foliar fertiliser does not depend on rainfall, providing advantages particularly in environments where decreased post-anthesis water supply may compromise soil N uptake. Blandino et al (2020) found no differences in GPC between foliar and soil fertilisation in humid Mediterranean environments. The addition of sulphur can partially explain trends in favour of higher GPC response to ammonium sulphate, by consequence of positive N by sulphur interaction (Duncan et al., 2018) that can have significant effects on N

assimilation and translocation to the grain (Tea et al., 2007; Salvagiotti et al., 2009). In addition, Salvagiotti et al. (2009) reported higher N recovery efficiency when sulphur was added, which was supported by our data and discussed in 1.5 Box 1.

1.4.3 Environmental effects on grain protein response to late season N

We identified GPC response patterns to late-season N application and their interaction with the environment. Environmental conditions in the critical period play a key role in determining the potential kernels per area, which reflect wheat sink strength (Fischer, 1985; Slafer et al., 2014, 2022). Reduced sink strength can relate to shortening of grain filling, reducing carbon and N accumulation (Triboi et al., 2006). Thus, a greater GPC response to late-season N application in environments with favourable growing conditions during the critical period could potentially be explained through a larger sink size that allowed for greater translocation of the late-applied N to the grains. Furthermore, we observed from our data that favourable conditions for crop growth in the critical period were related to greater grain N recovery efficiency, which can partially explain greater grain N accumulation on crops fertilised with late-season N (1.5 Box 1). We could not confirm any effects of temperature during the grain filling, as the confidence intervals overlapped between high and low clusters in terms of response to late-season N. Under controlled-temperature environment, however, Dupont et al., (2006) isolated the interactive effects of grain filling temperature and N availability on GPC accumulation, concluding that GPC only increased due to N application under low temperature after anthesis. The narrow range of temperatures during grain filling sampled in our study can also partially account for the lack of temperature effect on our results (Appendix Table A.1).

1.4.4 Physiological drivers of GPC response to late-season N

Late-season N applications can increase N source size by enhancing N uptake after anthesis and consequently improve GPC (Monaghan et al., 2001; Triboi et al., 2006; Lollato et al., 2021). Martre et al. (2003) suggested that grain N accumulation is source-regulated under limiting pre-anthesis N conditions and as a consequence, fertilisation at anthesis can enhance the fraction of storage proteins. Furthermore, the level of source-regulation of GPC deposition seems to be genotype-dependent (Martre et al., 2003), which can partially explain unaccounted variations in our model (Figure 1.7). Greater sink size achieved through more kernels per area can increase N demand during grain filling, which can be matched by greater N mobilization from vegetative tissues and post-anthesis N uptake (Triboi and Triboi-Blondel, 2002). Therefore, increasing C sink size (*via* greater grain number) could enhance grain N demand and thus GPC response to late N. However, N available during grain filling contributes to coupling increased grain N demand and reduce potential GPC dilution. Here, we showed that there is still inconsistency on the effects of stover N uptake and stover N concentration on GPC response to late-season N, suggesting that other factors such as N mobilization efficiency and sink-source relations can play a role in determining accumulated grain N (Kong et al., 2016).

In agreement with our findings, de Oliveira Silva et al. (2020a) suggested that plant N concentration was more strongly related to plant N uptake than biomass. Moreover, we found that GPC associated with stover N concentration and not with stover biomass. Concentration of amino acids in the flag leaf is positively related to GPC deposition (Barneix, 2007). As discussed by Barneix (2007), free amino acids synthesised from recently absorbed NO_3^- represents the shoot N fraction that is directly linked to N exports to the grain under non-limiting N. This opens

the inquiry of whether the free amino acids fraction in plant tissue can potentially predict post-anthesis N uptake and grain N accumulation.

1.4.5 Impact of GPC response on dough rheological properties

Increased GPC with late N fertilisation improved dough extensibility. This relation was reported by numerous studies that generally showed lack of association between N management and dough tenacity (Dong et al., 2009; Blandino et al., 2015; Corassa et al., 2018). The clearest effect derived from enhancing GPC was the increased alveogram index, as reported before (Borghi et al., 1997; Lloveras et al., 2001) and depended sometimes in a combination of factors such as N source, N rate, and soil textural class (Blandino et al., 2015). Moreover, under controlled-conditions, Xue et al. (2016) showed that even when late N did not improve GPC, positive effects in baking quality can be expected by altering flour gliadin proportion and gluten content. Previous literature highlighted the positive association between gliadin to glutenin ratio and dough extensibility (Uthayakumaran et al., 1999; Mirsaeedghazi et al., 2008). However, the effect of increased gliadin to glutenin proportion on bread-making quality could depend on the cultivar (Rekowski et al., 2019).

1.5 Box 1

Nitrogen recovery efficiency is the difference in grain N removal between an unfertilised control and a N-fertilised treatment per unit N applied (Mosier et al., 2004). We hypothesise that late-season N applications may increase N recovery compared to pre-sowing or basal N applications because the crop canopy and root system are fully developed, potentially minimising N losses by enhancing N uptake efficiency (Wuest and Cassman, 1992; Foulkes et al., 2009). This is supported by some preliminary evidence though the benefit of N applied at anthesis to N recovery depended on early-season N availability (Wuest and Cassman, 1992).

Smith and Whitfield (1990) also suggested N application at heading increased grain ^{15}N recovery efficiency as compared to earlier tillering and booting N applications in rainfed crops. However, most research measured N recovery efficiency from basal N fertilisation. Here, we quantified the recovery efficiency of late-season N fertiliser by comparing the grain N removal of crops receiving late-season N to the grain N removal of its respective reference receiving the same amount of early-season N, divided by the amount of late-season N applied. Across all sources of variation, N recovery efficiency averaged 0.30 kg grain N kg late N $^{-1}$ and ranged from -0.82 to 1.79 kg grain N kg late N $^{-1}$ (Figure 1.9A). Conditions favouring crop growth during the critical period (high photothermal quotient, long duration, and low temperatures) were related to high late N recovery efficiency (Figure 1.9B). There was no association between recovery efficiency of late N with environmental attributes in the grain filling period (Figure 1.9B). Late N placement, source, and timing had no impact on the recovery of late N fertiliser though some trends were observed (Appendix Figure A.2). Our results suggested that late-season N application increased N recovery efficiency thus the proportion of grain N. However, we note that the mean and range N recovery efficiency from late-season N in this meta-analysis was similar to that reported for long-term field experiments evaluating pre-plant N applications (mean: 31 %, range: -33 to 166 %; Lollato et al., 2019), a meta-analysis evaluating the co-application of nutrients (Duncan et al., 2018), and to that reported for cereals in a global analysis (33%, (Raun and Johnson, 1999). Addition of sulphur to the late-season N can partially explain trends of slightly higher late N recovery on ammonium sulphate fertilisers (Appendix Figure A.2) which is in line with previous research showing that the addition of sulphur enhanced recovery efficiency of N fertiliser (Duncan et al., 2018; Salvagiotti et al., 2009). Further increases in late-season N recovery efficiency can be expected under favourable conditions for

crop yield formation, as high photothermal quotient in the critical period is linked to grain number and grain set, favouring greater sink strength which enhances crop N demand and thus recovery efficiency of late N (Fischer, 1985; Slafer et al., 2014, 2022).

1.6 Conclusion

We showed that late N application was neutral for yield and improved GPC, shifting the yield-GPC correlation upwards. The response of GPC to late fertilisation was larger with a greater proportion of late N relative to the total N, when applied later within the GS 37 to 71 window, and using foliar fertiliser sources. Greater responses also occurred in high-yielding environments where weather conditions were favourable around the critical period. Improved GPC from late N also improved dough quality parameters. Future research could focus on approaches to forecast the effects to late N on post-anthesis N uptake and GPC considering plant N nutritional status at the moment of application, and addressing late N-fertiliser recommendations depending upon the crop yield potential.

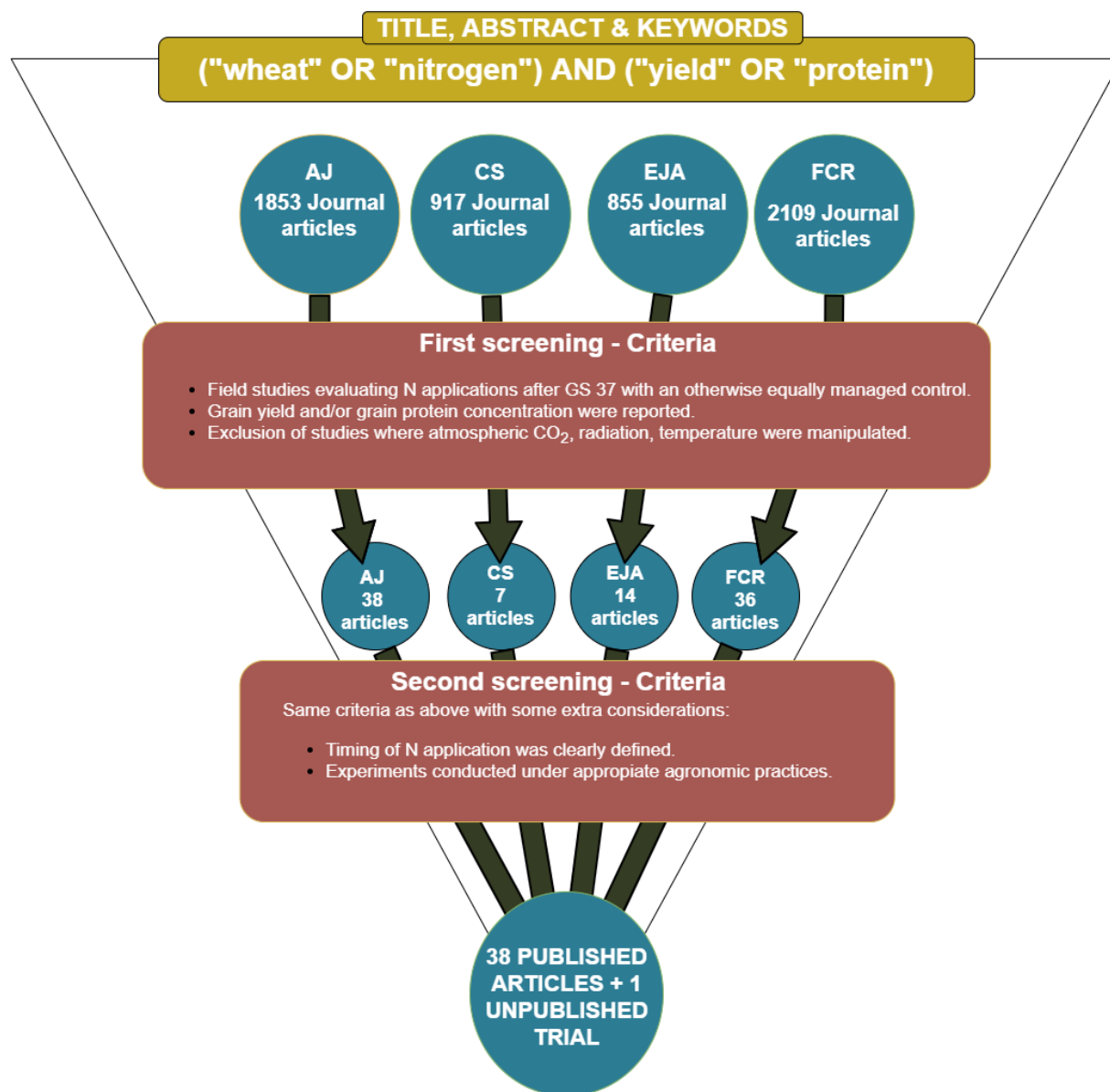


Figure 1.1. Approach to screen articles from AJ (Agronomy Journal); CS (Crop Science); EJA (European Journal of Agronomy); and FCR (Field Crops Research).

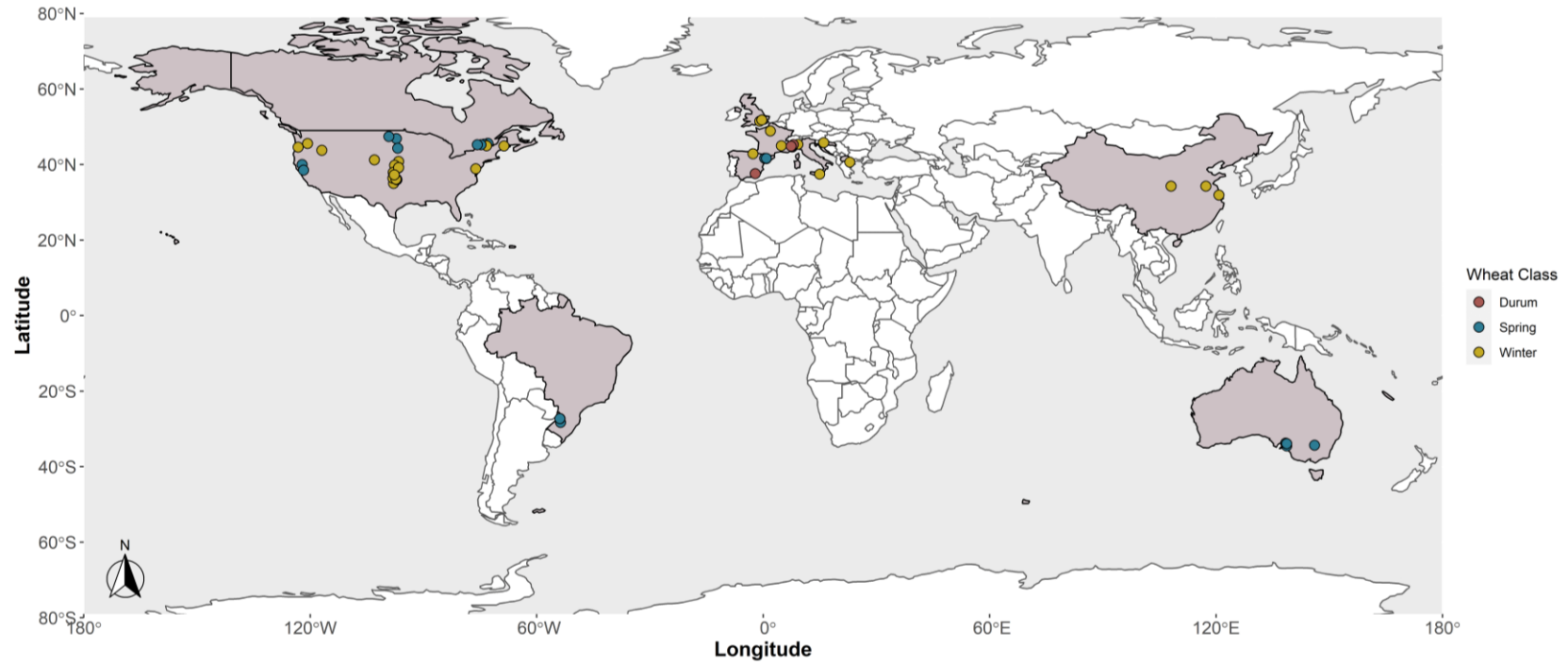


Figure 1.2. Distribution of field trials evaluating wheat response to late-season N application in the current meta-analysis.

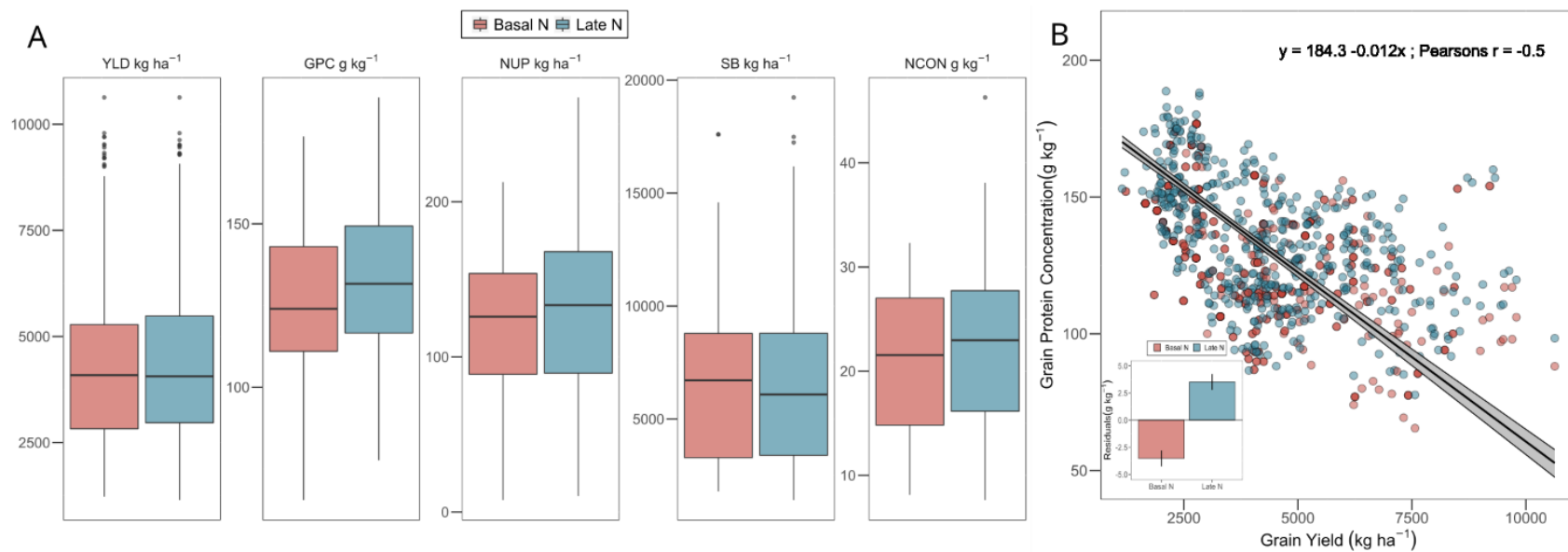


Figure 1.3. (A) Comparisons of wheat grain yield (YLD), grain protein concentration (GPC), stover nitrogen uptake (NUP), stover biomass (SB) and stover nitrogen concentration (NCON) between basal N (red) and late N crops (blue). Basal N crops received N fertiliser before and late N after GS 37. Boxplots show the range, the median and inter-quartile range. (B) Grain yield-grain protein concentration relation across all studies and sources of variation; red symbols are basal N and blue are late N crops. The line is the SMA regression with its 95% bootstrapped confidence interval. Inset compares residuals for basal N (red) and late N (blue) (mean and s.e.).

Table 1.1. Comparison of mean yield ($\pm$ s.d.) and mean grain protein concentration GPC ($\pm$ s.d.) of wheat in basal N and late N crops. PWC is the number of pairwise comparisons; Env. is the number of environments; wheat type is D (durum wheat), W (winter bread wheat), S (spring bread wheat). Studies are arranged according to the mean yield of the basal N treatment in each study. n.a.: data not available.

Yield (Mg ha ⁻¹)		GPC (g kg ⁻¹)		Country	PWC	Env.	Wheat type	Reference
Basal N	Late N	Basal N	Late N					
8.58 $\pm$ 1.39	8.04 $\pm$ 1.39	101 $\pm$ 8.66	108 $\pm$ 10.74	France	5	2	W	David et al (2005)
8.56 $\pm$ 0.67	8.49 $\pm$ 0.67	118 $\pm$ 5.63	124 $\pm$ 5.14	UK	6	5	W	Gooding et al (2007)
8.51 $\pm$ 0.69	8.85 $\pm$ 0.69	n.a.	n.a.	China	8	2	W	Chen et al (2018)
7.97 $\pm$ 0.66	8.21 $\pm$ 0.66	152 $\pm$ 7.66	155 $\pm$ 6.27	Italy	6	3	D	Blandino and Reyneri (2009a)
7.81 $\pm$ 0.66	8.13 $\pm$ 0.66	104 $\pm$ 5.37	124 $\pm$ 5.65	US	15	3	W	Brown and Petrie (2006)
7.69 $\pm$ 0.63	7.69 $\pm$ 0.63	89 $\pm$ 2.92	103 $\pm$ 3.08	UK	12	2	W	Rossman et al (2019)
7.46 $\pm$ 0.63	7.70 $\pm$ 0.63	112 $\pm$ 5.19	117 $\pm$ 4.79	Croatia	8	1	W	Varga and Svečnjak (2006)
7.12 $\pm$ 0.61	7.24 $\pm$ 0.61	82 $\pm$ 3.77	89 $\pm$ 3.96	Spain	2	1	W	Fuertes-Mendizabal et al (2010)
6.97 $\pm$ 0.62	7.26 $\pm$ 0.62	100 $\pm$ 5.12	118 $\pm$ 5.30	US	30	3	S	Wuest and Cassman (1992)
6.70 $\pm$ 0.58	6.62 $\pm$ 0.58	107 $\pm$ 5.09	115 $\pm$ 4.77	Australia	8	1	S	Fischer (1993)
6.08 $\pm$ 0.57	6.26 $\pm$ 0.57	120 $\pm$ 5.67	124 $\pm$ 5.00	Macedonia	8	2	W	Papakosta and Gagianas (1991)
6.03 $\pm$ 1.23	6.24 $\pm$ 1.23	n.a.	n.a.	China	4	1	W	Xu et al (2022)
6.01 $\pm$ 0.56	6.04 $\pm$ 0.56	134 $\pm$ 6.44	136 $\pm$ 5.40	Spain	8	4	S	Lloveras et al (2001)
5.96 $\pm$ 0.56	6.20 $\pm$ 0.56	126 $\pm$ 6.00	131 $\pm$ 5.30	US	20	2	W	Kratochvil et al (2005)
5.50 $\pm$ 0.52	5.28 $\pm$ 0.52	150 $\pm$ 7.78	155 $\pm$ 6.30	US	5	5	S	Otteson et al (2007)
5.36 $\pm$ 0.24	5.45 $\pm$ 0.24	129 $\pm$ 9.81	130 $\pm$ 7.22	Italy	6	3	W	Borghi et al (1997)
5.35 $\pm$ 0.51	5.15 $\pm$ 0.51	n.a.	n.a.	US	5	5	S	Otteson et al (2008b)
4.96 $\pm$ 0.50	4.94 $\pm$ 0.50	119 $\pm$ 4.87	120 $\pm$ 4.77	US	36	6	W	Lollato et al (2021)
4.51 $\pm$ 0.48	4.59 $\pm$ 0.48	101 $\pm$ 4.85	113 $\pm$ 4.88	US	8	1	W	Altman et al (1983)
4.51 $\pm$ 0.35	4.50 $\pm$ 0.35	109 $\pm$ 3.53	110 $\pm$ 3.31	US	32	8	W	Lollato 2020 (unpublished)
4.20 $\pm$ 0.60	4.45 $\pm$ 0.60	96 $\pm$ 5.98	100 $\pm$ 4.86	US	16	4	W	Mallory et al (2013)
4.13 $\pm$ 0.87	4.19 $\pm$ 0.87	124 $\pm$ 8.50	134 $\pm$ 8.50	Italy	16	4	W, D	Blandino et al (2015)

4.12±0.46	4.18±0.46	126±6.07	133±5.50	Spain	3	1	D	Garrido-Lestache et al (2005)
3.85±0.44	3.71±0.44	153±7.78	155±6.24	Spain	12	4	D	Abad et al (2004)
3.80±0.45	3.86±0.45	n.a.	n.a.	Italy	12	6	D	Blandino et al (2009b)
3.74±0.45	3.85±0.45	121±5.91	129±5.37	US	72	6	W	Dick et al (2016)
3.61±0.43	3.61±0.43	n.a.	n.a.	US	4	4	W	Bhatta et al (2017)
3.47±0.44	3.43±0.44	n.a.	n.a.	Canada	3	3	S	Ayoub et al (1994)
3.46±0.42	3.43±0.42	116±3.54	122±3.00	Brazil	27	3	S	Corassa et al (2018)
3.30±0.36	3.23±0.36	130±7.69	135±6.91	US	24	6	W, S	Bly et al (2003)
3.20±0.36	3.18±0.36	152±8.80	155±5.91	US	72	4	W	Cruppe et al (2017)
3.11±0.15	3.29±0.15	n.a.	n.a.	Australia	16	2	S	Kitonyo et al (2018)
2.98±0.41	3.20±0.41	135±6.09	127±4.70	Australia	16	4	S	Hooper et al (2015)
2.90±0.40	3.02±0.40	161±8.12	161±6.49	US	1	1	W	Heitholt et al (1990)
2.72±0.45	2.79±0.45	149±7.27	160±7.25	US	60	6	W	Woolfolk et al (2002)
2.62±0.39	2.55±0.39	140±7.11	147±6.07	Canada	16	2	S	Subedi et al (2007)
n.a.	n.a.	151±7.66	155±6.16	US	1	1	S	Otteson et al (2008a)
n.a.	n.a.	101±4.80	109±4.64	China	6	2	W	Wang et al (2014)
n.a.	n.a.	105±4.84	109±4.44	US	8	4	S	Webster and Jackson (1993)

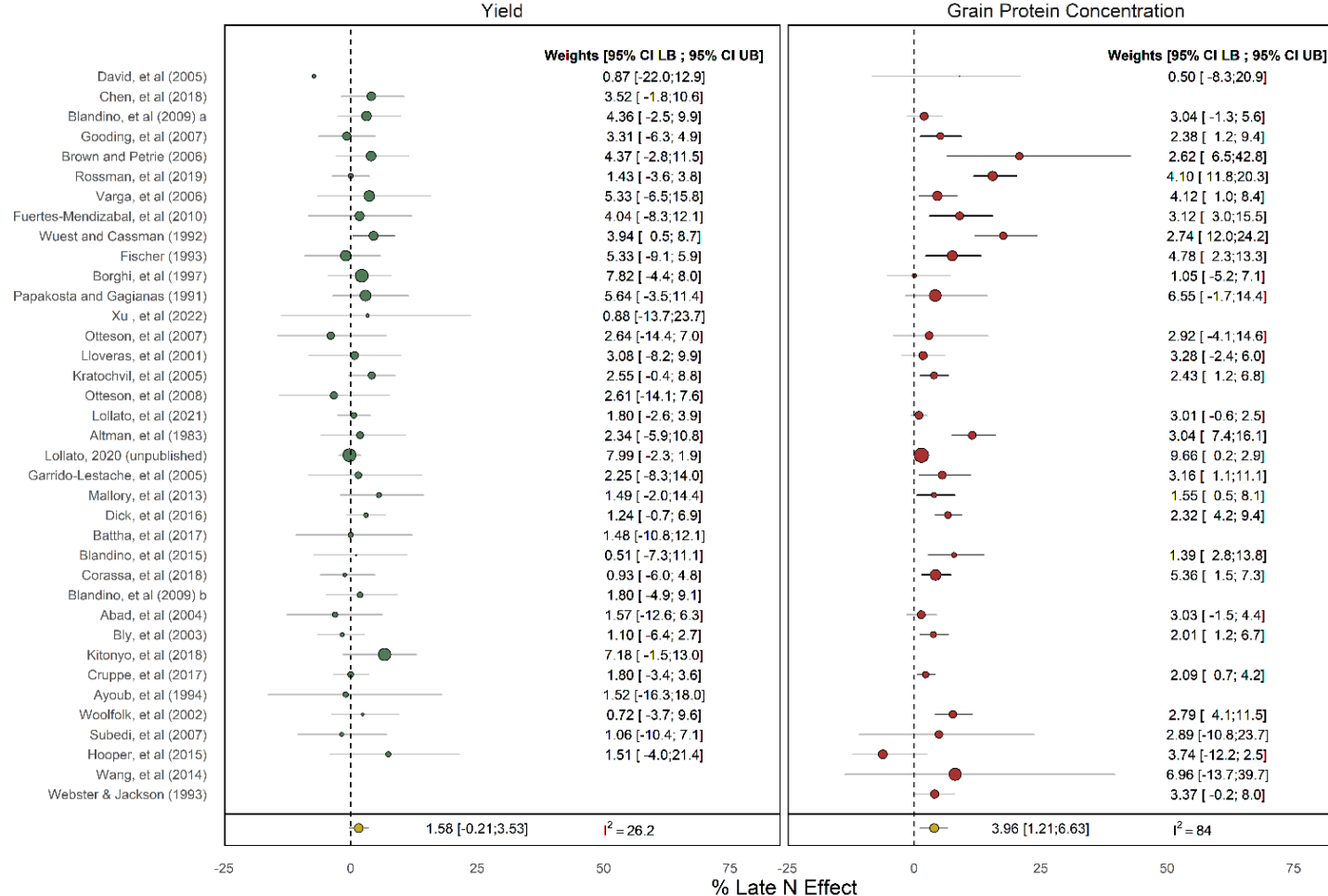


Figure 1.4. Pooled effects for grain yield (green symbols) and grain protein concentration (red symbols). Symbols and their whiskers represent the mean effect and 95% bootstrapped CI for each of the studies in this analysis. The yellow symbols are the mean estimate and its 95% bootstrapped confidence interval. Opacity of whiskers is relative to the significance of each estimate, and size of the points is relative to the weight of each study. Studies are sorted according to the mean yield of the basal N treatment in each study in decreasing order from top to bottom. Abbreviations: confidence interval (CI), lower bound (LB), upper bound (UB), I^2 = I-squared statistic (%).

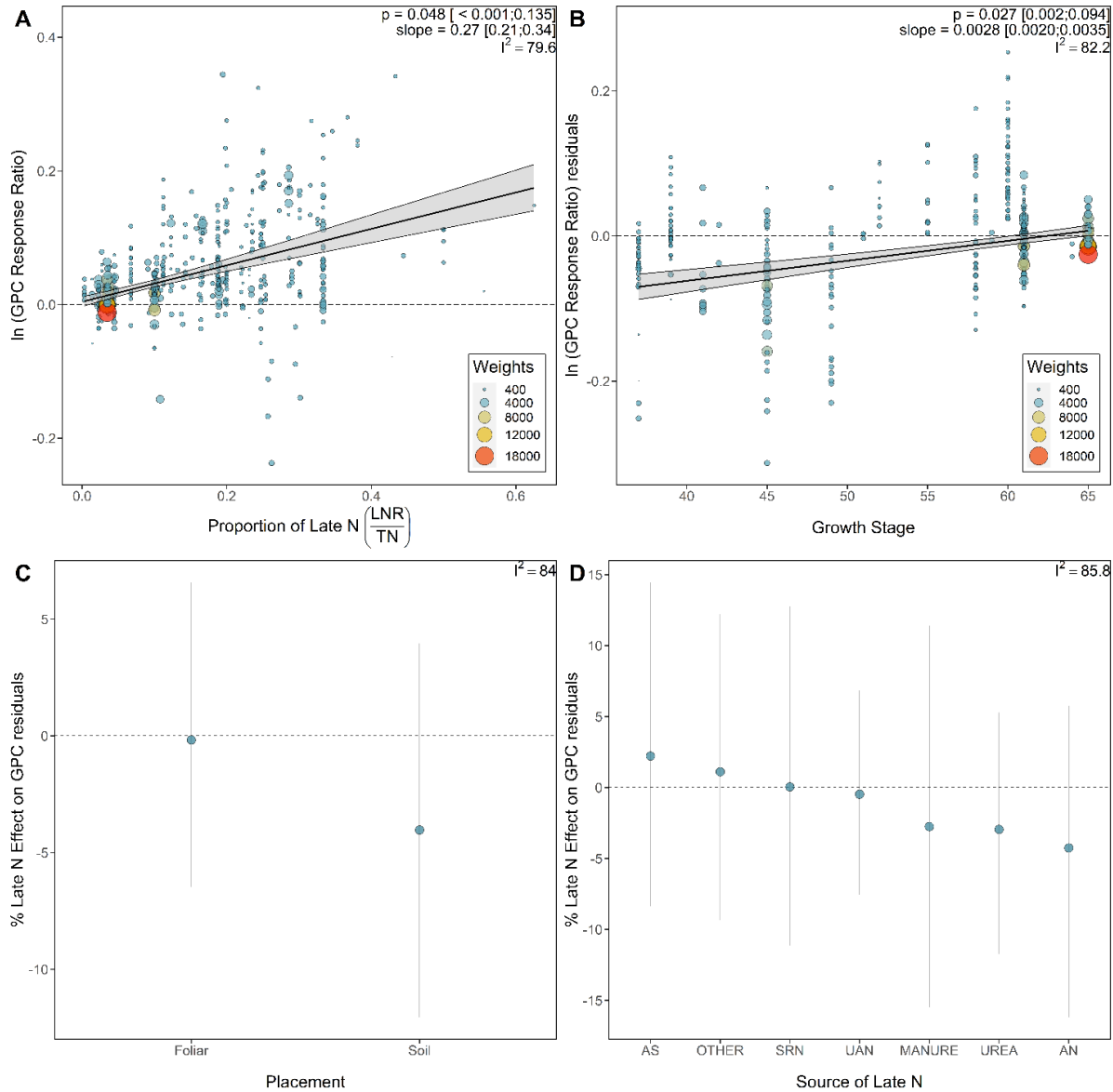


Figure 1.5. Impact of late nitrogen management practices on grain protein concentration response: (A) Grain protein concentration increased with the proportion of the late applied N (LNR) relative to the total N available (TN). Effect of different late N fertiliser timings of application (B), placement (C) and sources (D) on the residuals of the proportion of late N and GPC response to late N relationship (Panel A). Size of the individual datapoints is relative to the weight of each observation. In panels A and B: p -values represent the slope significance (mean and confidence interval (CI) of a resampling distribution); slope mean estimate and 95% bootstrapped CI are represented. I^2 = I-squared statistic. Ribbons around the fitted line indicate 95% bootstrapped CI for the slope of the meta-regression. In panels C and D: points represent the mean effect and whiskers correspond to the bootstrapped CI; grey whiskers indicate non-significant effects corresponding to the 97.5% quantile of the bootstrapped p -values. Key: AN (ammonium nitrate), AS, (ammonium sulphate), SRN (slow-release nitrogen), UAN (urea ammonium nitrate), UREA (granulated urea).

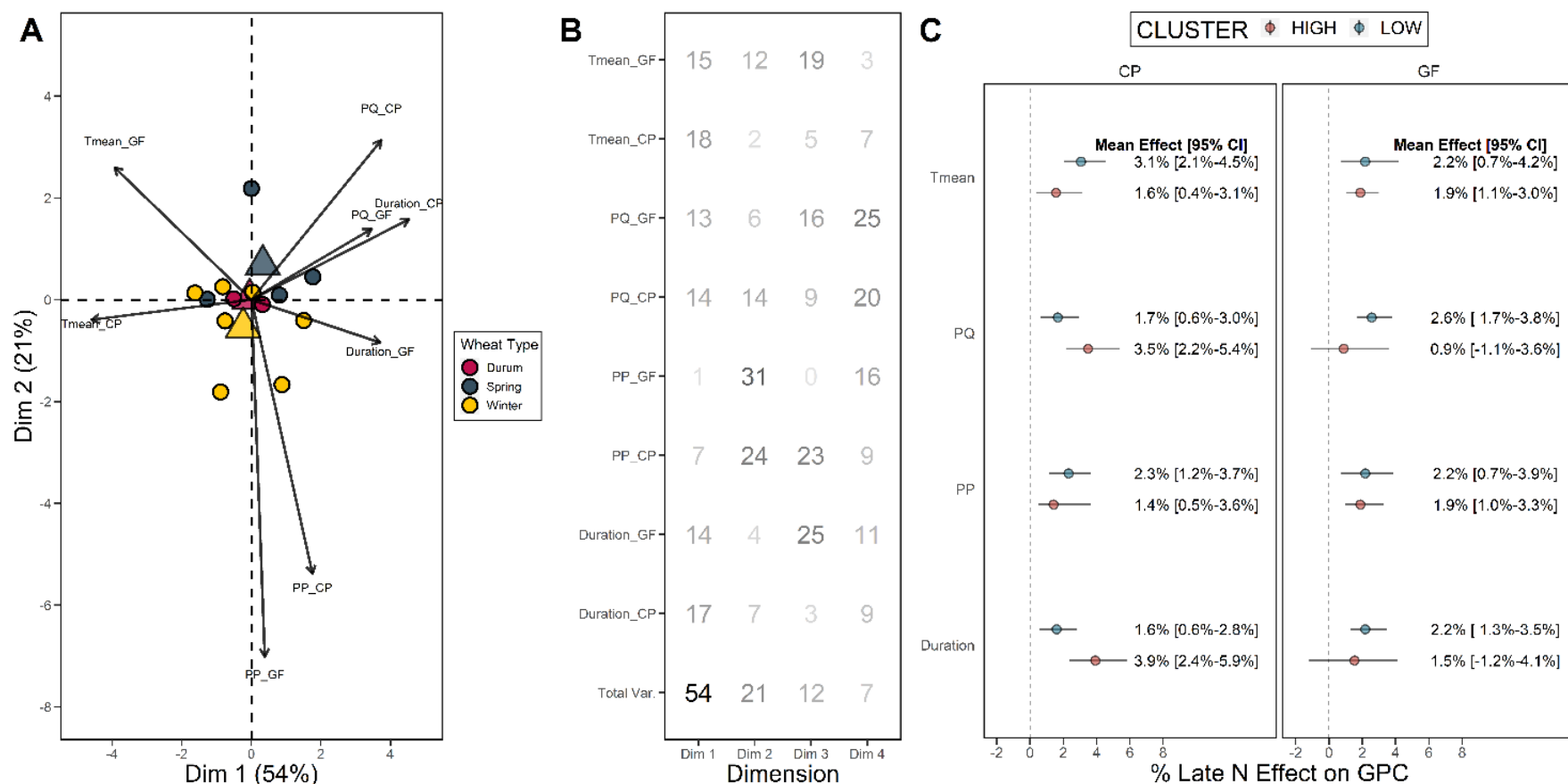


Figure 1.6. Environmental descriptors of the GPC response to late-season N fertilisation. (A) Bi-plot with first two dimensions of the principal component analysis, points represent studies and triangles the corresponding centroids for wheat type clusters; (B) individual contribution of the weather attributes in the first 4 dimensions, ‘Total Var’ represents the total variance explained by each of the dimensions; (C) effect of environmental descriptors on GPC response in the two clusters: HIGH (red) and LOW (blue) for the critical period (CP) and grain filling period (GF). In panel C whiskers represent the 95% bootstrapped CI. Significance of the means comparisons are provided in Appendix Table A.1. Variables evaluated were: mean temperature (Tmean), photothermal quotient (PQ), duration of the period (Duration), accumulated precipitation (PP).

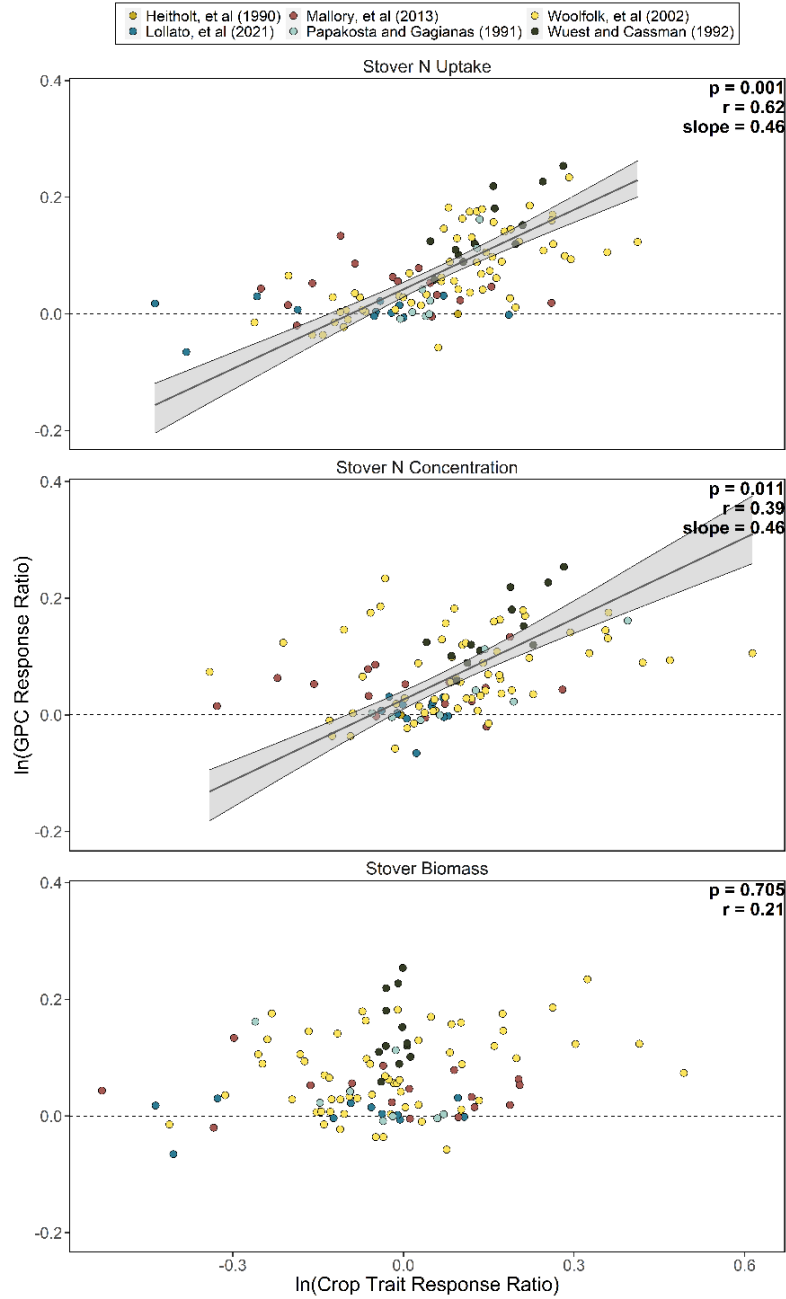


Figure 1.7. Relationship between relative GPC response ratio and stover N uptake response ratio, stover nitrogen concentration response ratio and stover biomass response ratio. Colours represent studies. P -values correspond to the 0.975 quantile of a resampling distribution. Grey area indicates 95% bootstrapped CI for the slope of the SMA regression. Mean slope and Pearsons r from a resampled distribution are represented.

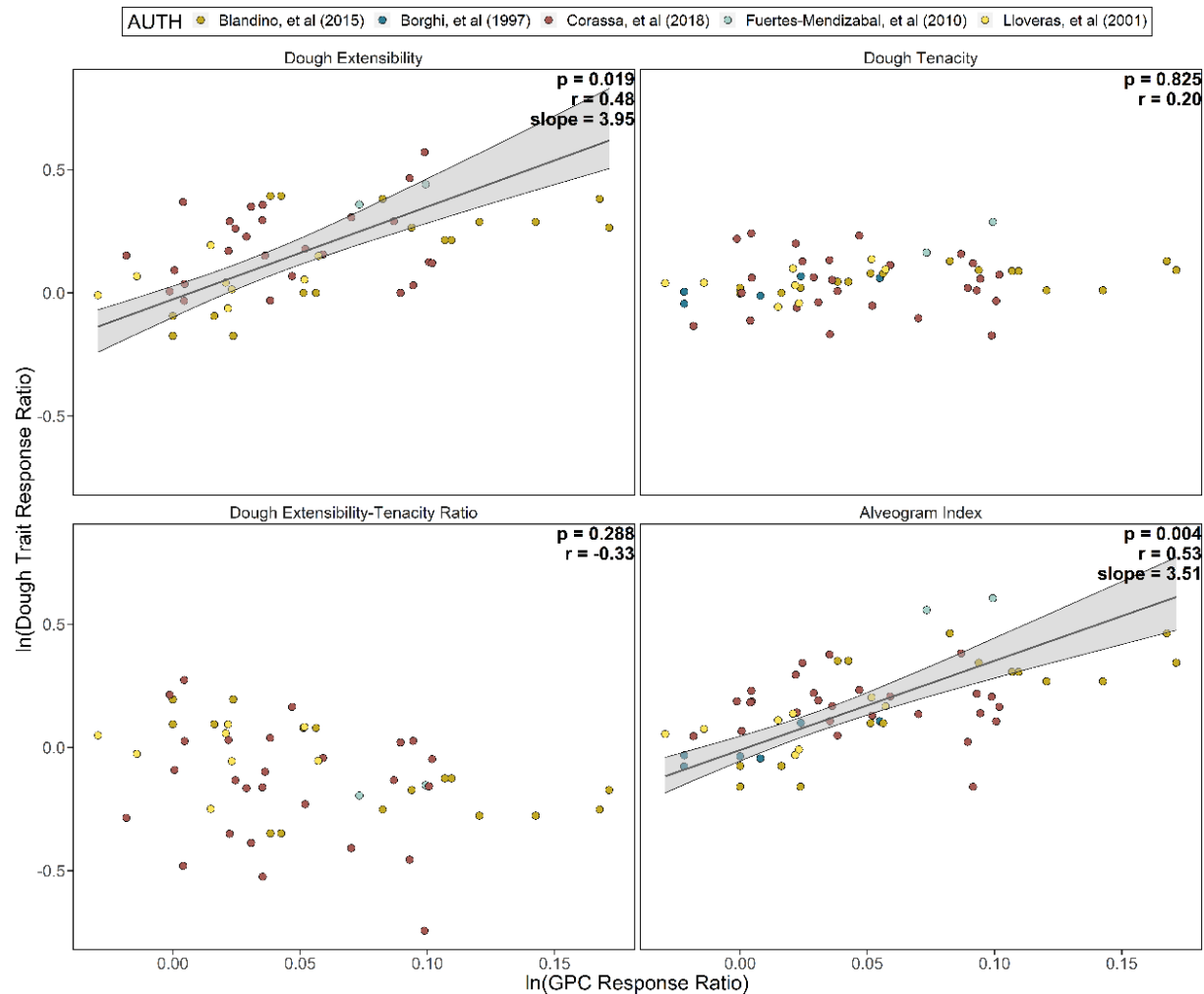


Figure 1.8. Grain protein concentration response ratio and its relation with the response in different dough traits: dough extensibility, dough tenacity, dough extensibility-tenacity ratio and alveogram index. P -values correspond to the 0.975 quantile of a resampling distribution. Grey area indicates 95% bootstrapped CI for the slope of the SMA regression. Mean slope and Pearson's r from a resampling distribution are represented.

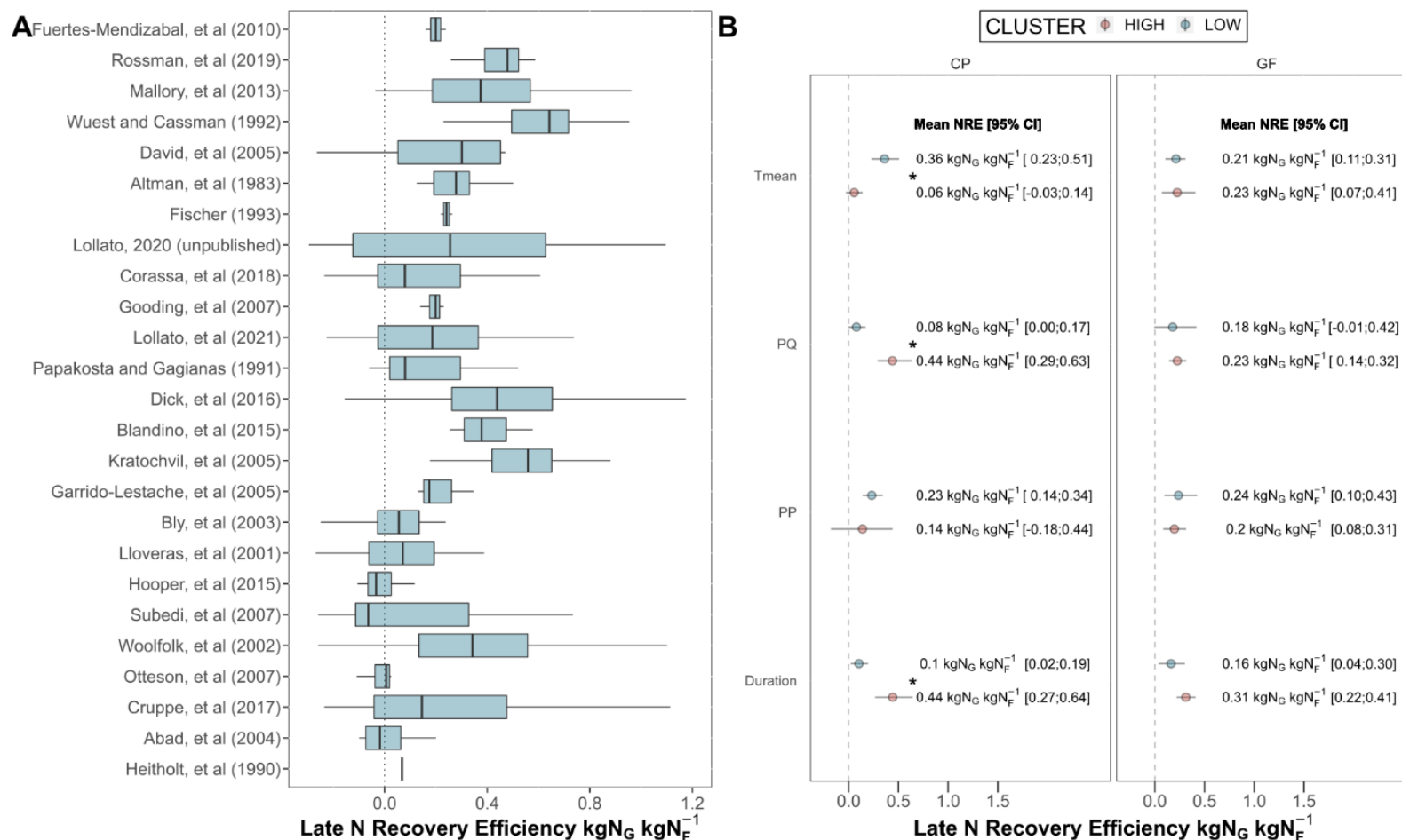


Figure 1.9 (A) Late N recovery efficiency for all studies included in the analysis. Studies are sorted according to the mean grain protein concentration of the basal N treatment in each study in decreasing order from top to bottom. (B) Effect of environmental descriptors on late N recovery efficiency in the two clusters: HIGH (red) and LOW (blue) for the critical period (CP) and grain filling period (GF). In panel B, whiskers represent the 95% bootstrapped CI and stars represent significant differences indicated by non-overlapping 95% bootstrapped CI. Abbreviations: grain N removal (N_G), late N fertiliser rate (N_F), mean temperature (Tmean), photothermal quotient (PQ), duration of the period (Duration), accumulated precipitation (PP).

Chapter 2 - Cultivar-specific phenotypic plasticity of yield and grain protein concentration in response to nitrogen in winter wheat

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Abstract

Context: Owing to the interaction between genotype and environment (G x E), identifying traits to increase wheat yield and grain protein concentration simultaneously or increasing one without affecting the other remains a challenge. Phenotypic plasticity is an insightful perspective to understand G x E.

Objective: To explore the relations of wheat yield and grain protein concentration in response to N input and its physiological basis from the perspective of phenotypic plasticity.

Method: We established a factorial experiment combining 14 winter wheat cultivars and four N fertilization rates (0, 45, 90 and 135 kg ha⁻¹) in eight environments. We analyzed the interaction of cultivar and N combining a phenotypic plasticity framework and a three-phase model of grain yield and protein response to N input. The phases are: phase I, N supply limits both yield and grain protein; phase II, N supply limits grain protein but not yield; and phase III, N supply does not limit yield or grain protein concentration

Results: Grain yield plasticity was positively associated to yield in high-yielding environments without N limitations (phase II) with no cost in low yielding environments, and associated to harvest index. Grain protein plasticity was a positively associated to protein in high protein environments without N limitations (phase III). Plasticity of grain protein concentration was negatively associated to grain number m⁻², resulting in moderate negative association of

protein plasticity and yield. Grain C:N ratio associated weakly and positively with yield plasticity and strongly and negatively for grain protein plasticity.

Conclusion: This work proposes a yield-protein plasticity framework combined with a three-phase model that allows to disclose $G \times N$ interactions. Under our experimental conditions, we identified physiological mechanisms associated to yield and protein plasticity.

Implications: Yield and protein plasticity can contribute guiding grower's cultivar selection towards high yield plasticity cultivars when aiming to high yield with acceptable protein levels or high protein plasticity cultivars to ensure high protein at the expense of lower yields. Yield plasticity brings opportunity to breed for high yielding cultivars while maintaining grain protein concentration. Accuracy of N recommendations models and mechanistic crop models can be improved by accounting for $G \times N$ interactions through plasticity of yield and grain protein.

2.1 Introduction

Nitrogen (N) management is crucial to sustainability avoiding both over-fertilization releasing reactive N to the environment and under-fertilization leading to yield gaps and soil mining (Alvarez et al., 2014; Jobbágy and Sala, 2014; Angus et al., 2017; Jaenisch et al., 2021). Understanding and predicting the response of crop yield and grain protein concentration to N fertilization is a long-standing concern in agriculture (Patterson, 1904; Moser, 1932) that remains unsolved due to lagging theoretical frameworks (Cossani and Sadras, 2021; Sadras et al., 2022) to capture the interactions between genotype, environment and management, $G \times E \times M$ (Van Sanford and MacKown, 1987; Savill et al., 2018; Nehe et al., 2020; Ivić et al., 2021; Lollato et al., 2021).

The association between grain yield and protein concentration is usually negative (Malloch and Newton, 1934; Benizian and Lane, 1981; Triboi et al., 2006; Bogard et al., 2010; Giordano et al., 2023). This is especially important for wheat (*Triticum aestivum* L.), a crop that provides approx. 20% of the human calories (Shewry and Hey, 2015) and the majority of essential amino acids except for lysine, which is the limiting amino acid in all cereals (Shewry, 2007; Shewry and Hey, 2015). The association between yield and grain protein concentration has a genetic component (Monaghan et al., 2001a; Oury and Godin, 2007; Nigro et al., 2019; Mosleth et al., 2020), but the interaction with environment (Oury and Godin, 2007) and N supply (Mosleth et al., 2015) can mask genetic effects (e.g., Lollato et al., 2021). The physiological basis of this negative association depends on the degree of source-sink limitation for grain starch and grain N accumulation (Benizian and Lane, 1981; Triboi and Triboi-Blondel, 2002; Triboi et al., 2006; Acreche and Slafer, 2009). Thus, identifying traits to increase yield and protein simultaneously remains a major challenge.

Phenotypic plasticity represents environmentally-induced changes on trait expression of a given genotype (Dewitt and Scheiner, 2004). Phenotypic plasticity depends on the genotype (species, cultivar), the trait (e.g., grain protein concentration, root depth), and the environmental source of variation (e.g., soil moisture, availability of soil N). Its genetic modulation is partially independent of the modulation of the trait *per se* (Bradshaw, 1965; Reymond et al., 2003a; Alvarez Prado et al., 2014a; Sadras et al., 2016; Kusmec et al., 2018; Laitinen and Nikoloski, 2019; Diouf et al., 2020). The perspective of phenotypic plasticity has offered understanding on $G \times E \times M$ interactions for agronomically important traits (Sadras et al., 2009; Sadras and Rebetzke, 2013; Alvarez Prado et al., 2014a; Sadras et al., 2016, 2019a; Lollato et al., 2020b; Diouf et al., 2020; de Felipe and Alvarez Prado, 2021).

In this paper, we explore the relations of wheat yield and grain protein concentration in response to N input and its physiological basis from the perspective of phenotypic plasticity. We advance a conceptual framework that leads to testable hypotheses, and report results from experiments designed to test them.

2.2 Conceptual Framework

2.2.1 Phenotypic plasticity

Phenotypic plasticity can be quantified as the variance ratio, which is the quotient between the individual variance for a given cultivar VT_{ik} and the variance of the population of cultivars VT_{ip} in a group of environments (Dingemanse et al., 2010; Sadras and Richards, 2014):

$$PP_{ik} = \frac{VT_{ik}}{VT_{ip}} \quad \text{Eq. 1}$$

Figure 2.1 illustrates trait-plasticity relations using yield as an example. In Figure 2.1 (A) plasticity is primarily related to yield responsiveness to favorable conditions, *i.e.* a highly-plastic cultivar outyields its less plastic counterpart under favorable conditions with no difference under low yielding environments. In Figure 2.1 (B) plasticity associates with sensitivity to stress with no difference under favorable conditions. In Figure 2.1 (C) plasticity associates with both higher yield under favorable conditions and lower yield under stress.

2.2.2 Evaluation of yield and grain protein response to N for cultivars with contrasting plasticity

The responses of grain yield and grain protein concentration to N supply are usually explored with empirical functions (Gastal et al., 2015a) despite their limitations (Sadras et al., 2019b). The relationship of yield and grain protein concentration to N supply can be divided in three phases (Stone and Savin, 1999), as depicted in Figure 2.2.

In phase I, N supply limits both yield and grain protein concentration. Here, increase in N supply increases grain yield at a diminishing return until a point in which N becomes non-limiting. In this phase, increasing yield associates with reduced grain protein concentration. The large response of yield to N supply in phase I associates with enhanced tillering, leaf expansion, increasing capture of radiation and canopy photosynthesis (Gastal et al., 2015a). The reduction in grain protein concentration is due to a dilution effect, as starch accumulates faster than protein (Triboi et al., 2006).

In phase II, grain yield plateaus but N supply still limits grain protein concentration. In this phase, N suffices for maintaining both high crop photosynthetic capacity and rate of carbon deposition in grain. Grain protein accumulation relies primarily on mobilization of vegetative N (Van Sanford and MacKown, 1987; Martre et al., 2003) complemented with N uptake during grain fill (Barneix, 2007; Bogard et al., 2010), when there is a tradeoff between maintenance of shoot N required to sustain radiation use efficiency and allocation of N to grain protein (Sinclair and de Wit, 1976).

In phase III, N supply ensures maximum grain yield and grain protein concentration and increases in N supply are neutral for both. In some cases, excessive N supply can reduce grain yield, *e.g.*, in crops relying on stored soil water, by increasing water use early in the season at the expense of water use during reproduction, and reducing carbohydrate reserves (van Herwaarden et al., 1998; Lollato et al., 2019a; Sadras et al., 2019b).

We hypothesize that (i) phenotypic plasticity of yield and grain protein concentration are negatively related; (ii) yield plasticity will be associated to yield in high yield environments without trade-offs under low yielding environments; (iii) protein plasticity is associated to protein in high protein environments without trade-offs under low protein environments (Figure

2.1A). Nitrogen supply contributes to environmental variation defining a range of yield and grain protein expression environments conceptualized in Figure 2.2. Therefore, we also hypothesize that differences among phenotypes with contrasting plasticity are more likely under non-N limiting conditions (phase II for yield and phase III for grain protein).

This paper focuses on N management to simultaneously improve grain yield and protein concentration (or improving one without negatively affecting the other) of winter wheat cultivars with the objective to answer the following questions:

- (i) Are yield and grain protein plasticity associated to responsiveness to favorable conditions, stress tolerance, or a combination of both (Figure 2.1)?
- (ii) How does N supply modulate the phenotype (yield and grain protein) of cultivars with contrasting plasticity? At which phases of trait response to N supply do differences among cultivars arise?
- (iii) Which are the physiological mechanisms associated to phenotypic plasticity under varying N supply?

2.3 Method

2.3.1 Crop husbandry, plant material, and experimental design

Rainfed field experiments were conducted in eight environments resulting from the combination of seasons and locations in Kansas, US (Table 2.1). A factorial experiment was established in each environment that combined four N rates (0, 45, 90 and 135 kg N ha⁻¹) and 14 high-yielding, agronomically adapted winter wheat cultivars with contrasting grain protein concentration (Table 2.2). The combination of locations and seasons with N rates originated 32 N-environments in which cultivars were evaluated. Treatments were arranged in a split-plot design with three or four replicates depending on the location, with N rates assigned to main plot

and varieties to subplots. Fertilizer N was applied as granulated urea (46-0-0) during spring tillering following winter dormancy at GS25 (Zadoks et al., 1974). All plots received 56 kg ha⁻¹ of diammonium phosphate at sowing (10 kg of N ha⁻¹ and 11 kg of P ha⁻¹) and 22 kg ha⁻¹ of sulfur as gypsum (0-0-0-23S) together with N application, to avoid sulfur limitations (Salvagiotti et al., 2009; Jaenisch et al., 2020).

Trials at Viola, Ashland Bottoms, Manhattan, and Great Bend were sown under no-tillage after soybean (*Glycine max L. Merrill*), and the trials in Hutchinson were established under conventional tillage after winter canola (*Brassica napus L.*) in 2020 and no-till after soybean in 2021. Crop husbandry was similar across locations and seasons (Table 2.1). Imidacloprid insecticide and tebuconazole fungicide were applied to the seed. Each variety was sown at a rate of 260 seed m⁻² (adjusting for variety-specific seed size) with a Great Plains 506 no-till drill. Plots were 9.1 m long (trimmed to 7.2 m prior to harvest) and 7 rows wide with a row spacing of 0.19 m. Weeds and insects were controlled as needed using commercial pesticides during the season. To avoid confounding effects of differential disease resistance among varieties (Cruppe et al., 2021a), crops were treated with foliar fungicides at anthesis with 89 ml ha⁻¹ of picoxystrobin [(Methyl (αE)- α-(methoxymethylene)-2-[[[6-(trifluoromethyl)-2-pyridinyl]oxy]methyl]benzeneacetate] plus 36 ml ha⁻¹ cyproconazole [α-(4-chlorophenyl)-α-(1-cyclopropylethyl)-1H-1,2,4-triazole-1-ethanol].

2.3.2 Measurements

Initial mineral soil N and texture were characterized before sowing in a composite sample of 15 individual soil cores at each 0-15 and 15-60 cm soil depth (Table 2.2, Appendix Table B.1). Initial mineral soil N content was determined by N-KCl extraction. Daily weather data were retrieved from Kansas Mesonet stations (Patrignani et al., 2020) located near the field

experiments. Weather data was summarized for (i) the critical period for yield determination between -300°Cd and 100°Cd centered on anthesis using a base temperature of 4.5°C (Fischer, 1985; Cossani and Sadras, 2021) and (ii) grain fill, from 100 °Cd to 600 °Cd after anthesis using a base temperature of 0°C (Dupont et al., 2006).

At physiological maturity (GS 93), shoot biomass was collected from an area of 0.19 m⁻² in a middle row of each plot and immediately dried at 60 °C for 72 h. Following shoot sampling, the entire plots were harvested with a Massey Ferguson 8XP small plot combine. Grain weight and moisture were measured on-site during harvest with Harvest Master monitor (Juniper Systems, Inc., Logan UT, USA) incorporated to the combine, and yield adjusted to dry matter accounting for the plot area plus borders. Dry shoot samples were partitioned to determine yield components: heads m⁻², grains head⁻¹, grains m⁻², thousand kernel weight, shoot biomass, and harvest index. We determined grain N and stover N concentration with LECO TruSpec CN Carbon/Nitrogen combustion analyzer (LECO Corporation, St. Joseph, MI, 2005.) and calculated (i) N harvest index (the ratio between N in the grain and N in shoot); (ii) N utilization efficiency, as the amount of grain produced per unit shoot N uptake; and (iii) stover and shoot N uptake.

2.3.3 Phenotypic plasticity

Phenotypic plasticity was quantified with Equation 1, for each cultivar and trait of interest, across all combinations of four N rates and eight location-seasons (32 N-environments). To establish whether plasticity was primarily related to responsiveness to favorable conditions, stress tolerance, or a combination of both (Figure 2.1) we plotted trait-plasticity relations (Sadras and Richards, 2014; Sadras et al. 2016) and fitted bayesian hierarchical linear-regression models, described below, using the data for the 10th and 90th percentile. The 10th percentile corresponds to environments with low trait expression (*e.g.*, low grain yield, low grain protein

concentration) and the 90th percentile corresponds to environments of high trait expression (*e.g.*, high yield, high protein concentration). Thus, whether the percentiles corresponded to stressful or favorable environments depended on the trait. Percentiles in our dataset seek to return an objective measure of upper and lower limits of traits, excluding undue influence of extremes (Sadras et al 2017).

2.3.4 Bayesian process models and statistical analysis

Bayesian statistics are attracting interest in ecology and agriculture (Dorazio, 2016), including in the analysis of grain yield response to N fertilization in maize (*Zea mays* L.)(Correndo et al., 2021b) and wheat (Ouedraogo and Brorsen, 2018). In contrast to frequentist approaches in which model parameters are estimated as fixed over true quantities (Dennis, 1996; Ellison, 2004), bayesian models (i) use the sample data to update prior knowledge (beliefs and hypotheses); (ii) grant inference over model parameters, as they are considered random; (iii) base inference on posterior distributions and credible intervals rather than strict p-values and confidence intervals; and (iv) allow for a direct measurement of the probability of an event to be true (Hooten and Hefley, 2019).

To quantify the association between phenotypic plasticity and N with grain yield and protein concentration we fitted bayesian hierarchical models using the *brms* package (Bürkner, 2017) in R (R Core Team, 2022). The models were fitted with a Markov Chain Monte Carlo algorithm, combining three chains with 10,000 iterations each, discarding the first 5000 as burn in interval. Thinning rate was set to 5 and an adapt delta to 0.99. Samples were used for estimating median and 95% credible intervals of posterior distributions. We used uninformative priors derived from previous published literature (de Oliveira Silva et al., 2020a) and unpublished data from N response studies conducted in Kansas (five studies conducted in 27

site-years and adding to 1,492 observations) to describe yield and protein concentration response process to phenotypic plasticity, N supply, and crop N traits. Weather data was used to explore associations between grain yield, protein concentration using principal component analysis (PCA).

2.3.4.1 Phenotypic plasticity response models

Based on previous studies (Sadras et al., 2016, 2019a) yield and grain protein concentration association with phenotypic plasticity was defined with the following process model:

$$y_i \sim N(\mu_i, \sigma_i^2), \quad \text{Eq. 2}$$

$$\mu_i = \beta_0 + \beta_1 x_i, \quad \text{Eq. 3}$$

where β_0 is the intercept and β_1 the slope of the association between plasticity of a given trait and the trait itself under high (90th percentile) and low (10th percentile) trait expression environments. Percentiles defining trait expression environment were obtained by splitting the predictor variable into equally spaced intervals and fitting the corresponding model using the 10th and 90th percentile across all data contained within each interval (Sadras et al., 2016, 2019a). We used uniform priors for the intercept β_0 that allow the model to cover all possible variability (Appendix Table B.4). For β_1 we defined an uninformative and normally distributed sample prior with an expected value of zero and standard deviation of 50. To explore associations of grain yield and protein plasticity and yield components and N traits, we also implemented bayesian hierarchical linear models described above with their respective priors provided in Appendix Table B.4.

2.3.4.2 Grain yield and protein concentration response to N supply models

For cultivars with contrasting phenotypic plasticity for yield, we described their differential yield response to N supply (mineral soil N at sowing + N fertilizer) with quadratic-plateau models for high (90th percentile) and low (10th percentile) yielding environments:

$$yield_i(tn\ ha^{-1}) \sim N(\mu_i, \sigma_i^2), \quad Eq. 4$$

$$\mu_i = \begin{cases} \beta_0 + \beta_1 x_i + \beta_2 x_i^2 & x_i < AON \\ \beta_0 + \beta_1 AON + \beta_2 AON^2 & \text{otherwise} \end{cases}, \quad Eq. 5$$

$$\beta_0 \sim N(1.0, 1.7),$$

$$\beta_1 \sim N(0.02, 0.06),$$

$$AON \sim N(130, 50),$$

Eq. 6

$$\sigma_i^2 \sim \text{half} - \text{student} - t(3, 0, 2.5),$$

where β_0 is the yield when N supply equals zero and β_1 the linear component and β_2 was decomposed as the term $\frac{-\beta_1}{2 \times AON}$ where AON is the agronomic optimum N supply, which is equivalent to the first derivative equal to zero (Figure 2.2). This model assumes that total N supply comes from two sources: mineral soil N at sowing, fertilizer N; thus, mineralization of N from organic matter and atmospheric N depositions are part of the error of the model. Thus, β_0 represents the expected grain yield when N supply from soil and fertilizer is zero.

Grain protein concentration was modeled using a generalized additive model (GAMs) that allows flexibility on the shape of the relationships between the predictor and explanatory variables with smoothing functions or splines (Pedersen et al., 2019). We defined GAM models for high (90th percentile) and low (10th percentile) protein environments:

$$protein_i(\%) \sim N(\mu_i, \sigma_i^2), \quad Eq. 7$$

$$\mu_i = \beta_0 + \beta_1 + f(Nsupply), \quad Eq. 8$$

$$\beta_0 \sim \text{half} - \text{student} - t(3, 14.4, 2.5),$$

$$X\beta_{1:3} \sim \text{Cauchy}(0, 1), \quad \text{Eq. 9}$$

$$\sigma_i^2 \sim \text{half} - \text{student} - t(3, 0, 2.5),$$

where μ_i is the predicted grain protein concentration in the i^{th} percentile, β_0 is the intercept and β_1 is the effect of the cultivar and $f(N_{\text{supply}})$ represent the smoothing effects of N supply on grain protein concentration. We implemented uninformative priors provided by the default option in *brms* package in R (Eq. 9).

To analyze yield and protein response to N against our three-phase model described in Figure 2.2, we compared cultivars at the starting point of the phases by including traits derived from yield (Eq. 8) and protein (Eq. 9) response to N models (Figure 2.5) as described in Table 2.3.

2.3.4.3 Relationships between phenotypic plasticity, yield components and crop N traits

Linear bayesian regression models were used to quantify the associations between yield components and N traits (section 2.2) with yield and grain protein plasticity as follows:

$$\text{crop\_trait}_{ij} \sim N(\mu_{ij}, \sigma_{ij}^2), \quad \text{Eq. 10}$$

$$\mu_{ij} = \beta_0 + \beta_1 x_{ij}, \quad \text{Eq. 11}$$

where μ_{ij} is the expected value of the j^{th} trait of the i^{th} cultivar with plasticity equal to x_{ij} , β_0 is the intercept and β_1 is the slope indicating the change in a given crop trait per unit yield or protein plasticity.

The relationship between shoot N uptake and grain yield was described with the following process model:

$$\text{yield}_i(\text{tn ha}^{-1}) \sim N(\mu_i, \sigma_i^2) \quad \text{Eq. 12}$$

$$\mu_i = \begin{cases} \beta_0 + \beta_1 x_i + \beta_2 x_i^2 & x_i < NC \\ \beta_0 + \beta_1 NC + \beta_2 NC^2 & \text{otherwise} \end{cases} \quad \text{Eq. 13}$$

$$\begin{aligned} \beta_0 &\sim \delta(0), \\ \beta_1 &\sim N(0.0347, 2), \\ NC &\sim U(0, 400), \end{aligned} \quad \text{Eq. 14}$$

$$\sigma_i^2 \sim \text{half} - \text{student} - t(3, 0, 2.5),$$

where β_0 was set to zero by implementing a point mass distribution prior centered to zero, x_i represents the aboveground N uptake (kg N ha^{-1}); β_1 and β_2 are the linear and quadratic terms respectively, and NC is the critical N uptake that represents the N uptake that maximizes grain yield. Nitrogen utilization efficiency at NC (*i.e.*: NUtE; $\text{kg grain/kg N uptake}$) was derived from the quotient between the posterior distribution of grain yield at the NC and NC.

Similarly, the relationship between grain N yield and shoot N uptake was modeled as:

$$N_{\text{yield}_i} (\text{kg N ha}^{-1}) \sim N(\mu_i, \sigma_i^2), \quad \text{Eq. 15}$$

$$\mu_i = \begin{cases} \beta_0 + \beta_1 x_i + \beta_2 x_i^2 & x_i < NC \\ \beta_0 + \beta_1 NC + \beta_2 NC^2 & \text{otherwise} \end{cases} \quad \text{Eq. 16}$$

$$\begin{aligned} \beta_0 &\sim \delta(0), \\ \beta_1 &\sim N(0.76, 10), \\ AON &\sim U(0, 400), \end{aligned} \quad \text{Eq. 17}$$

$$\sigma_i^2 \sim \text{half} - \text{student} - t(3, 0, 2.5),$$

where β_0 was set to zero by implementing a point mass distribution prior centered to zero, x_i is shoot N uptake (kg N ha^{-1}), β_1 is the linear term and NC is the critical N uptake that maximizes grain N yield.

We used a quadratic model to describe the relationship between NHI and HI as follows:

$$Nyield_i \sim N(\mu_i, \sigma_i^2), \quad \text{Eq. 18}$$

$$\mu_i = \beta_0 + \beta_1 x_i + \beta_2 x_i^2, \quad \text{Eq. 19}$$

$$\beta_0 \sim \delta(0),$$

$$\beta_1 \sim N(1, 2),$$

$$MaxNHI \sim U(0, 1),$$

$$\sigma_i^2 \sim \text{half-student-t}(3, 0, 2.5),$$

Eq. 20

where β_0 was set to zero by implementing a point mass distribution prior centered to zero, β_1 is the linear term and β_2 was expressed as the first derivative equal to zero ($MaxNHI = \frac{-\beta_1}{2 \times \beta_2}$).

2.3.4.4 Model selection

For representing the most convenient relationship between grain yield and protein concentration in response to N supply, we compared two models for each trait: (i) a model in which the parameters were estimated across cultivars and (ii) a model with parameters estimated for each cultivar. We compared linear-plateau and quadratic-plateau models and selected the model with the best fit. Comparisons were performed using *model_performance* function from the *performance* package in R (Lüdtke et al., 2021). Models with the lowest widely applicable information criterion were retained.

2.4 Results

2.4.1 Environments, yield, and grain protein

Growing season rainfall ranged from 358 to 511 mm, and accumulated reference evapotranspiration ranged from 552 to 714 mm (Appendix Figure B.1). Across environments, mean seasonal T_{min} ranged from 1.2 to 2.7 °C; mean seasonal T_{max} ranged from 13.2 to 16.1 °C; the photothermal quotient ranged from 1.37 to 2.19 MJ m⁻² d⁻¹ °C⁻¹ in the critical period and from 0.90 to 1.15 m⁻² d⁻¹ °C⁻¹ during grain fill (Appendix Figure B.1).

Across all sources of variation, grain yield averaged 3.16 Mg ha^{-1} and ranged from 0.79 to 5.65 Mg ha^{-1} (Table 2.2). Average grain yield increased from 2.50 Mg ha^{-1} ($Q_{2.5\%} = 1.14 \text{ Mg ha}^{-1}$; $Q_{97.5\%} = 4.60 \text{ Mg ha}^{-1}$) in the unfertilized control to 3.60 Mg ha^{-1} ($Q_{2.5\%} = 2.24$; $Q_{97.5\%} = 5.15 \text{ Mg ha}^{-1}$) with the highest N rate (Figure 2.3A). Average grain protein concentration was 10.9% and increased from 9.9% ($Q_{2.5\%} = 5.7 \%$; $Q_{97.5\%} = 15.9 \%$) in the unfertilized control to 12.1% ($Q_{2.5\%} = 7.8 \%$; $Q_{97.5\%} = 16.8 \%$) with the highest N rate (Figure 2.3B). The variation in yield and grain protein in unfertilized crops can be partially explained by contrasting initial mineral soil N and organic N mineralization across environments (Table 2.1, Appendix Figure B.1), while the range in the highly fertilized crops suggests that N supply did not limit grain yield (Goos et al., 1982).

Yield associated positively with photothermal quotient during the critical period, the duration of the grain filling period, and to a lesser extent, to the duration of the critical period (Figure 2.3C). Yield correlated negatively with time to anthesis and with mean temperature during the critical period. Grain protein concentration increased with photothermal quotient and mean temperature during grain fill (Figure 2.3C).

2.4.2 Phenotypic plasticity of grain yield and grain protein concentration

Grain yield plasticity varied 1.6-fold, from 0.70 for LCS Chrome to 1.13 for Bentley (Table 2.2). Grain yield plasticity associated with responsiveness to high yielding environments, whereas all cultivars returned similar yield in low yield environments (Figure 2.4A). A comparison of the same analysis using a frequentist approach return similar results and is in Appendix Figure B.3.

Plasticity of grain protein concentration varied 1.6-fold, from 0.73 for WB4269 to 1.18 for Green Hammer (Table 2.2). Grain protein plasticity associated with divergent trait-plasticity

relations for the 90th and 10th percentiles, *i.e.*, highly plastic phenotypes increased protein concentration more markedly in high than in low protein environments (Figure 2.4B, inset Figure 2.4B). A frequentist approach of this same analysis returned similar results and is in Appendix Figure B.3.

2.4.3 Grain yield and protein concentration response to N for cultivars with contrasting plasticity for yield and grain protein concentration

Under high yielding conditions, plasticity was unrelated to yield on phase I (*i.e.*: minimal N supply) and associated positively to yield in phase II (Figure 2.6E). For instance, Bentley, the cultivar with highest phenotypic plasticity for yield, outyielded LCS Chrome by 0.59 Mg ha⁻¹ (C.I._{95%} = 0.17 – 1.01 Mg ha⁻¹). Under low yielding conditions, there were no yield differences among cultivars (Figure 2.5A-D, Appendix Figure B.4, Appendix Table B.3).

Cultivar-specific grain protein response to N supply was only observed under high grain protein environments (Figure 2.5E-H, Appendix Figure B.4), which is denoted by a better performance (lower WAIC; Appendix Table B.3) of the model when parameters were estimated for each of the cultivars. Under low protein environments, the pooled model performed better (Appendix Table B.3), indicating similar grain protein response to N supply among cultivars. In high protein environments, plasticity of grain protein concentration associated with higher protein in phase III (Figure 2.6J).

Yield at critical N uptake was positively associated to yield plasticity (Figure 2.8A). To exemplify, the plastic cultivar for yield Bentley outyielded the stable LCS Chrome by 0.57 Mg ha⁻¹ (C.I._{95%} = 0.28 – 0.87 Mg ha⁻¹) (Figure 2.7A, Figure 2.8A-B). Yield plasticity was unrelated to critical N uptake, N utilization efficiency and N yield (Figure 2.8C, 2.8F, 2.8H). Protein plasticity was negatively related to grain yield at critical N uptake (Figure 2.8B). For instance,

grain yield at critical N uptake was 0.81 Mg ha^{-1} ($\text{C.I.}_{95\%} = 0.43 - 1.25 \text{ Mg ha}^{-1}$) higher in WB4269, stable for protein, compared to Green Hammer, with high plasticity for grain protein concentration (Figure 2.7C, Figure 2.8D). Critical N uptake negatively associated with protein plasticity (Figure 2.8D), which is reflected in the greater N uptake of WB4269 with low plasticity for grain protein concentration compared to the more plastic Green Hammer ($Q_{50\%} = 32.6 \text{ kgN}$; $\text{C.I.}_{95\%} = 4.51 - 58.4 \text{ kgN}$) (Figure 2.7C-D; Figure 2.8D). Protein plasticity was unrelated to N utilization efficiency (Figure 2.8G) and negatively related to N yield (Figure 2.8I).

2.4.4 Associations between phenotypic plasticity and crop traits

Grain yield plasticity was unrelated to protein in high and low yielding environments (Figure 2.9A). Under high yielding conditions, yield plasticity was positively associated to harvest index (Figure 2.9C), while under low yield scenarios yield plasticity associated positively to heads m^{-2} (Figure 2.9L). Yield was unrelated to other physiological traits in high yielding environments (Figure 2.9).

Grain protein plasticity was unrelated to yield in low protein environments and negatively associated to yield in high protein environments (Figure 2.9B). At low protein conditions, protein plasticity associated negatively to harvest index, grains m^{-2} and heads m^{-2} (Figure 2.9D, Figure 2.9I, Figure 2.9M) and positively to kernel weight (Figure 2.9K). In high protein environments, protein plasticity was negatively associated with grain yield, partially due to lower grain m^{-2} and heads m^{-2} (Figure 2.9B, Figure 2.9I, Figure 2.9M).

Figure 2.10A and Figure 2.10B shows the allometric relationship between NHI and HI for cultivars with contrasting phenotypic plasticity. Grain yield plasticity was weakly positively related to HI per unit NHI (Figure 2.10C). In contrast, protein plasticity was negatively associated with HI per unit NHI (Figure 2.10D).

2.5 Discussion

We combined a three-phase model of yield and grain protein concentration in response to N supply with a perspective of phenotypic plasticity to analyze the interaction between cultivar and N fertilization under contrasting environmental conditions in winter wheat. Our findings are bounded by the combination of eight environments and 14 modern semi-dwarf cultivars with a narrow range in plant height (Wang et al., 2023a). Location-season and N fertilization contributed to the variation in environmental conditions (Figure 2.3), in addition to cultivar $\times$ environment interactions typical of agronomic settings (Appendix Figure B.1).

In our experiments initial N supply was sufficient to support tillering potential (Table 2.1). Reflecting common practice in the region (Jaenisch et al., 2021) crops were fertilized during spring after winter dormancy (GS 25). Timing of N application can contribute to synchronizing crop N supply and N demand (Hawkesford, 2012; Giordano et al., 2023). For instance, N applications at or after jointing will most likely increase grain protein concentration rather than yield (Lollato et al., 2021; Souza et al., 2022; Giordano et al., 2023). Understanding the interaction between yield and protein plasticity and late-season N application over grain yield and protein remains to be investigated.

Yield plasticity was agronomically adaptive as it associated with greater yield in high yielding environments, in line with previous studies in the study region (Grogan et al., 2016; Lollato et al., 2020b). For instance, on a trial conducted with 299 winter wheat cultivars across 11 environments in the study region, Grogan et al. (2016) found that plasticity of yield was related to maximum yields (slope = $2.737 \text{ Mg ha}^{-1}\text{plasticity}^{-1}$) and unrelated to yield across low yielding environments, supporting our findings in Figure 2.4A. At the expense of lower yield, and particularly in low grain protein environments (Figure 2.4B), plasticity of grain protein

concentration associated with high grain protein regardless of environmental variation. Nitrogen was a key factor related to the expression of phenotypic plasticity as the associations between trait and plasticity for yield and protein were only apparent under non-N limiting conditions, phase II for yield and phase III for grain protein concentration. Grain yield plasticity related positively to greater yield under favorable yielding conditions and was unrelated to grain protein content (Figure 2.9A), highlighting the possibility of breeding for high yield plasticity while maintaining protein concentration levels.

Protein plasticity associated negatively to critical N uptake (Figure 2.8D), highlighting that drivers of protein plasticity can be associated to the ability of the crop to capture N. Empirical evidence supports the co-regulation of crop N uptake by N supply and crop biomass accumulation (Gastal and Lemaire, 2002; Gastal et al., 2015a). Crop biomass accumulation, in turn, drives plant N demand (Devienne-Barret et al., 2000), which drives N uptake under high N supply (Gastal and Lemaire, 2002) through physiological mechanisms including: (i) density of N transporters per unit root length; (ii) intrinsic activity of N transporters; (iii) activity of N transporters modulated by photosynthesis signaling; and (iv) shoot N satiety signals (Gojon et al., 2009; Nacry et al., 2013).

The association between yield plasticity and yield in favorable environments was partially mediated by the higher harvest index of cultivars with higher yield plasticity (Figure 2.9C). In contrast, yield often associates more strongly with biomass (Slafer et al., 2014; de Oliveira Silva et al., 2020b; Jaenisch et al., 2022). This reinforces the notion that a trait and its plasticity are partially independent traits with partially independent genetics (Bradshaw, 1965; Reymond et al., 2003a; Alvarez Prado et al., 2014a; Diouf et al., 2020; Happ et al., 2021). Thus, selection for yield potential may favor low grain protein whereas selection for yield plasticity

could favor high yield in non-N limiting environments while maintaining acceptable grain protein concentration.

There were environment-dependent associations between plasticity of grain protein concentration and grain yield per se, whereby cultivars with higher plasticity for grain protein concentration had lower grain number and yield in low protein environments (Figure 2.9I). Higher protein plasticity associated with higher kernel weight (Figure 2.9K), which is linked to the number of endosperm cells in the grain, in turn associated with grain N sink capacity (Fradgley et al., 2021). High kernel weight and grains per head in cultivars with high protein plasticity did not compensate the lower grain number; this is consistent with the high plasticity of grain number and the stability of grain weight (Bradshaw, 1965; Sadras, 2007, 2021; Sadras and Slafer, 2012; Slafer et al., 2014, 2022). Thus, cultivars with higher plasticity of grain protein concentration largely expressed the trade-off between grain number and grain weight, partially related to the reduction in survival of distal florets and lower proportion of constitutively small grain (Slafer et al., 2022).

Simultaneous improvement of yield and protein must consider the target trait and its interaction with management and the environmental source of variation. Grain protein deviation has taken countless research efforts (Monaghan et al., 2001a; Bogard et al., 2010; Mosleth et al., 2015) as a target trait to break the negative association of yield and protein. Nonetheless, a study mapping two populations of 159 and 189 locally adapted genotypes on six environments showed that selection for grain protein deviation was positively associated to protein but still negatively affecting grain yield (Rapp et al., 2018). In our research, yield plasticity was positively associated to yield in high yield, non-N limiting environments and was unrelated to protein, opening paths for increasing yield without affecting grain protein content. The positive

association between NHI and HI is widespread in crops (Ciampitti and Vyn, 2011; Tamagno et al., 2017) including wheat (Desai and Bhatia, 1978); it reflects a tight link between the allocation of carbon and N to grain. However, the strength of the association varies with grain protein concentration (Lemaire and Ciampitti, 2020). The negative association between the slope of the allometric relation between NHI and HI and protein plasticity partially explains the negative associations between protein plasticity and grain yield, as HI became less sensitive to variations in NHI with increasing phenotypic plasticity for grain protein concentration.

2.6 Conclusion

This article proposes a phenotypic plasticity framework to analyse yield and protein response to N, disclosing $G \times N$ interactions and identifying higher yielding cultivars that exploit non-N limiting conditions. Our findings have agronomic, breeding and modelling implications: (i) releasing grain yield and protein plasticity information on commercial wheat cultivars data sheet can guide growers towards high yield plasticity cultivars when aiming to high yield with acceptable protein levels or high protein plasticity cultivars to ensure high protein at the expense of lower yields; (ii) dissecting the genetic basis of wheat yield phenotypic plasticity remains a challenge. Yield plasticity has partially its own genetic regulation and was unrelated to grain protein concentration and protein plasticity in this dataset. Breeding programs may benefit as yield plasticity can be subject to direct selection in order to breed for high yielding cultivars while maintaining grain protein concentration levels; (iii) accuracy of N recommendations and mechanistic crop simulation models can be improved by accounting for $G \times N$ interactions through plasticity of yield and grain protein. This study provides a basis for wheat growth models to account for yield and protein plasticity through $G \times E$ dependent physiological processes such as grain carbon and N allocation.

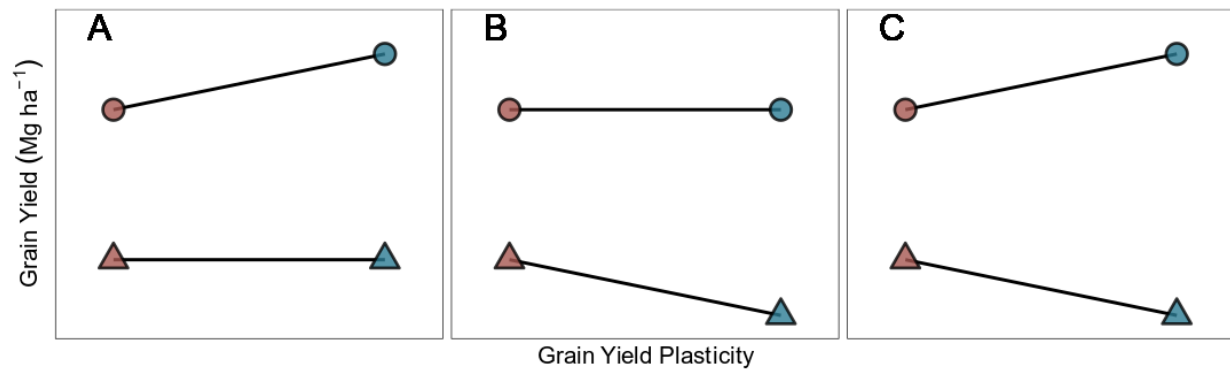


Figure 2.1. Hypothetical relations between trait and trait plasticity for a phenotype with high (blue) and low (red) plasticity under conditions that favor high (circles) or low (triangles) traits. The higher plasticity of the blue phenotype arises from (A) responsiveness to favorable conditions, or (B) higher sensitivity to stressful conditions, or (C) high responsiveness to both favorable conditions and stress.

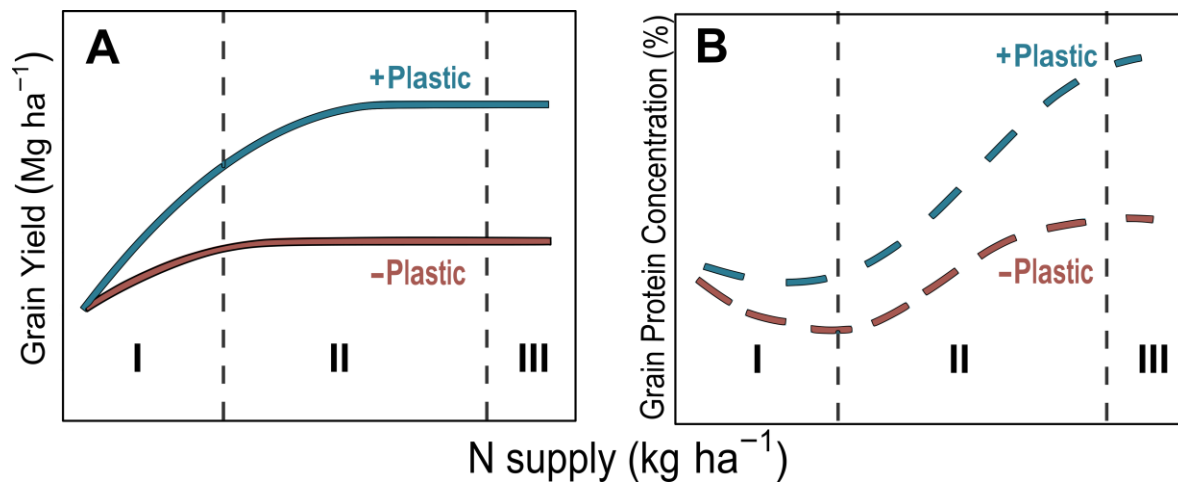


Figure 2.2. Conceptual model of grain yield (A; solid lines) and protein (B; dashed lines) in response to N supply for phenotypes with high (blue) and low (red) phenotypic plasticity. Vertical dashed lines are the boundaries of phases I, II, III in the response of yield and protein to N supply. In phase I, N supply limits both yield and grain protein; in phase II, N supply limits grain protein but not yield; and in phase III, N supply does not limit yield or grain protein concentration.

Table 2.1. Year, location, soil type, geolocation, crop husbandry, and mineral soil N (0-0.6 m) at sowing in eight location-seasons. Fungicide was applied at GS65. Abbreviation: DAS, days after sowing.

Year	Location	Env.	Soil	Latitude	Longitude	Sowing	N fertili- zation (DAS)	Fungi- cide (DAS)	Harvest (DAS)	Initial mineral soil N (kg ha ⁻¹)	
										NO ₃ -N	NH ₄ -N
2020	Ashland Bottoms	AM20	Belvue silt loam	39°08'31"N	96°37'52"W	10/25/2019	133	207	245	32.9	22.3
	Great Bend	GB20	Taver loam	38°21'46"N	98°52'10"W	10/16/2019	146	211	253	135.2	11.9
	Hutchinson	HU20	Ost loam	37°55'43"N	98°01'50"W	10/10/2019	153	209	263	222.9	51.9
	Viola	VI20	Nalim loam	37°18'36"N	98°40'12"W	10/17/2019	147	202	242	31.8	20.4
2021	Ashland Bottoms	AM21	Belvue silt loam	39°08'31"N	96°37'52"W	10/14/2020	146	208	250	54.3	39.8
	Ashland Bottoms	AB21	Bismark grove silt loam	39°07'57"N	96°37'11"W	10/13/2020	147	211	251	50.2	59.4
	Hutchinson	HU21	Ost loam	37°55'43"N	98°01'50"W	10/8/2020	151	209	251	72.3	53.2
	Manhattan	MA21	Kahola silt loam	38°24'00"N	98°54'00"W	10/7/2020	153	218	243	74.6	92.3

Table 2.2. Characteristics of the 14 winter wheat commercial cultivars included in the study: year of release, average protein deviation, maturity, plant height, drought tolerance and standability. Phenotypic plasticity (unitless), calculated as variance ratio (Eq. 1), is shown for yield, its components, grain protein concentration, and crop N traits. Abbreviations: year of release (YOR), grain protein deviation from the grain yield ~ grain protein regression line (GPD), maturity (MAT, 1 = early; 5 = medium; 9 = late), plant height (PH), drought tolerance (DT, 1 = excellent; 5 = good; 9 = poor straw strength: 1 = excellent; 5 = good; 9 = poor), standability (Sta), harvest index (HI), N uptake (Nup), N harvest index (NHI), N utilization efficiency (NUtE). *sources: <https://bookstore.ksre.ksu.edu/pubs/mf991.pdf>; <http://www.ramwheatdb.com/database.php>

Cultivar	YOR	GPD	MAT*	PH	DT*	Sta*	Phenotypic Plasticity (dimensionless)												
		(%)		(cm)			Yield	Protein	Biomass	HI	Grains m ⁻²	Grain weight	Heads m ⁻¹	Grains head ⁻¹	Biomass Nup	Above- ground Nup	Stover N concentra- tion	NHI	NUtE
Everest	2009	-0.14±0.01	2	69.7±6.5	7	2	0.99	0.87	0.68	0.74	0.8	0.49	0.75	0.68	0.97	0.94	1.05	0.81	0.88
WB Grainfield	2012	-0.49±0.05	5	78.3±7.3	5	4	1	0.97	1.08	1.01	1.1	1	0.85	0.8	0.99	0.94	0.72	0.91	1.18
WB4458	2012	0.57±0.05	4	73.8±6.9	6	2	1.11	1.07	0.79	0.53	0.66	0.56	0.57	0.78	0.96	1.04	1.01	0.86	0.79
DoubleStop	2013	0.92±0.09	6	75.6±7.0	5	4	0.92	0.98	1.47	0.58	0.82	0.94	1.09	0.47	1.19	1.24	0.9	0.84	0.64
SY Monument	2014	-0.25±0.02	6	75.6±7.0	6	5	0.9	0.85	1.19	0.74	0.99	0.73	0.92	0.62	1.08	1.08	0.93	0.8	0.99
Bentley	2015	-0.12±0.01	4	79.6±7.4	4	7	1.13	0.92	0.98	0.93	1.07	0.89	0.88	0.92	0.95	1.13	0.83	0.82	0.98
WB4269	2015	-0.16±0.01	4	68.4±6.3	5	3	1.12	0.74	0.67	0.71	1.24	0.56	1.29	0.61	0.96	0.9	0.92	0.74	0.63
WB4303	2015	0.12±0.01	3	72.5±6.7	6	1	0.98	1	0.82	1.17	1.03	0.9	0.49	1.87	1.09	1	1.29	1.18	0.86
Larry	2016	-0.26±0.02	5	75.0±7.0	6	3	0.89	0.93	0.97	1.09	0.83	0.73	0.65	0.77	0.88	0.9	0.85	0.99	1.05
LCS Chrome	2016	0.43±0.04	8	80.4±7.5	4	3	0.71	1.07	1.12	1.21	0.79	0.99	0.77	0.59	0.97	0.86	1.27	1.58	0.97
Tatanka	2016	-1.18±0.11	6	73.2±6.8	6	7	1.04	0.89	0.77	0.61	1.33	0.63	1.31	0.55	1.04	0.93	0.89	0.83	1.3
Zenda	2016	-0.28±0.03	4	76.6±7.1	7	3	0.9	0.8	0.95	0.57	0.87	0.53	0.77	0.61	1.07	0.87	0.98	1.04	0.85
Bob Dole	2017	0.11±0.01	4	83.5±7.8	6	5	0.96	1.07	1.25	0.79	0.74	0.97	0.7	0.83	1.01	0.89	0.74	0.98	1.15
Green Hammer	2018	0.89±0.08	4	78.2±7.3	4	1	0.97	1.18	0.96	0.63	0.78	0.82	0.56	0.96	0.86	1.32	1.5	1.28	0.82

Table 2.3. Analytical solutions implemented for identifying the starting point of the phases described in Figure 2 and fitted in Figure 5. In phase III, only those cultivars that reached maximum protein were compared. Abbreviations: N supply (N_s).

Phase	Analytical solution	Description
I	$N_s(kgN\ ha^{-1}) = \min(N_s)$	Grain yield and protein comparisons at minimum N supply.
II	$\frac{dYield}{dN_s} = 0,$ $where\ \frac{dYield}{dN_s} = \lim_{w \rightarrow 0} \frac{Yield(N_s + w) - Yield(N_s)}{w}$	Grain yield and protein comparisons at the agronomic optimum N supply (AON). Where AON is the starting point of phase II and represents the N supply that maximizes yield which is represented by the first derivative equal to zero and $w = \Delta N_s$ value approaching zero.
III	$\frac{dProtein}{dN_s} = 0,$ $where\ \frac{dProtein}{dN_s} = \lim_{w \rightarrow 0} \frac{Protein(N_s + w) - Protein(N_s)}{w},$ $for\ N_s > \frac{dYield}{dN_s} = 0$	Comparisons of grain protein at N supply that maximizes protein (NMP). Where NMP is the starting point of phase III and represents the N supply that maximizes protein which is represented by the first derivative equal to zero and $w = \Delta N_s$ value approaching zero.

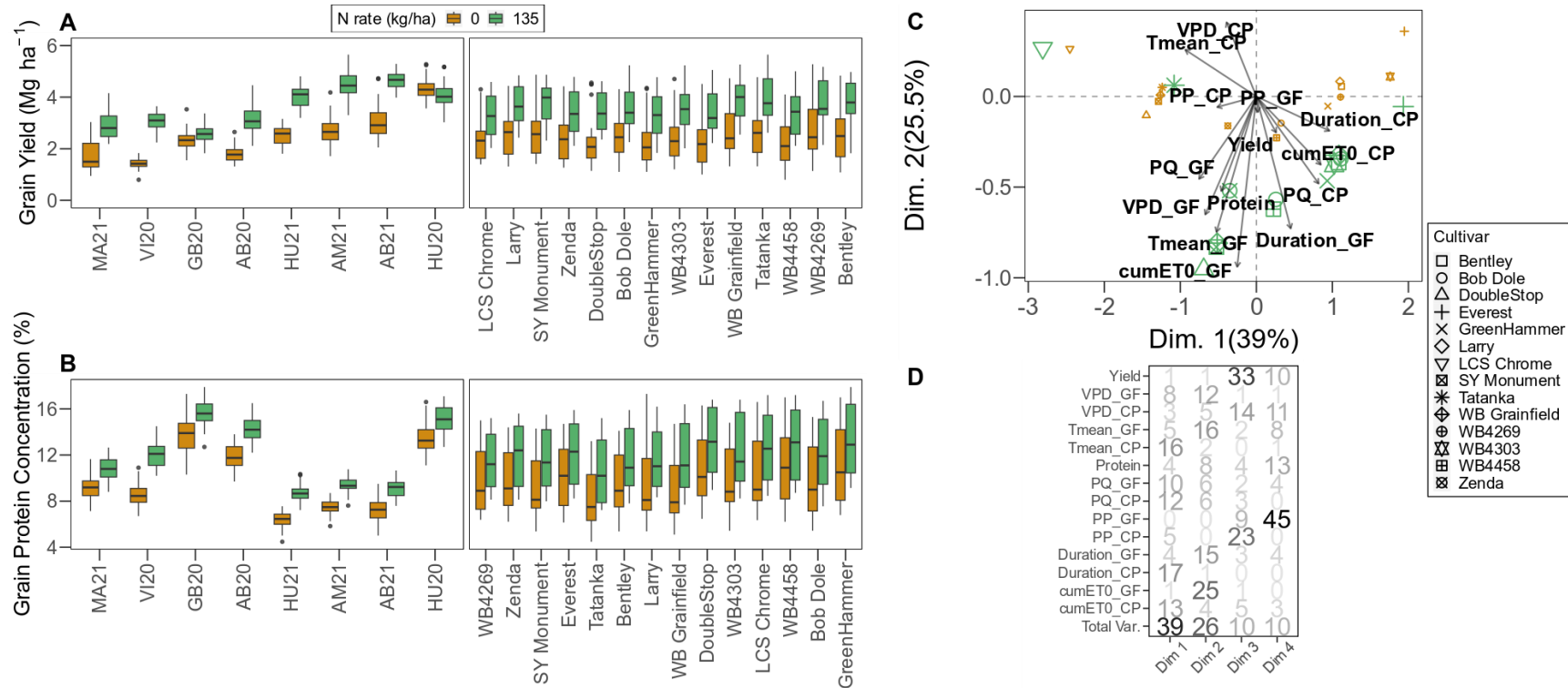


Figure 2.3. Frequency distribution of grain yield (A) and grain protein concentration (B) pooled for cultivars and location-season on the most contrasting N rates of 0 and 135 kg N ha⁻¹. The box represents the interquartile range and the line inside the box the median. Whiskers represent 1.5x the interquartile range. Cultivars are sorted in increasing order according to their phenotypic plasticity of yield (A) and protein (B); and location-seasons are sorted from left to right according to the mean grain yield in increasing order. Principal component analysis for grain yield, grain protein concentration and environmental variables: biplot (C) and variance contribution within dimension (D) in experiments carried out in Kansas in 2020 and 2021. In C and D, the color of the points represents the extreme N rates (0 kg N ha⁻¹ orange, 135 kg N ha⁻¹ green), while shapes represent cultivars. Abbreviations: Ashland Bottoms 2A2 field (AB), Ashland Bottoms M3 field (AM), Great Bend (GB), Hutchinson (HU), Manhattan (MA), Viola (VI), season 2019-2020 (20), season 2020-2021 (21), mean temperature (Tmean), vapor pressure deficit (VPD), photothermal quotient, (PQ), cumulative reference evapotranspiration (cumET0), critical period (CP) and grain filling period (GF).

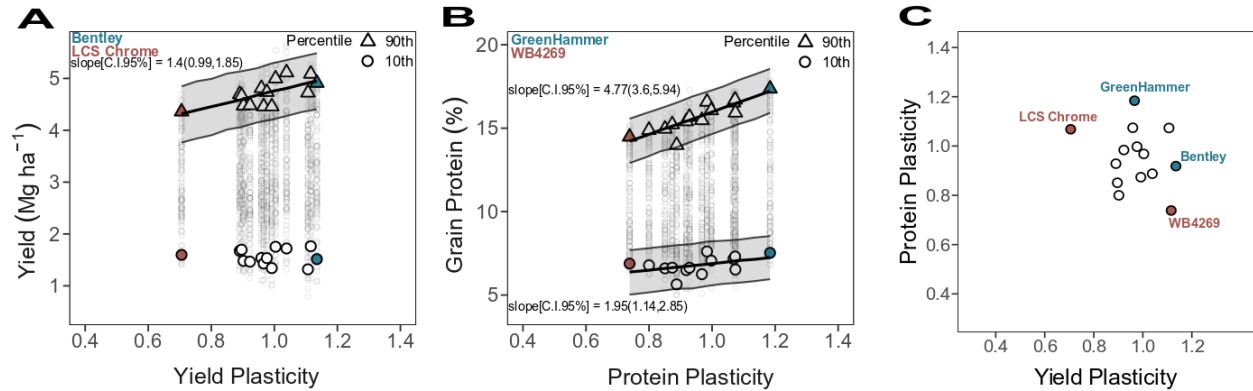


Figure 2.4. Trait-plasticity relationships for grain yield (A) and protein (B), and relationship between plasticity of grain protein and yield (C). Colors highlight the least (red) and the most plastic (blue) cultivars for each trait. Solid lines (posterior median) and ribbons (posterior 95% credible interval) are shown when the 95% credible interval of the slope of the relation is not overlapping zero. Inset text shows the slope posterior median and 95% credible interval.

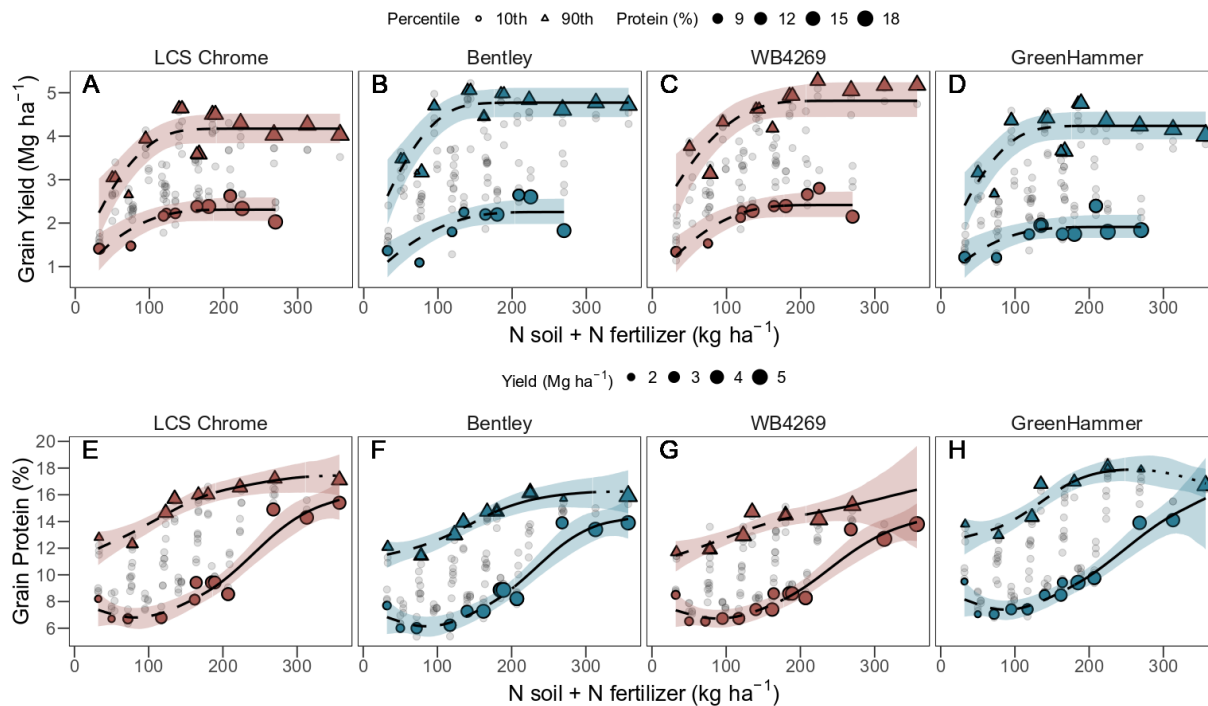


Figure 2.5. Wheat grain yield (A-D) and protein (E-H) response to N supply under conditions conducive to high (90th percentile, triangles) and low (10th percentile, circles) trait expression for cultivars with contrasting phenotypic plasticity. Red symbols are for cultivars with low plasticity for yield (LCS Chrome) and protein (WB4269), and blue is for cultivars with high plasticity for yield (Bentley) and protein concentration (Green Hammer). Linetype indicates the phases conceptualized in Figure 2: dashed (phase I), solid (phase II), dotted (phase III). Lines represent the posterior medians and ribbons the 95% estimation credible interval for model predictions. The size of the symbol shows protein concentration in the yield panels (A-D) and yield in the protein panels (E-H).

Phase

Percentile ○ 10th △ 90th

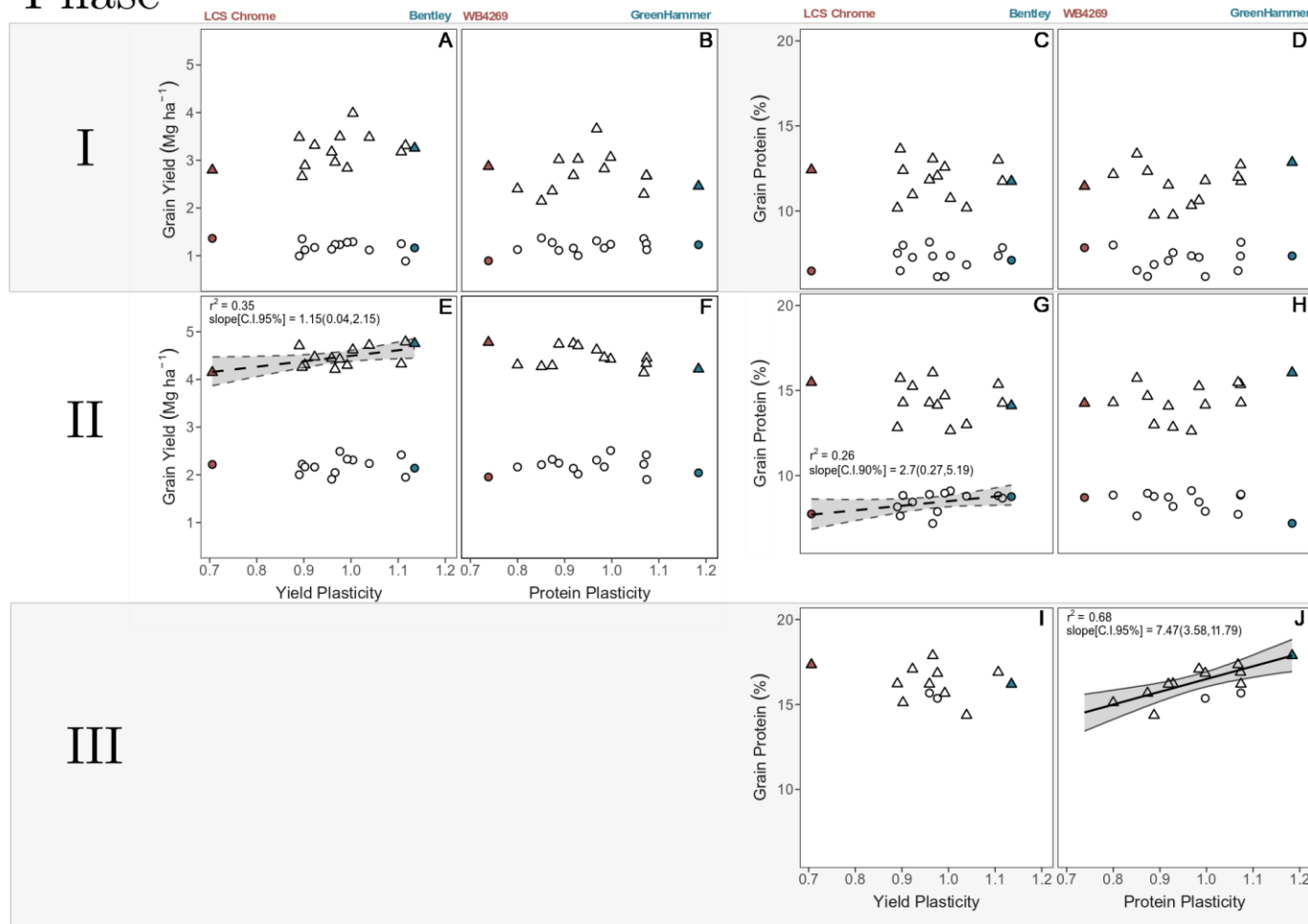


Figure 2.6. Association of yield and protein plasticity with grain yield (A, B, E, F) and protein (C, D, G, H, I, J) at the starting point of phases described in Figure 2 and Table 3 (phase I - N limits yield and protein; phase II, N limits for protein but not for yield; phase III – non-N limitation). In yield panels shapes represent high (triangles) and low (circles) yielding environments; in protein panels shapes represent high (triangles) and low (circles) protein environments. Lines shown only when the slope's credible interval not overlaps zero at different confidence levels (95% - solid lines; 90% - dashed lines).

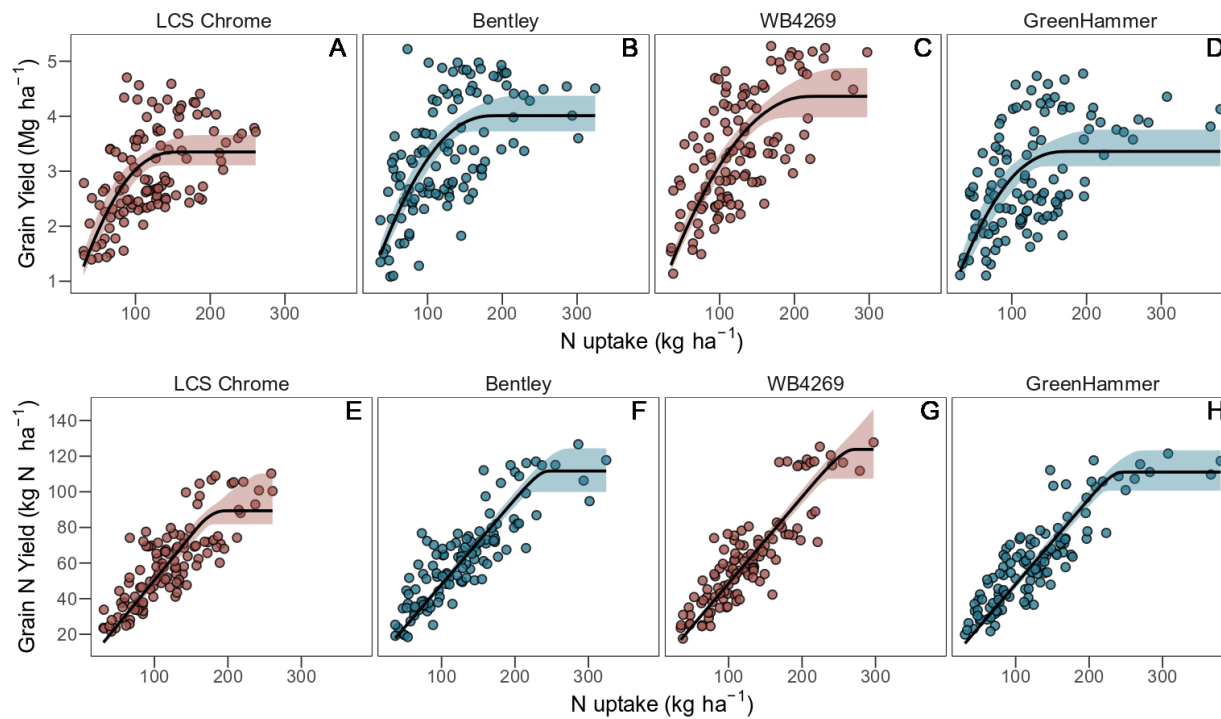


Figure 2.7. Wheat grain yield (A-D) and N yield (E-H) response to N uptake across environments for cultivars with contrasting plasticity for yield (LCS Chrome, Bentley) and protein (WB4269, Green Hammer). Solid lines represent the posterior medians and ribbons the 95% estimation credible interval for model predictions.

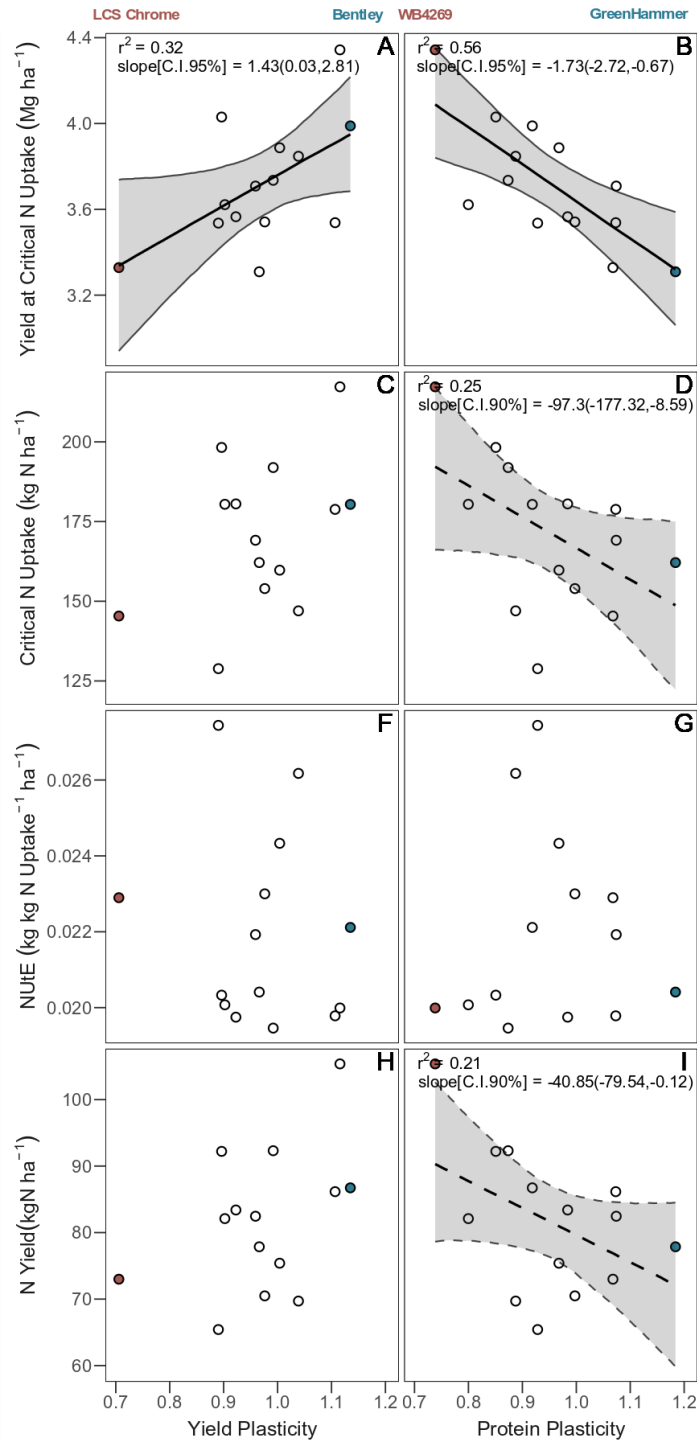


Figure 2.8. Association between yield and protein plasticity and yield at the critical N uptake, critical N uptake, N utilization efficiency (NUE) and N Yield for contrasting yield and protein plasticity cultivars pooled across environments. Lines shown only when the slope's credible interval does not overlap zero at 95% (solid line) and 90% (dashed lines). Inset slopes represent the median and credible interval.

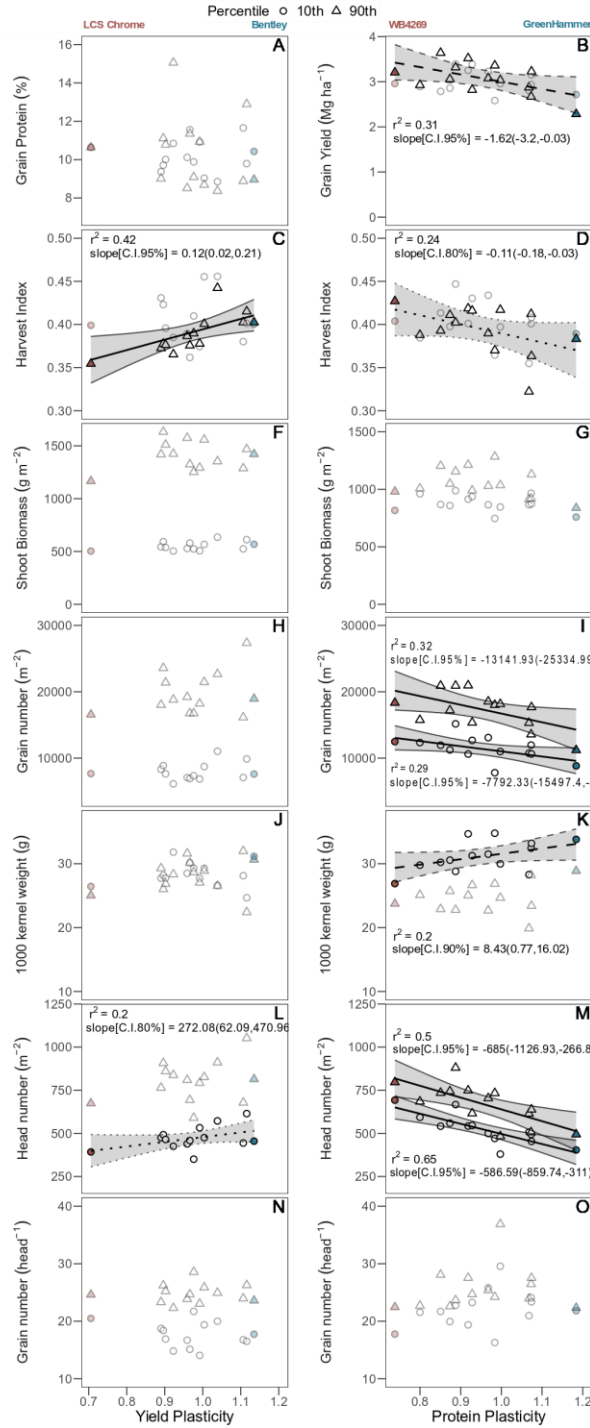


Figure 2.9. Relations between grain yield phenotypic plasticity (A, C, F, H, J, L, N) and protein (B, D, G, I, K, M, O) phenotypic plasticity and crop traits (grain protein, grain yield, harvest index, shoot biomass, grain number m⁻², thousand kernel weight, head number m⁻², and grain number head⁻¹) for crops grown in low (10th percentile, circles) and high (90th percentile, triangles) yield and protein environments. Points and lines shown only when the slope's credible interval does not overlap zero at 95% (solid lines), 90% (dashed lines) and; 80% (dotted lines). Inset slopes represent the median and credible interval.

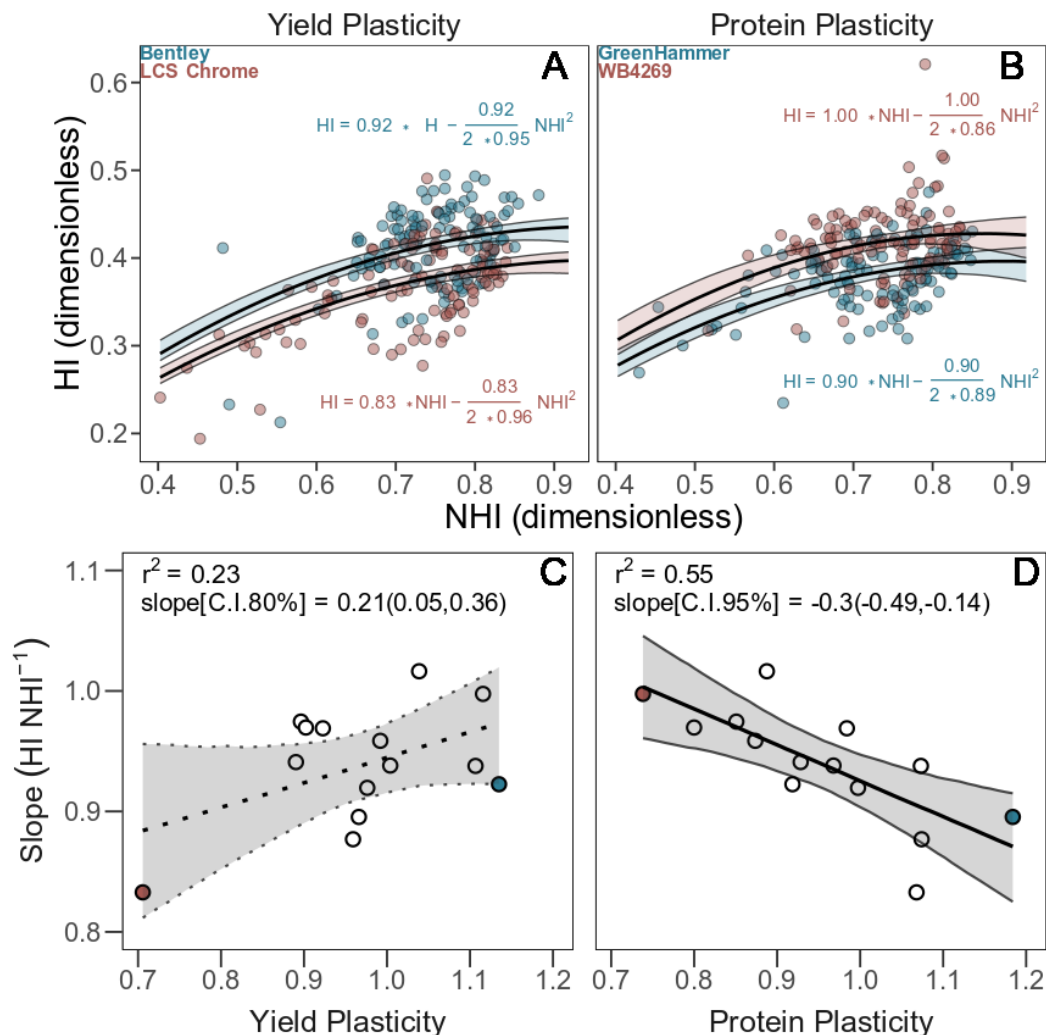


Figure 2.10. Allometric relation between N harvest index (NHI) and harvest index (HI) for contrasting yield (A) and protein (B) plasticity cultivars; $R^2 = 0.34$. Association between yield (C) and protein (D) plasticity and the linear term of the quadratic models presented above. Lines shown only when the slope's credible interval not overlaps zero at different confidence levels (95% - solid lines; 90% - dashed lines; 80% - dotted lines). Inset slopes represent the median and credible interval.

Chapter 3 - A Bayesian framework to model variance of grain yield response to plant density

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Abstract

Background: The expected grain yield response to plant density in winter wheat (*Triticum aestivum* L.) follows a diminishing returns function. To our knowledge, all previous studies dealing with plant density have assumed constant variance. The gap relies on quantifying the optimum plant density that optimizes grain yield at the lowest risk. Here, we propose a Bayesian hierarchical framework to model the variance of grain yield response to plant density. We demonstrate our framework by identifying the plant density in each seed size, seed treatment and environment combination that maximizes the expected yield and minimizes yield variance.

Results: To fit the model, we used data from field experiments conducted in the Canadian Prairies to identify informative priors and Kansas experiments to demonstrate and validate our framework. Kansas experiments were conducted in 25 environments and consisted of a complete factorial combination of three seed cleaning methods leading to three different seed sizes (light, moderate, heavy), two or three seeding rates, and two seed chemical treatments (insecticide + fungicide vs. none). We described both expected yield and variance of yield in response to plant density. The proposed model allowed us to quantify the minimum risk plant density (*minRPD*), which represents the minimum plant density at which grain yield variance becomes constant. Plant density at the *minRPD* was always greater than the agronomic optimum plant density (*AOPD*, i.e.: the plant density that maximizes expected yield); thus, *minRPD* could be used to

estimate the minimum plant density that maximizes expected yield and minimizes yield variance. When compared at the *AOPD*, four seed cleaning × chemical treatments combinations resulted in similar yield advantages over the control under high and low yielding environments. However, in low-yielding environments, only two cleaning × chemical treatments combinations resulted in smaller variance when compared at the *minRPD* against the control. All seed cleaning × chemical treatments combinations resulted in similar *AOPD*. However, two cleaning × chemical treatments combinations had greater *minRPD* in low-yield environments compared to the control.

Conclusion: Modeling grain yield response to plant density with the proposed framework is suitable for heteroscedastic data scenarios. Future research may focus on exploring how genotypes, environments and their interaction modulate the difference between *AOPD* and *minRPD* and, extend the framework to a variety of processes involving crop management decisions.

Abbreviations: *AOPD*: agronomic optimum plant density; *minRPD*: minimum risk plant density; *maxVPD*: maximum variance plant density; $q_{.50}$: quantile 0.50; $q_{.25}$: quantile 0.025; $q_{.975}$: quantile 0.975.

3.1 Background

The response of winter wheat to plant density has been widely studied (Fischer et al., 1976, 2019; Dahlke et al., 1993; Beres et al., 2010). Previous studies focused on the average effects (*i.e.*, expected value) of plant density on yield (Whaley et al., 2000; Valério et al., 2009; Bastos et al., 2020) in interaction with cultivars (Briggs and Ayten-Fisu, 1979; Baker, 1982; Wiersma, 2002; Valério et al., 2009, 2013; Mehring et al., 2020), seeding management strategies (*e.g.*, seed size and seed treatment ; Beres et al., 2016), sowing date (Spink et al., 2000) and environment (Lloveras et al., 2004). These studies have always used similar models that assume constant variance (*i.e.*, ‘spread of the data’) for all plant densities, which is oftentimes overlooked (*e.g.*: Figure 8, Darwinkel, 1978). Despite this fact, no attempts have been made to model yield variance in response to plant density thus far.

Variance models were developed for heteroscedastic data scenarios and have been used for decades (Taylor, 1961; Goldfeld and Quandt, 1965; Engle, 1982; Engle et al., 1985) in fields as diverse as macroeconomics (Engle, 1982), epidemiology (Johnson et al., 2018) and ecology (Seekell et al., 2012). More recently, Bayesian modeling has been successfully implemented for modeling heteroscedastic data (Parker et al., 2021), with multiple advantages compared to frequentist approaches allowing to integrate multiple sources of information (*e.g.*: selecting informative priors ; Banner et al., 2020) and providing the means for making inference based on probabilities (Hooten and Hefley, 2019).

Adopting a fully Bayesian analysis requires specifying objective priors reflecting the current state of knowledge. In a Bayesian setting, informative priors are based on data that weights model parameters. Similarly, in hierarchical modelling structures, which are widely accepted and applied in the scope of agronomy (Makowski et al., 2020; Lacasa et al., 2023),

model parameters are informed based on a given process model. Hence, using informative priors supported on previous data not only reflects the appropriate use of Bayesian models but also can increase parameter precision (*i.e.*, narrowing credible intervals) without reducing accuracy (*e.g.*, targeted median *minRPD*), when specified correctly (Morris et al., 2015).

The expected wheat yield response to plant density follows a diminishing returns function (Willey and Heath, 1969; Fischer et al., 2019) which is supported by crop eco-physiological processes (Whaley et al., 2000). The mathematical equation of expected yield response to plant density can vary from quadratic (Lloveras et al., 2004; Mehring et al., 2020), quadratic-plateau (Willey and Heath, 1969), linear-plateau (Lollato et al., 2019b; Bastos et al., 2020) or exponential rise to maximum (Willey and Heath, 1969; Spink et al., 2000; Lollato et al., 2024). Across proposed mathematical models, light interception limits yields under low plant densities (Whaley et al., 2000; Fischer et al., 2019). At higher plant densities yield reaches a plateau (Tokatlidis, 2014; Fischer et al., 2019; Bastos et al., 2020). The nature of the plateau relies on compensation mechanisms to maintain grain yield while increasing plant density, including (i) reduction in the number of shoots per plant, (ii) reduction in the green area per shoot, (iii) lower radiation use efficiency through less evenly light distribution across the vertical canopy profile and (iv) changes in the resource partitioning within the plant related to sink size (Whaley et al., 2000).

Environmental factors interact with crop management practices to influence the optimum plant density required to maximize grain yield (Beres et al., 2016; Jaenisch et al., 2019, 2022). The inherent uncertainty of environmental conditions within a cropping season requires us to think about alternative approaches that account for the uncertainty on optimum plant density quantification. Thus, we developed a Bayesian hierarchical framework to model the variance of

grain yield response to plant density. We demonstrate the model by combining information in two datasets of similar characteristics (see sections 2.2, 2.3) aiming to identify the plant density in each seed size, seed treatment and environment combination that maximizes expected yield and minimizes yield variance.

3.2 Methods

3.3.1 Modeling grain yield response to plant density

To model the density-yield relationship we implement a hierarchical Bayesian framework as follows:

$$y_{ij} \sim N(\mu_{ij}, \sigma_{ij}^2), \quad (1)$$

$$\mu_{ij} = \begin{cases} \beta_{1j}s_{ij} + \beta_{2j}s_{ij}^2, & s_{ij} < AOPD_j \\ \beta_{1j}AOPD_j + \beta_{2j}AOPD_j^2, & \text{otherwise} \end{cases}, \quad (2)$$

$$\sigma_{ij}^2 = \begin{cases} 0, & s_{ij} = 0 \\ e^{\alpha_{1j}s_{ij} + \alpha_{2j}s_{ij}^2}, & s_{ij} < minRPD_j. \\ e^{\alpha_{1j}minRPD_j + \alpha_{2j}minRPD_j^2}, & s_{ij} > minRPD_j \end{cases} \quad (3)$$

In Equation 1 y_{ij} represents an observation of the response variable grain yield at the i th plot ($i = 1, 2, \dots, n$) in the j th combination of seed size, seed treatment and yielding environment ($j = 1, 2, \dots, 12$) and follows a normal distribution with an expected value μ_{ij} and variance σ_{ij}^2 . The physiological mechanisms described in the previous section support that μ_{ij} is affected by plant density (s_{ij}) following a quadratic plateau function described in Equation 2. The quadratic-plateau expression in Equation 2 is biologically meaningful and allows to interpret model parameters from an agronomic perspective. Here, β_{1j} and β_{2j} are the linear terms specific to the j th seed size $\times$ seed treatment $\times$ environment and $AOPD_j$ is the agronomic optimum planting density, which is the smallest value of s_{ij} that maximizes μ_{ij} . In other words, $AOPD_j$ can be

interpreted as the lowest plant density required to reach yield plateau. We note that the intercept in this process model (Eq. 2) is set to zero, as we assume μ_{ij} is equal to zero when s_{ij} is zero.

The knowledge gap lies on how yield variance (σ_{ij}^2) is affected by s_{ij} . Thus, we propose Equation 3 to describe the non-linear process of σ_{ij}^2 as a function of s_{ij} . First, σ_{ij}^2 is equal to zero when s_{ij} is zero. Secondly, σ_{ij}^2 increases with s_{ij} , following an exponential-quadratic function until a maximum. Last, σ_{ij}^2 decreases until a point where further increases in plant density do not modify σ_{ij}^2 (i.e., σ_{ij}^2 is constant). The value of s_{ij} where σ_{ij}^2 becomes constant is defined by the parameter $minRPD_j$ (minimum risk plant density). In other words, $minRPD_j$ represents the minimum value of plant density that minimizes yield variance on the right-hand side of the maximum variance. Likewise, $minRPD_j$ is a separate value from the $AOPD_j$, that identifies the minimum plant density required to minimize risk while still within the optimum yield range.

The model described in Equations 1-3 can be easily adapted to commonly used experimental designs of agricultural experiments, such as experiments testing the interaction of plant density and genotype (i.e.: Valério et al., 2009) or row spacing (i.e.: Fischer et al., 1976). To facilitate the implementation and extensions of our model, we provide a detailed description of the model fitting process in supporting material and its implementation within the R programming language (https://github.com/giordanon/yield_variance_plant_density; R Core Team, 2021).

To fully specify our Bayesian model, we need to define the priors for the parameters in Equations 1 to 3. Instead of explicitly specifying our priors for β_{2j} and α_{2j} , we chose to consider $AOPD_j$ and $maxVPD_j$ respectively because they are more interpretable quantities (i.e., their units

are in plants m⁻²), thus resulting in a more conscious prior selection. Assuming μ_{ij} and s_{ij} are constants, then the $AOPD_j$ can be expressed as a function of β_{1j} and β_{2j} (Eq. 4):

$$\begin{aligned}\frac{\partial \mu_{ij}}{\partial s_{ij}} = 0 &= \beta_{1j} + 2\beta_{2j}AOPD_j \rightarrow \\ AOPD_j &= \frac{-\beta_{1j}}{2\beta_{2j}}.\end{aligned}\tag{4}$$

Likewise, $maxVPD_j$, maximum variance plant density, is the value of plant density that maximizes σ_{ij}^2 (Eq. 5) and can be expressed as a function of α_{1j} and α_{2j} .

$$\begin{aligned}\frac{\partial \sigma_{ij}^2}{\partial s_{ij}} = 0 &= (\alpha_{1j} + 2\alpha_{2j}maxVPD_j) e^{\alpha_{1j}maxVPD_j + \alpha_{2j}maxVPD_j^2} \rightarrow \\ maxVPD_j &= \frac{-\alpha_{1j}}{2\alpha_{2j}}.\end{aligned}\tag{5}$$

3.3.2 Developing informative priors: Canadian Prairies data

Prior hyperparameters were defined using data of winter wheat response to density in the Canadian Prairies (see details below) and previous literature (Fischer et al., 2019; Eq. 6-10). We acknowledge that the Canadian Prairies and Kansas are widely differing environments; however, priors used for the purpose of this study have a support wide enough for model parameters acceptable to both regions. The procedure consisted of: 1) defining flat priors based on previous literature (Fischer et al., 2019, see Appendix C for details on flat priors); 2) fitting the proposed model (Eq. 1-3) to the Canadian Prairies dataset adopting flat priors; 3) derive quantities (*e.g.*, the expected value, standard deviation, and quantiles) from the fitted model in step 2 and; 4) parametrize priors in the desired model.

Detailed procedures for this trial comprised of field experiments conducted in 26 environments across Canada during three cropping seasons between 2010 and 2013 are cited in

Beres et al. (2016). Briefly, this study consisted of a factorial combination of two seeding rates (200 and 400 seeds m⁻²), three seed size levels (small, moderate, or heavy), and two seed treatment levels (check-no seed treatment and fungicide). Seeding rate treatments were imposed to generate a range of plant density (*i.e.*, plants emerged) wide enough to study yield response to plant density. Treatments were applied to the experimental units (*ith* plot) which were laid out in a randomized complete block design. Seed sizes were determined by passing the bulk seed lot over a no. 9 round top screen and a no. 8 round bottom screen. Scalped seeds from the top of the no. 9 round screen were categorized as “heavy,” while those that scalped off of the no. 8 round screen were deemed “light” and while remaining seeds between both screens resulted in “moderate” seed size. Cultivar CDC Buteo, a hard-red winter wheat cultivar widely adapted to the Canadian Prairies, was sown in all trials. Seed germination was approx. 98% (data not shown). Stand counts were performed during late October-early November in each season by counting 2 linear row meters. Once the crop reached physiological maturity and grain moisture was lower than 15%, plots were harvested with a plot combine. Grain yields were corrected to 13% moisture content.

In order to build the priors indicated in Eqs. 6-10, we fitted the model described in Eqs. 1-3 across all of the environments in the Canadian dataset. For this instance, we defined flat priors based on previous literature (Fischer et al., 2019) allowing a reasonable range of values for our parameter of interest. These flat priors specifications are described in Appendix C. Equations 6-10 show the resulting priors combining the Canada dataset and previous literature (Fischer et al., 2019) that were used to analyze data from Kansas (see section 3.3.3):

$$\beta_{1j} \sim \psi(0.08, 0.01, 0, 0.20), \quad (6)$$

$$AOPD_j \sim \psi(105.29, 8.72, 10, 200), \quad (7)$$

$$\alpha_{1j} \sim \psi(0.031, 0.004, 0, 0.04), \quad (8)$$

$$\max VPD_j \sim \psi(91.88, 7.76, 0, 111.87), \quad (9)$$

$$\min RPD_j \sim \psi(160.19, 15.04, 0, 198.94). \quad (10)$$

We selected the truncated normal (ψ) distribution for ease of analysis and its capacity to clearly define the support of acceptable values for each of our priors. The ψ distribution is defined by four parameters. In the order listed hyperparameters of the ψ distribution are: the expected value (μ), the precision (σ) and the lower (a) and upper (b) truncation points. Evidence for the lower truncation point for the $AOPD_j$ of 10 plants m^{-2} was obtained from Fischer et al. (2019). This study was conducted under irrigated conditions with plants sown in raised beds in a honeycomb design in the Yaqui Valley of Mexico (27°22'13", -109°55'39"). The combination of low-latitude environments where freeze damage is unlikely, and agronomic management adopted allows wheat crops to express its tillering plasticity and maximize yields with a plant stand as low as 10 plants m^{-2} (Fischer et al., 2019). While environmental conditions and agronomic management explored in this study differ from that of Fischer et al. (2019), we utilize their evidence to inform the model about the lowest plausible plant density that can maximize yield in Kansas, where environments are much more restrictive for tillering and stand establishment compared to the Yaqui Valley.

3.3.3 Data analysis: Central Great Plains, Kansas US

Our data to demonstrate the model comprised of rainfed field experiments conducted in Kansas, US during three cropping seasons (2018-2021) in a total of 25 environments (site-year combinations). Each experimental unit (*ith* plot) was 9 m long by seven rows (0.19m spaced). A split-split plot design with three to four replications was used to establish 18 treatments, which

were created by combining three seeding rates (148, 222 and 297 seeds per m⁻²), three levels of seed cleaning [none (light), air screen (moderate), and gravity table + color sorting (heavy)], and two seed treatments (none and insecticide + fungicide). In order to generate a wide range of plant density (*i.e.*, plants emerged), we imposed seeding rate treatments. Seed treatment consisted of 5 oz ac⁻¹ of Cruiser Maxx (thiamethoxam and mefenoxam–fludioxonil) and 0.75 oz ac⁻¹ Cruiser 5FS (thiamethoxam). The wheat variety evaluated at all locations was 'SY Monument,' which was the most widely sown winter wheat variety in Kansas during the study period (USDA-NASS, 2024). Weeds, insects, and diseases were controlled as needed using standard practices so that they were non-limiting to grain yield. Other practices (*e.g.*, sowing date, tillage, etc.) were specific to each environment (Appendix Table C.1, Appendix Table C.2) , not allowing us to explore their interactions with the treatments. Stand counts were done 3-4 weeks after sowing on 1 linear row-meter. Once the crop reached physiological maturity and grain moisture was lower than 15%, experimental units were harvested using a Massey Ferguson XP8 small-plot combine. To avoid border effect, the plot ends were trimmed at harvest time. Grain yields were corrected to 13% moisture content.

Using a k-means clustering algorithm, we classified all 25 environments based on attained yield as high or low yielding environments. The number of clusters was set to two (k=2). The individual environment classification comprised the following rules: in a given environment if more than 50% of the plot level yield observations fell in the high-yielding cluster the environment was classified as high, or *vice versa* for low-yielding environments (Messina et al., 2015; Sciarresi et al., 2019; Bastos et al., 2020).

In order to rapidly quantify our parameters of interest (*AOPD* and *minRPD*) in each seed size × seed treatment × environment combination, we adopted a *divide and conquer* approach

(Wang and Srivastava, 2023). This approach consisted of fitting the preceding model (Eq 1-6) to 12 subsets of our data corresponding to each permutation of seed size, seed treatment, and environment. Note that the *divide and conquer* approach does not modify the statistical model but rather serves as a computational advantage. It is easily applicable in this case, since each response curve (for both μ_{ij} and σ_{ij}^2) is specific to each seed size $\times$ seed treatment $\times$ environment combination.

In order to analyze how different treatments, seed sizes and environments impacted yield response to plant density, we compared all treatments against the control treatment (untreated, light seed) in each environment cluster (high or low-yielding environments). For the ease of interpretation of the variable units, the variance of yield values was converted to standard deviation. From the posterior distribution of model parameters and predictions we calculated the median ($q_{.50}$), the upper ($q_{.025}$) and lower ($q_{.975}$) limits of the 95% credible interval. Comparisons between treatments imposed were calculated as:

$$\Delta x_j = x_j - x_{Control}, \quad (11)$$

where x is one of the following μ_j , σ_j , $AOPD_j$, $minRPD_j$.

We evaluated the economic impacts of the following plant density recommendations by the $minRPD_j$ against $AOPD_j$:

$$Net\ Income_j = y_{ij} * 220 - PD_j * 6.16 * 10^{-5}, \quad (12)$$

$$\Delta Net\ Income_j = Net\ Income_{minRPD_j} - Net\ Income_{AOPD_j}, \quad (13)$$

where the $Revenue_j$ is calculated as the difference between income and cost of seed. Income is calculated as the product between the posterior distribution of grain yield y_{ij} and the price of wheat grain assumed to be 220 \$ Mg⁻¹. Seed costs are expressed by the product between, a given plant density recommendation PD_j , where PD_j can be either $minRPD_j$ or $AOPD_j$, and 6.16 *

10^{-5} \$ seed⁻¹. Price per unit seed was calculated by assuming 40 \$ seed bag⁻¹, a bag weight of 22.7 kg and grain weight of 35 mg grain⁻¹. $\Delta Revenue_j$ represents the difference in revenue from recommendations following $minRPD_j$ against $AOPD_j$.

3.3 Results

3.3.1 Informative priors: Canadian Prairies

Yields in the Canadian Prairies averaged 4.42 Mg ha⁻¹ ($q_{0.025} = 1.35$ Mg ha⁻¹; $q_{0.975} = 8.18$ Mg ha⁻¹). Plant density ranged from 4 to 501 plants m⁻². Across all treatments and environments, the $AOPD$ ranged from 79 to 128 plants m⁻². Meanwhile, $minRPD$ was consistently higher than the $AOPD$ (posterior probability = 0.0001) and ranged from 138 to 199 plants m⁻². Capturing the whole range of probable values for $AOPD$ and $minRPD$ parameters allowed to design informative priors reflecting the current knowledge and its associated uncertainty (Figure 3.1).

3.3.2 Yield response to plant density under varying seed size, seed treatment and environment in Kansas

Across all treatments and Kansas environments, grain yield averaged 4.10 Mg ha⁻¹ ($q_{0.025} = 1.87$ Mg ha⁻¹; $q_{0.975} = 7.25$ Mg ha⁻¹) and plant density ranged from 8 to 275 plants m⁻². In low-yielding environments grain yield was on average 3.37 Mg ha⁻¹ ($q_{0.025} = 1.62$ Mg ha⁻¹; $q_{0.975} = 4.64$ Mg ha⁻¹). In high yield environments grain yield averaged 5.59 Mg ha⁻¹ ($q_{0.025} = 3.79$ Mg ha⁻¹; $q_{0.975} = 7.42$ Mg ha⁻¹).

Plant density effects on expected yield and yield variance can be visually inspected (as a first check) for winter wheat seeded in Kansas US under untreated, light seeds treatments in low-yielding environments cluster (Figure 3.2). All the other seed treatments $\times$ seed size $\times$ environments combinations can be found in Appendix Figure C.2. Moreover, to compare how seed treatment, seed size and environment affected expected yield, yield variance and model

parameters, we derived quantities from models presented in Figure 3.2 and Appendix Figure C.2 using Equation 11 and explored in sections 3.2.1 and 3.2.2.

3.3.2.1 Seed treatment and size impacts expected yield and yield variance

Heavy and treated seeds conferred greater yields at the AOPD compared to the control seed management practice untreated light (Figure 3.3). Across environments, seed treatment and heavy seed size resulted in similar yield advantage over the control (Figure 3.3), averaging 0.27 Mg ha^{-1} ($q_{.025} = 0.06 \text{ Mg ha}^{-1}$; $q_{.975} = 0.47 \text{ Mg ha}^{-1}$). Results from the rest of seed treatment and size combinations are shown in Appendix Figure C.3. Three treatments (i.e., None_Moderate, None_Heavy, Treated_Moderate in Appendix Figure C.3) resulted in similar yield advantage over the control under high ($q_{.50} = 0.238 \text{ Mg ha}^{-1}$; $q_{.025} = -0.026 \text{ Mg ha}^{-1}$; $q_{.975} = 0.498 \text{ Mg ha}^{-1}$) and low ($q_{.50} = 0.167 \text{ Mg ha}^{-1}$; $q_{.025} = 0.001 \text{ Mg ha}^{-1}$; $q_{.975} = 0.331 \text{ Mg ha}^{-1}$) yielding environments (Appendix Figure C.3).

In low-yielding environments, seeding heavy or moderate size seeds and treated seeds resulted in lower yield variance (more stable yields) compared to the control (Figure 3.3B, Appendix Figure C.3), reducing yield variance on average by -0.13 Mg ha^{-1} ($q_{.025} = 0.02 \text{ Mg ha}^{-1}$; $q_{.975} = -0.31 \text{ Mg ha}^{-1}$).

3.3.2.2 Seed treatment and size effects on AOPD and minRPD.

Regardless of the environment, treated, heavy seeds resulted in similar AOPD as compared to the untreated, light seeds control (Figure 3.4, Figure 3.5). All other seed treatments and sizes resulted in similar AOPD compared to the control (Appendix Figure C.5). Seed treatment influenced the minRPD, particularly in low-yielding environments where two treatments [*Treated_Moderate* (posterior probability = 0.880) and *Treated_Heavy* (posterior

probability = 0.863)] had a higher minRPD compared to the control untreated, light seeds (posterior probability = 0.863; Figure 3.5B, Appendix Figure C.5).

3.3.2.3 Economic assessment of plant density recommendations

When comparing net income resulting from plant density recommendations following minRPD against AOPD, across seed chemical treatments and cleaning methods net income was on average 37 \$ ha⁻¹ higher ($q_{.025} = 6$ \$ ha⁻¹; $q_{.975} = 77$ \$ ha⁻¹) in low yielding environment (Figure 3.6A). In high yielding environments net income was 19 \$ ha⁻¹ higher ($q_{.025} = -8$ \$ ha⁻¹; $q_{.975} = 54$ \$ ha⁻¹) when following plant density recommendations based on the minRPD compared to the AOPD (Figure 3.6B).

3.4 Discussion

We introduced a model describing both expected yield and yield variance in response to plant density using comprehensive datasets from two hard red winter wheat growing areas. In addition, we elaborated this model to assess how seed management affected the optimal planting density. We determined the optimum planting density that maximizes yield and minimizes variance (*minRPD*) and showed how our framework could be used to compare yield-plant density relations between a combination of treatments (seed size and seed treatment) and environments. The novelty on the proposed framework lies on the assumptions behind the variance of yield response to plant density. Results showed this framework allows quantifying the minimum plant density that minimizes grain yield variance.

3.4.1 Limitations

One limitation of this study is the use of k-means clustering algorithm to perform environmental classification. First, k-means does not account for uncertainty associated with yield environment classifications (Hartigan and Wong, 1979; Ahmed et al., 2020). Second, k-

means classification approach requires *post hoc* yield data to classify environments, restricting its applicability in real world scenarios where growers have no knowledge of the conditions for the upcoming season. A feasible alternative that could be incorporated to overcome the latter limitation is to perform long-term assessment of drought patterns and yield environments in the region (e.g., Chenu et al., 2011, 2013), subsequently adopting management strategies that maximize yield and minimize variance for the most common environment in a region.

Another limitation of this study is that we evaluated a single cultivar, thus ignoring cultivar $\times$ plant density interactions that can occur in wheat (Faris and De Pauw, 1980; Baker, 1982; Valério et al., 2009; Tokatlidis, 2014). Previous studies showed the optimum plant density depended on the cultivar's tillering potential (Valério et al., 2009; Bastos et al., 2020), yield of a cultivar at very low planting density (*i.e.*: plant yield efficiency; Tokatlidis, 2014), and to lesser extent differences in leaf insertion angle (*i.e.*: planophile or erectophile; Fischer et al., 1976). Future research can focus on estimating the *minRPD* for cultivars varying tillering potential or other physiological characteristics.

3.4.2 Modeling assumptions

In our model, yield response to plant density is defined by models for two processes (one for expected yield and one for yield variance, Eq 2. and Eq 3.) and are based on mechanisms of wheat physiology (Whaley et al., 2000). From the expected yield perspective, we acknowledge multiple processes were proposed in the literature to model the yield-plant density relation (Willey and Heath, 1969; Spink et al., 2000; Lloveras et al., 2004; Lollato et al., 2019b; Bastos et al., 2020; Mehring et al., 2020). Critically thinking about the underlying biological basis behind the tested hypothesis (*i.e.*, the model selected) is crucial to provide meaningful inference (section 4 in Johnson and Omland, 2004). Thus, our designed process model relies on parameters and

derived quantities that are agronomically meaningful and interpretable to guide producers in their plant density decisions (*e.g.*, *minRPD* and *AOPD*). Contrastingly, model comparison and selection approaches according to the empirical support of a model (*e.g.*, selecting a model based on the lowest Akaike or Deviance Information Criterion, etc.) should only be utilized when the data shows support for more than one hypothesis (Johnson and Omland, 2004).

3.4.3 Agronomic and economic implications behind *minRPD*

Our research shows *minRPD* was always greater than the *AOPD* (Figure 3.4). This phenomenon could be partially explained by plant density $\times$ environment interactions within each environmental cluster (*i.e.*, low- or high- yielding environment), resulting in each environment having its own *AOPD*, as *AOPD* depends on the target environment (Bastos et al., 2020). Environmental factors influencing the optimal plant density (*i.e.*: *AOPD*), remain to be tested. Improved predictive performance of plant density recommendation models can seek to incorporate static (*i.e.*, those with lower variability within the same cropping season such as soil organic matter, and soil water holding capacity) environmental covariates. While dynamic environmental factors (those that have greater variability within the same cropping season) might be prone to better explain changes in yield response to plant population (*e.g.*: fall precipitation, average temperature, and cumulative radiation during the Fall and Winter as noted Bastos et al., 2020), their inherent uncertainty limits their use on predictive models.

There are multiple issues associated with modeling grain yield response to plant density for each individual environment. First, the range of plant density is constrained by densities explored in a single environment. Second, subgrouping sample size is limited to observations within a single environment resulting in less precise estimators (*i.e.*, greater uncertainty on model

parameters). Finally, it has no predictive power as environmental conditions resulting in a given *AOPD* are largely unpredictable.

Heavy seed sizes and treated seeds resulted in more stable yields compared with light untreated seeds only under low yielding environments (Figure 3.3B). Evidence in the Canadian Prairies suggest similar behavior, where the benefits of seed size and chemical treatment were more apparent under conditions conducive to thinner wheat stands (Beres et al., 2016). Mian and Nafziger (1992) found that the use of smaller seed sizes can translate into thinner wheat stands and even provide a yield advantage over heavier seed sizes under G x E combinations conducive to lodging. However, genetic progress in lodging resistance makes lodging conditions unlikely in more recently released wheat germplasm (Zhang et al., 2016). A probabilistic assessment of genotypes with varying tillering potential, and planting dates can contribute to classify G x E combinations where intensified seed management strategies can provide yield advantages.

Guiding plant density recommendations following *minRPD* comprise higher seed costs when compared against *AOPD*. However, our data shows that more stable yields resulting from adopting *minRPD* translate in higher net income compared to those following *AOPD*. Economic benefits from *minRPD* are higher in low yielding environments, as plant density modulates spikes per m⁻², a coarse regulator of grain yield (Slafer et al., 2014). An independent dataset shows empirical evidence from field trials conducted in the Central Great Plains region showing that winter wheat yield response to plant density is higher as environmental mean yield decreases (Figure 4A in Bastos et al., 2020), aligning with our findings. Future models can consider incorporating uncertainty in seed to grain price ratio as a component within the model (Correndo et al., 2021b), which would allow to quantify the impacts of plant density following *minRPD* on long term net returns. Therefore, delivering plant density recommendations following *minRPD*

can mitigate, at the expense of higher seeding costs, risks associated with plant density decisions in unpredictable environments.

3.5 Conclusion

We described both expected yield and yield variance in response to plant density. Our model consisted of process models generated with our expert knowledge on eco-physiological processes and the prior distributions were specified using previous data and past studies. We used this model to answer agronomically relevant questions regarding seed management (*e.g.*, yield and variance of yield response to seed size and treatment; *AOPD* and *minRPD* response to seed size and treatment). To facilitate the usability of our model, we developed a user interface (<https://ksuwheat.shinyapps.io/minrpd>) which allows informing seed management decisions based on probabilistic inference of the minimum risk plant density (*minRPD*). Under heteroscedastic data scenarios the proposed framework can be used to model grain yield response to plant density. Future research can (i) explore how genotypes, environments and their interaction modulate the difference between *AOPD* and *minRPD* and, (ii) extend the framework to a variety of processes involving crop management decisions.

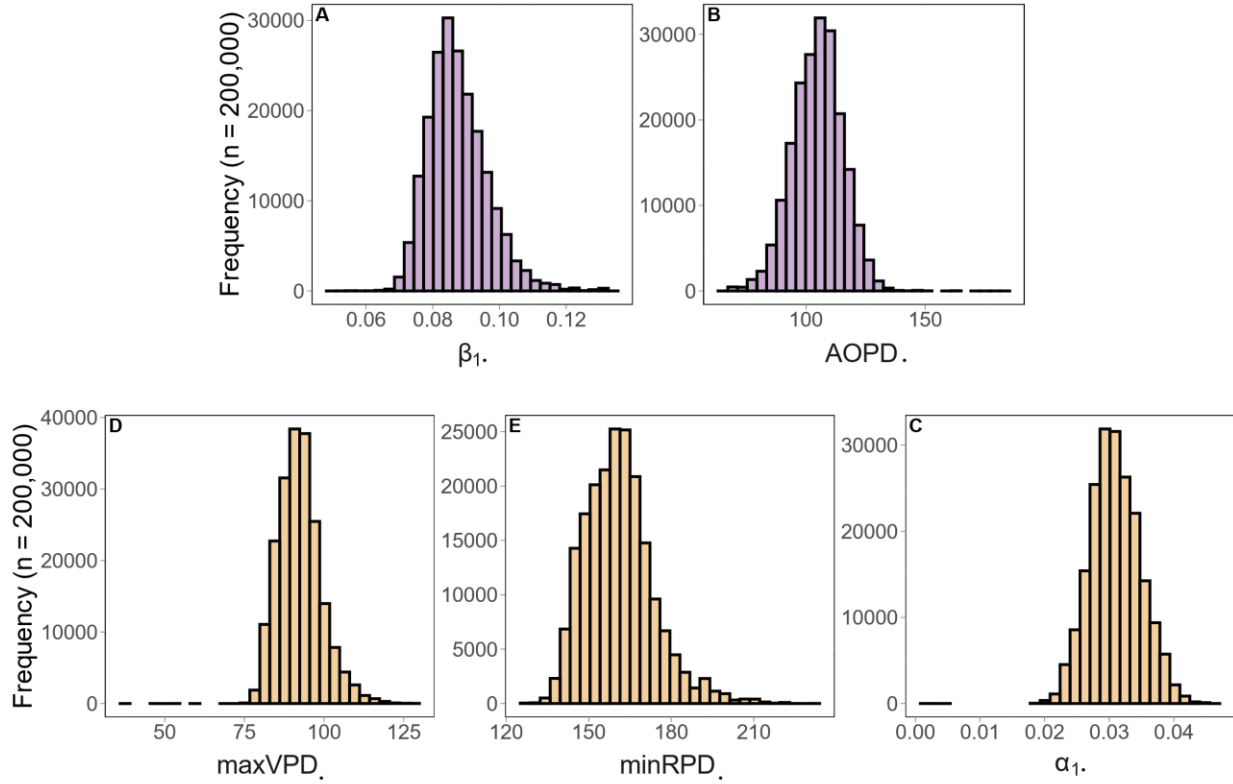


Figure 3.1. Posterior distributions of yield response to plant density model parameters (Eq. 2 and Eq. 3) pooling all 12 combinations of seed treatment, seed size and environment. Derived quantities from these distributions (e.g., the expected value, the standard deviation, and quantiles) were used to build informative priors described in Eq 6 – 10. Purple bars refer to parameters or quantities related to modelling the expected value (μ_{ij}) and yellow bars to parameters or quantities related to modelling the variance (σ_{ij}^2) of grain yield. Abbreviations: sample size (n), linear term of expected yield response to plant density (β_1), agronomic optimum plant density (AOPD), maximum variance plant density (maxVPD), minimum risk plant density (minRPD), linear term of variance of yield response to plant density (α_1).

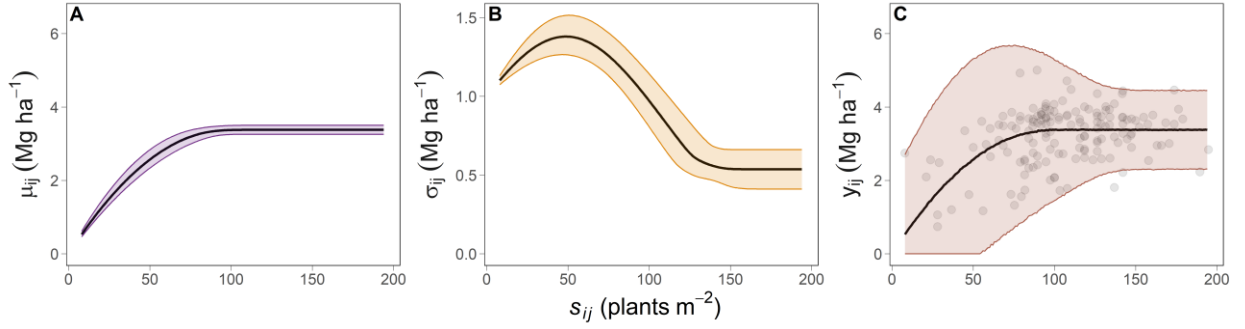


Figure 3.2. Panel A shows expected grain yield (μ_{ij}) in response to plant density (s_{ij} , purple); panel B shows standard deviation of yield (derived from yield variance, σ_{ij}^2) in response to plant density (yellow); panel C shows the posterior predictive distribution of grain yield (y_{ij}) response to plant density (brown) for the j th treatment $\times$ environment combination (in this example untreated, light seeds in low yield environment cluster). Solid black lines represent the median and ribbons the 95% credible interval. Purple refers to parameters or quantities related to modelling the expected value (μ_{ij}) and yellow to parameters or quantities related to modelling the variance (σ_{ij}^2) of grain yield.

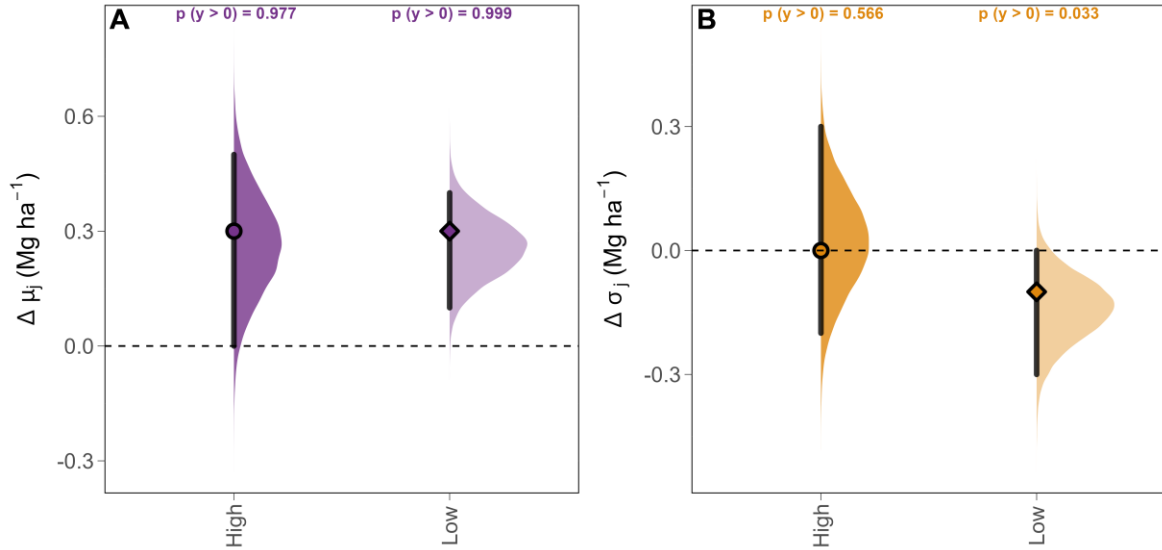


Figure 3.3. Posterior distributions of expected grain yield response to seed management evaluated at the AOPD (Eq. 11); B) standard deviation of yield response to seed management evaluated at the minRPD (Eq. 11) in high (circles, opaque) and low (diamond, transparent) yielding environments. Contrasts represent heavy, treated seeds against light seed, untreated control treatment (Eq. 11). Points represent the median and whiskers are the 95% credible interval; p represents the posterior probability of $\Delta\mu_j$, $\Delta\sigma_j$ being greater than zero. Purple refers to parameters or quantities related to modelling the expected value (μ_{ij}) and yellow to parameters or quantities related to modelling the variance (σ_{ij}^2) of grain yield.

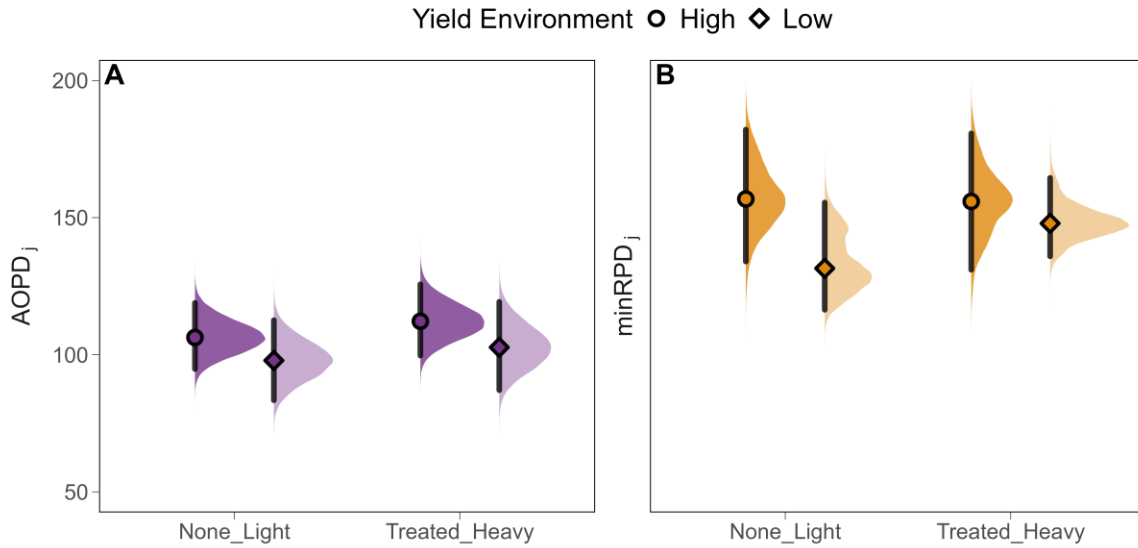


Figure 3.4. Posterior distributions of AOPD (A) and minRPD (B) for contrasting seed management treatments (no treatment and light seeds, “None_Light”; treated and heavy seeds, “Treated_Heavy”) under high (circles, opaque) and low (diamond, transparent) yielding environments. Points represent the median and whiskers are the 95% credible interval. Purple refers to parameters or quantities related to modelling the expected value (μ_{ij}) and yellow to parameters or quantities related to modelling the variance (σ_{ij}^2) of grain yield.

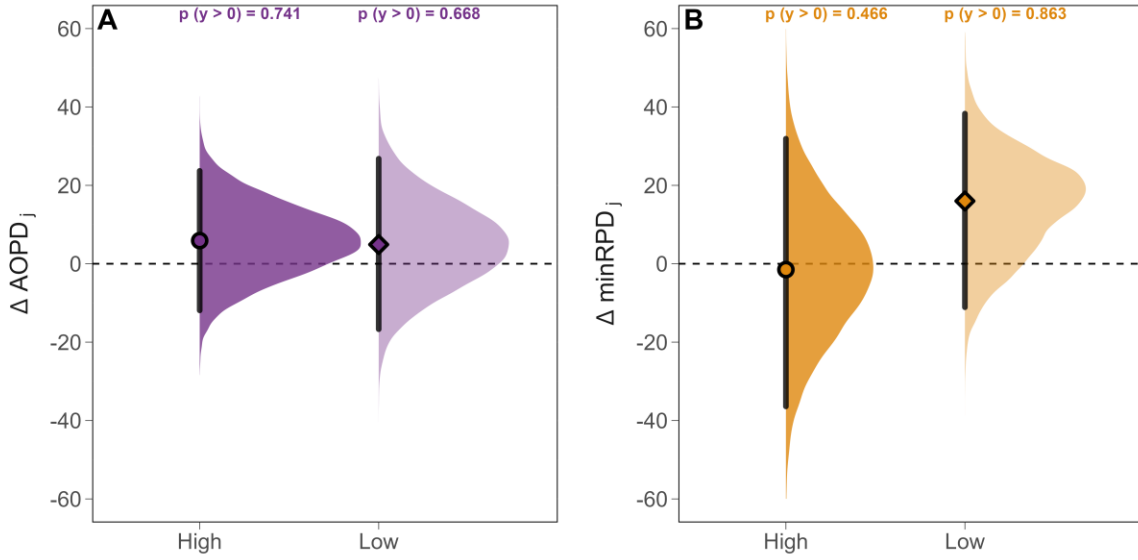


Figure 3.5. Posterior distributions of AOPD (A) and minRPD (B) as affected by seed management treatments under high (circles, opaque) and low (diamond, transparent) yielding environments. Contrasts represent heavy, treated seeds against light, untreated (control) seeds. Points represent the median and whiskers are the 95% credible interval. Equation 11 describes the calculations used for contrasts between treatments. Purple refers to parameters or quantities related to modelling the expected value (μ_{ij}) and yellow to parameters or quantities related to modelling the variance (σ_{ij}^2) of grain yield. Abbreviations: agronomic optimum plant density (AOPD), minimum risk plant density (minRPD).

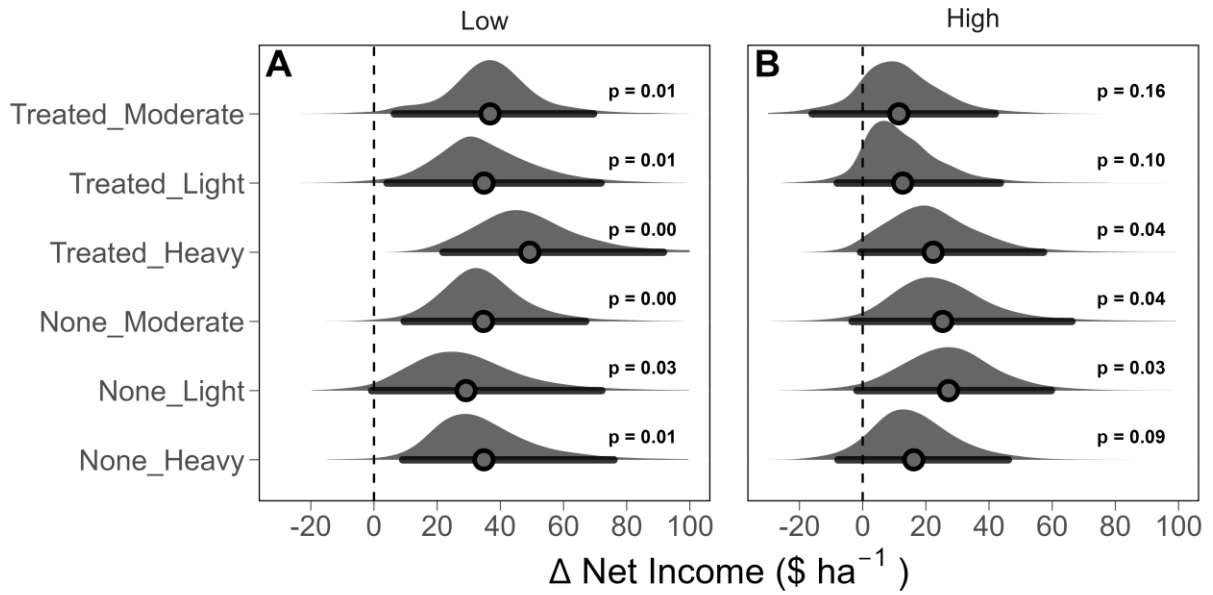


Figure 3.6. Posterior distribution of the difference in net income from plant density recommendations following minRPD compared to AOPD, under (A) low and (B) high yielding environments and varying seed chemical treatment and cleaning methods. Positive Δ Net Income values represent greater net income by following minRPD compared to AOPD (Eq. 12, 13). Points represent the mean and whiskers the 95% credible interval.

Chapter 4 - Genetic modulation of yield and phenotypic plasticity of yield in winter wheat

Abstract

For winter wheat in the US Central Great Plains, phenotypic plasticity of yield is agronomically adaptive, *i.e.*, genotypes with higher plasticity have higher yield in high yielding environments with no tradeoff in stressful, low yielding environments. Using data from variety trials conducted between 2000 and 2022 and cultivars released between 1967 and 2022, we explored time trends in phenotypic plasticity and heritability of yield. We hypothesize that i) newer cultivars will have higher yield plasticity; ii) heritability of yield is declining in the time series; and iii) genomic regions associated with yield depend on the environment and do not fully overlap with those associated with phenotypic plasticity of yield. Breeding for yield and agronomic adaptation increased phenotypic plasticity of yield at 0.5% year⁻¹; broad sense heritability of yield decreased from 0.23 in 1993 to 0.15 in 2017. Genome-wide-association analysis shows genomic regions associated with yield varied between high yielding and stressful environments and were partially independent of those associated with yield plasticity. Newer cultivars have a higher frequency of alleles associated with yield and its plasticity. We discuss implications for breeding and agronomy aimed to improve wheat phenotypes.

Abbreviations: Credible interval (c.i.), genotype × environment (G × E), Centro Internacional de Mejoramiento de Maiz y Trigo (CIMMYT), single nucleotide polymorphisms (SNPs), genome-wide-association study (GWAS).

4.1 Introduction

Wheat (*Triticum aestivum* L.) grain yield is a complex trait that varies with genotype (G), environment (E), agronomic management (M) and their two and three-way interactions. Increased winter wheat yield in the U.S. Central Plains between 1985 and 2010 (Fischer et al., 2014) has been attributed to improved management and genetics and the interaction between of G and E whereby genetic gains have been higher in higher yielding environments (Cox et al., 1988; Berzonsky and Lafever, 1993; Donmez et al., 2001; Khalil et al., 2002; Fufa et al., 2005; Stewart et al., 2010; Green et al., 2012; Battenfield et al., 2013; Maeoka et al., 2020). Looking at the interaction between genotype and environment from the perspective of phenotypic plasticity provides links with ecology, evolution and developmental biology with implications for breeding and agronomy (Sultan, 1987; Sadras and Slafer, 2012; Sadras and Richards, 2014; Ruiz et al., 2019; Cooper and Messina, 2023; Giordano et al., 2024).

Phenotypic plasticity is “the amount by which the expression of individual characteristics of a genotype are changed by different environments” (Bradshaw, 1965); it depends on the trait, the genotype, and the environmental sources of variation (Bradshaw, 1965; Dewitt and Scheiner, 2004). Figure 4.1 illustrates genotype-dependent phenotypic plasticity of yield in a sample of wheat producing regions. In three out of six cases (Argentina, Australia, Alberta), yield plasticity was agronomically adaptive; this is, genotypes with higher plasticity had higher yield in high yielding environments with no tradeoff in more stressful, low yielding environments (Figure 4.1). A closer examination of the Canadian wheat belt shows plasticity was neutral for yield in Manitoba and positive in Alberta (Figure 4.1). In the Central Great Plains, one of the major wheat producing regions (USDA-NASS, 2024) and the focus of this study, previous investigations showed yield plasticity is agronomically adaptive (Grogan et al., 2016; Lollato et

al., 2020a; Giordano et al., 2024). Thus, whether plasticity is agronomically adaptive depends on the environment, the germplasm pool (Figure 4.1), and the costs and limitations of phenotypic plasticity (DeWitt et al., 1998; Valladares et al., 2007; Auld et al., 2009).

The rate of genetic gain in the yield of wheat is slowing down in major wheat producing regions (Brisson et al., 2010; Fischer et al., 2014; Lo Valvo et al., 2018; Maeoka et al., 2020). Common explanations for slower rates include diminishing returns and traits like harvest index approaching their biological limit (Hay, 1995; Fischer and Rebetzke, 2018). Declining heritability as a potential factor slowing down genetic gain has been overlooked; two perspectives, phenotypic plasticity and phenotypic connectance, converge to predict declining heritability of yield in some breeding settings. First, where selection for yield and agronomic adaptation favors higher phenotypic plasticity of yield (*e.g.*, Sadras and Lawson, 2011; de Felipe and Alvarez Prado, 2021), heritability might be declining because trait plasticity correlates negatively with heritability (Donovan et al., 2011; Sadras and Slafer, 2012; Alvarez Prado et al., 2014b). Second, from the perspective of phenotypic connectance defined as the level of linkage between organs and traits in the developing organism (Amzallag, 2000), lower heritability has been predicted for a historic collection of Australian wheat for which phenotypic connectance of grain yield has increased over five decades (Sadras, 2024), and heritability and phenotypic connectance are negatively correlated (Amzallag, 2000).

Bradshaw (1965) formalized the notion that plasticity is a trait of its own, with its own genetic modulation and Scheiner (1993) advanced three models to explain the genetics of plasticity: i) the overdominance model, where plasticity is negatively related to the degree of heterozygosity; ii) the pleiotropic model, where genes have pleiotropic effects, influencing multiple traits simultaneously and iii) the epistatic model, which assumes the genetic

independence of the trait *per se* and its plasticity. At present, the overdominance model is largely irrelevant in wheat varieties that are highly inbred and predominantly homozygous. Empirical evidence supports pleiotropic and epistatic models accounting for the partial genetic independence of phenotypic plasticity and the trait *per se*, *e.g.* for grain weight (Alvarez Prado et al., 2014b) and grain yield in *Zea mays* (Kusmec et al., 2018) and for flowering time and fruit weight in *Solanum lycopersicum* (Diouf et al., 2020).

Using yield data of hard winter wheat collected between 2000 and 2022 from cultivars released between 1967 and 2022 in the U.S. Central Plains, we explore time trends in phenotypic plasticity and heritability of yield. Being that yield plasticity is agronomically adaptive in the Great Plains, our working hypotheses are: i) newer cultivars will have higher yield plasticity; ii) heritability of yield is declining in the time series, and iii) genomic regions associated with yield depend on the environment and do not fully overlap to those associated with yield phenotypic plasticity.

4.2 Method

4.2.1 Field experiments

Grain yield data were obtained from hard winter wheat (HWW) variety trials conducted in the United States Central Great Plains between 2000 and 2022. During the last 10 years, the states of Kansas, Colorado and Oklahoma have sown about 6.1 Mha of HWW and produced an average 15.0 Mt (USDA-NASS, 2024) annually, with average yields from 1.8 to 3.7 Mg ha⁻¹. This study analyzed the dataset comprising of 111,026 observations of 888 genotypes, including commercial cultivars and advanced experimental lines within breeding pipelines, hereafter both referred as cultivars, across 853 environments resulting from the combination of site and year; not all wheat cultivars were tested in all environments. The trials spanned over the states of

Colorado, Kansas and Oklahoma (Figure 4.2A). Cultivars were released from breeding programs between 1967 and 2022. Details of field experiments can be found in Figure 4.2B and in Munaro et al. (2020).

4.2.2 Yield data

We filtered yield data to all cultivars replicated in at least 25 environments, since the predicted standard deviation of plasticity based on the exponential decay model was 0.03 with this number of environments (Appendix Figure D.1). This resulted in a set of 234 cultivars (Appendix Table D.2). We estimated yield phenotypic plasticity as the slope of a reaction norm (Woltereck, 1909) between observed grain yield and environment mean yield. This approach requires assumptions on the shape of the reaction norm but is less sensitive to uneven sample size from each genotype when compared to estimates from variance ratios that do not need these assumptions (Dingemanse et al., 2010). To capture non-linear trends in yield plasticity we defined nonlinear plasticity following Eberhart and Russel (1966), as the deviation from the yield-yielding environment regression line of each cultivar (Kusmec et al., 2017), quantified by the root mean squared error (RMSE). In this context, nonlinear yield plasticity can be interpreted as how predictable the yield of a cultivar is across the range of environmental conditions. Yield plasticity was estimated with a Bayesian hierarchical approach (Equation 1, 2) using a Gibbs sampler developed for this purpose (Su et al., 2006) and implemented using the *FW* package available in R (Lian and Campos, 2015; R Core Team, 2021).

$$y_{ijk} \sim N(\mu_{ijk}, \sigma^2), \quad (1)$$

$$\mu_{ijk} = \mu_0 + g_i + e_j + \beta_i e_j + \epsilon_{ijk},$$

$$e \sim N(0, E\sigma_e^2), \quad (2)$$

$$g \sim N(0, A\sigma_g^2),$$

$$\beta \sim N(0, A\sigma_b^2).$$

In Equation 1, y_{ijk} is the observed yield at the k^{th} replicate ($k: 1, 2, \dots, n$), of the i^{th} genotype ($i: 1, 2, \dots, 234$) at the j^{th} environment ($j: 1, 2, \dots, 234$). The number of n replicates was on average four and varied with environment. In the process model μ_0 is the overall intercept, while g_i and e_j are the main effects of genotypes and environments respectively, quantified as deviations from μ_0 . Thus, g_i can be also interpreted as the intercept of the reaction norm and β_i is the slope used to estimate phenotypic plasticity of yield. ϵ_{ijk} is the error term assumed normally distributed with expected value equal to zero and variance σ_e^2 . Prior distributions are all multivariate normal, **A** and **E** describe the covariance structure between levels of random effects g_i , β_i and e_j , respectively (Equation 2). By retrieving variance components from model in Equations 1 and 2, we calculated broad sense heritability (H^2) of grain yield as:

$$H^2 = \frac{\sigma_g^2}{\sigma_g^2 + \frac{\sigma_\beta^2}{n_i} + \frac{\sigma_\epsilon^2}{n_\epsilon}}. \quad (3)$$

In Equation 3, σ_g^2 is the genotypic variance of genotype main effects (g_i). The denominator in the equation is the total phenotypic variance, where σ_β^2 is the variance from the slope of the reaction norm (β_i) and the residual error variance σ_ϵ^2 , both scaled by their respective degrees of freedom n_i and n_ϵ . H^2 of yield in the population was estimated using a sliding window of 10 years over the cultivars year of release starting in 1989 until 2022. Data before 1989 were excluded as only three cultivars were representative of the entire population in that period.

We explored how phenotypic plasticity of yield changed with cultivar year of release. A linear Gaussian model was used to assess the association of yield plasticity and year of release:

$$y_i \sim N(\beta_0 + \beta_1 YOR_i, \sigma^2). \quad (4)$$

Quantile regression was used to estimate genotype-specific grain yield at high (95th percentile) and low yielding environments (5th percentile, Equation 5). The model was fitted using an asymmetric Laplace distribution, which allows specifying τ parameter to 0.95 for 95th percentile and 0.05 for 5th percentile:

$$y_{ij} \sim \text{ALD}(\mu_i, \phi_i, \tau), \quad (5)$$

where y_{ij} is the observed grain yield at the j^{th} replicate ($j: 1, 2, \dots, n$), of the i^{th} genotype ($i: 1, 2, \dots, 234$), with expected value equal to μ_i and the dispersion ϕ_i .

Four yield phenotypes were then defined as: i) yield plasticity; ii) yield in low yielding environments (5th yield percentile, *i.e.*, μ_i when $\tau = 0.05$ in Equation 5); iii) mean cultivar yield (g_i , Equation 2) and; iv) yield in high yielding environments (95th yield percentile, *i.e.*, μ_i when $\tau = 0.95$ in Equation 5).

The association between yield phenotypic plasticity and yield in low yielding environments (5th yield percentile), yield mean and yield in high yielding environment (95th yield percentile) were explored using linear regression:

$$y_i \sim \Gamma(\alpha_0 + \alpha_1 1 + \beta_i, \phi), \quad (6)$$

where y_i follows a Gamma distribution and represents the estimated value for each yield level for the i^{th} genotype ($i: 1, 2, \dots, 234$). The expected value is represented with α_0 being the intercept and α_1 the slope of the association of yield plasticity, β_i , and three levels of yield, while ϕ is the dispersion.

4.2.3 Environmental data

Daily weather data were retrieved from Daymet (Thornton et al., 2014) using the *daymetr* package available in R (Hufkens et al., 2018). Daymet provides daily weather gridded estimates

of 1 km × 1 km spatial resolution from ground-based meteorological stations (<https://daymet.ornl.gov/overview>). Weather data were summarized for (i) the critical period for yield determination between -300°Cd and 100°Cd centered on anthesis using a base temperature of 4.5°C (Fischer, 1985; Cossani and Sadras, 2021), (ii) grain fill, from 100 °Cd to 600 °Cd after anthesis using a base temperature of 0°C (Dupont et al., 2006). Anthesis date was simulated from a locally calibrated model for the region (Lollato et al., 2020b). We explored the association of 13 environmental descriptors (Appendix Table D.3) and mean environmental yield (e_j , Equation 2) using regression tree with *rpart* function available in R (Therneau and Atkinson, 1999). We selected hyperparameters by grid search and retained the simplest model that maximized the R^2 and minimized the root mean squared error.

4.2.4 Genotypic data

A panel of 234 wheat cultivars (Appendix Table D.2) were genotyped by genotyping-by-sequencing (GBS). The cultivars were obtained directly from private and public breeding programs, USDA-ARS National Plant Germplasm System or USDA Regional Performance Nursery Program. DNA was isolated from leaf tissues collected at three leaf stage using hexadecyltrimethylammonium bromide (CTAB) method (Doyle and Doyle, 1987), and GBS libraries were prepared using *Pst*I and *Msp*I restriction enzymes (Poland et al., 2012). Size selected libraries were sequenced using NextSeq2000 sequencer (Illumina, San Diego) at the USDA Central Small Grain Genotyping Lab, Manhattan, Kansas. Single nucleotide polymorphisms (SNPs) were called using the Chinese Spring (CS) reference genome RefSeq v2.1 (Zhu et al., 2021) developed by International Wheat Genome Sequencing Consortium (IWGSC), which generated 117,391 SNPs. The SNPs were filtered by retaining those with >5% minor allele frequency (MAF), <20% missing data and <5% heterozygous calls. After filtering,

15,224 high-quality SNPs were imputed using K-nearest neighbors imputation algorithm available within TASSEL v5.0 software (Bradbury et al., 2007).

Genome-wide-association study (GWAS) was conducted to explore the associations between 15,224 SNPs and four yield phenotypes (Equations 2, 5) using a multi-locus, fixed and random model circulating probability unification (FarmCPU) available within the GAPIT package in R (Wang and Zhang, 2021). The model was implemented by testing three to 20 principal components (PCs) as covariates to account for population structure. Eigenvectors were obtained from principal component analysis of the genotypic matrix. The most parsimonious model was selected based on visual inspection of quantile-quantile plots between predicted and observed p -values. The final model included 10 PCs as covariates plus one SNP in chromosome 2A detected to have strong influence capturing structure of the population analyzed. SNP-trait associations were explored using a threshold of $-\log_{10}(P) = 3.0$, where ‘P’ represents the p -value of the association of a given SNP with the trait of interest.

We explored the allelic frequency changes with year of cultivar release using a sliding window of 10 years starting in 1989 until 2022. For each SNP, we calculated the effect size of homozygous alleles on the four yield traits using linear regressions. Effect sizes were estimated as the difference between favorable and unfavorable alleles for each SNP $\times$ trait combination.

4.3 Results

4.3.1 Rainfall and photothermal quotient associated with yield

Mean cultivar yield averaged 3.4 Mg ha^{-1} and ranged from 2.5 Mg ha^{-1} to 4.0 Mg ha^{-1} (Figure 4.2A). Variation in yield between genotypes ranged from 0.4 to 2.5 Mg ha^{-1} in low yielding environments and from 4.0 to 8.4 Mg ha^{-1} in high yielding environments (Figure 4.2A). Mean environmental yield averaged 3.5 Mg ha^{-1} , ranged from 0.7 to 8.8 Mg ha^{-1} (Figure 4.2B)

and correlated with rainfall in both the critical period and grain filling, and with the photothermal quotient in the critical period (Figure 4.2C, 2D). Regression tree including rainfall and photothermal quotient explained 20% of the variance in environmental mean yield with a root mean squared error of 1.1 Mg ha⁻¹ (Figure 4.2C).

4.3.2 Genotype-dependent phenotypic plasticity of yield is agronomically adaptive in the Central Plains

Yield plasticity varied 2-fold, from 0.66 in cultivar `2163` to 1.32 in `LCS Revere` (Figure 4.3A, Appendix Table D.2). Plasticity calculated as slope of reaction norms correlated with plasticity estimated as a ratio of variances (Appendix Figure D.2). Yield plasticity was agronomically adaptive, *i.e.*, phenotypes with higher plasticity had substantially higher yield in high yielding environments, captured in a rate of yield increase of 3.4 Mg ha⁻¹ per unit plasticity, and slightly higher yield in low yielding environments, with a rate of 0.3 Mg ha⁻¹ per unit plasticity (Figure 4.3B).

4.3.3 Phenotypic plasticity of yield increased and heritability of yield decreased over decades

Yield plasticity increased at 0.5 % year⁻¹ (c.i.: 0.4 – 0.7 % year⁻¹, Figure 4.4A). The cultivar with the lowest yield plasticity, `2163`, was released in 1989 and its counterpart with highest plasticity, `LCS Revere`, in 2018 (Figure 4.4A). The cultivar with the lowest yield plasticity, `Goodstreak`, was released in 2002 and its counterpart with highest plasticity, `LCS Revere`, in 2018 (Figure 4.4A). Nonlinear plasticity increased at an average rate of 7.3 kg ha⁻¹ year⁻¹ (c.i.: 6.1 – 8.6 kg ha⁻¹ year⁻¹, Figure 4.4B). Heritability of yield declined on average from 0.23 in the decade centered on 1993 to 0.15 in the decade centered on 2017 (Figure 4.4C). Declining heritability was partially attributed to declining variance from yield plasticity (σ_{β}^2),

increasing variance from non-linear plasticity (σ_{ε}^2) and to a lesser extent declining genetic variance (σ_g^2 , Figure 4.4D).

4.3.4 Partial independence in the genetic modulation of yield phenotypes

The 2N^vS translocation from *Aegilops ventricosa* Tausch captured population structure in the genotypic data (Figure 4.5A). The frequency of the 2N^vS translocation in the germplasm pool increased with cultivar year of release, from 6% in 1994 when `Jagger` was released to 68% in 2017 (Figure 4.5B). Presence of the 2N^vS translocation associated positively with all four yield traits (Figure 4.5C-F). Presence of the 2N^vS translocation associated with yield more strongly in higher than in lower yielding environments (Figure 4.5 D vs F, H vs J).

We found 46 SNPs above the exploratory threshold of $-\log_{10}(P) = 3.0$ to be associated with yield traits including 8 associated with phenotypic plasticity of yield, 12 associated with 95th yield percentile, 12 associated with mean yield, and 14 with 5th yield percentile (Figure 4.6A-D).

Frequency of favorable alleles contributing to yield phenotypes changed over time (Figure 4.7A-D). Increasing yield plasticity with time of cultivar release (Figure 4.4A) could be partially associated with higher frequency of favorable alleles at SNPs S6A_13708715, S2B_781222236 (Figure 4.7A). Three SNPs (S6B_412147528, S5D_134802435, S1A_14289872) associated with yield in high yield environments had higher frequency of favorable alleles in newer cultivars (Figure 4.7B). The frequency of the favorable alleles associated with mean yield, SNPs S2B_13713678, S3A_691148254 and S2D_206645004, increased from older to newer cultivars (Figure 4.7C). The frequency of favorable alleles associated with yield in low yield environments, SNPs S2A_17606976 and S7D_13070614, increased with time of cultivars release (Figure 4.7D).

4.4 Discussion

As expected, differences among contrasting plasticity cultivars arose under high yielding environments, with no trade-offs under stress (Figure XXX). This phenomenon was observed in independent datasets across major wheat producing regions (Figure 1, Calderini and Slafer, 1999) and crops (citation). Our and prior evidence shows wheat grain yield in the Central Great Plains is associated with drought, heat and windy events, which are largely unpredictable (citations). Selection in high-yielding environments is crucial to capture differences among contrasting plasticity cultivars (citations). However, testing in low yielding sites is required in order to capture well adapted cultivars to most frequent environmental sources of stress in the region. Enhancing adoption of envirotyping models that characterize frequency, duration and timing of drought (citation), heat (citations) and windy events (citations), can inform breeders to increase selection pressure on years when stresses are more frequent given the climate history of a given testing site.

4.4.1 Agronomically adaptive changes on wheat yield phenotypes

Evidence in wheat (Calderini and Slafer, 1999; Araus et al., 2008; De Vita et al., 2010), suggests that newer cultivars are more plastic for yield, when plasticity associated with responsiveness to high yielding conditions. In this study we showed from two different scales of biological organization, crop level (Figure 4.4A) and molecular level (Figure 4.7) that increasing phenotypic plasticity of yield and changes in favorable allele frequency associated with yield plasticity were a consequence of wheat breeding that drives agronomically adaptive changes. The outcome is that newer cultivars have better adaptation to high rainfall-high photothermal quotient scenarios and cope better with drought stress.

From an agronomic perspective, cultivars with high yield plasticity allow for greater impacts of enhanced agronomy on yield in high yielding environments (Jaenisch et al., 2019; Raj et al., 2023; Giordano et al., 2024). To support the synergy between genetics and agronomy underlying yield gains in farmers' fields, we introduce three examples of experiments conducted in the region with a sample of cultivars evaluated in this study. Jaenisch et al., (2019) evaluated wheat yield response to a factorial combination of six agronomic practices including nitrogen, sulfur, chloride, foliar fungicides and plant growth regulators and found that management intensification increased environmental mean yield; Raj et al., (2023) reported a divergent bundle of reaction norms of yield with increasing environmental mean yield when the source of variation was management intensity; Giordano et al., (2024) found that cultivars with high yield plasticity outyielded their counterparts with lower plasticity under high yield non-nitrogen limiting environments. Our findings in the current study reinforce associations where, i) enhanced agronomic management improves yield in high yielding environments, ii) a stronger association between yield and yield plasticity in higher yielding environments (Figure 4.1, Figure 4.3, 3) and consequently iii) selection for cultivars with higher yield plasticity favors response to enhanced agronomic management.

From a breeding perspective, response to selection (*i.e.*, genetic gain) for a given trait depends on the intensity of selection, the trait heritability, and genetic and phenotypic variance for the trait in the population (Lush, 1937; Cooper and Messina, 2023). A more recent formulation of the genetic gain equation, includes terms of selection accuracy (Cooper and Messina, 2023), which could be the one most impacted when making selections in high yielding environments, where yield differences among cultivars with contrasting plasticity are more evident (Figure 4.3B). Recent evidence suggested wheat genetic gains are decelerating in the US

hard winter wheat region (Maeoka et al., 2020). Our findings showed declining heritability is not associated with depleting genetic variance, but rather increasing phenotypic variance through lower predictability of cultivars yield across the range of environmental conditions (Figure 4.4C, Figure 4.4D), which might be partially attributed to increasing environmental variability in the context of climate change (Asseng et al., 2011; Tack et al., 2015; Zhao et al., 2017; Zhang et al., 2024). Declining variance in yield phenotypic plasticity in the time series can be partially associated with higher phenotypic connectance, aligning with the proposition suggested by Sadras (2024), where connectance associates with lower trait heritability and high phenotypic plasticity.

4.4.2 Genetic modulation of yield phenotypes

There are bi-directional relationships between the phenotype and both the genome and gene expressivity (West-Eberhard, 2003b; Noble, 2010; Baverstock, 2021; Shapiro, 2022). Here we show that the associations of SNPs with yield varied between favorable and droughted environments, and that plasticity has its own partially independent genetic modulation (Figure 4.6), aligning with Bradshaw's (1965) insightful proposition. Empirical evidence from 5,000 *Zea mays* recombinant inbred lines, showed that for 23 agronomically relevant traits, trait means and their plasticities have partially independent genetic modulation and associated candidate genes forming structurally and functionally distinct groups (Kusmec et al., 2017). Reymond et al. (2003b) established reaction norms relating maize leaf expansion rate and meristem temperature, air vapor pressure deficit and predawn leaf water potential, showing that the intercept and slope of the reaction norms associated with different QTL. With this approach, they pre-empted QTL x E interaction: instead of asking for QTL associated with leaf expansion rate, and then dealing with the interaction, they asked what QTL associate with the response of the trait to the

environment. This approach complements statistical methods to untangle G x E (*e.g.*, Gauch Jr. et al., 2011) but is biologically more insightful. Likewise, we ask: which genomic regions associate with phenotypic plasticity of yield, effectively pre-empting the G x E component of yield variation (Figure 4.6A).

The 2N^vS translocation from *Aegilops ventricosa* captured most of the population structure on the genome-wide-association analysis (Figure 4.5). This translocation was first introduced to commercial breeding programs through cultivar `Jagger`, released in 1994. The frequency of the 2N^vS in the germplasm pool in this study increased over time (Figure 4.5B). The 2N^vS translocation has 535 high-confidence genes (Gao et al., 2021) some found to be associated with resistance to biotrophic parasites such as root knot nematodes (*Meloidogyne spp.*, Williamson et al., 2013) and fungal diseases including leaf rust (caused by *Puccinia triticina*, Xue et al., 2018), stripe rust (caused by *P. striiformis f. sp. tritici*, Fang et al., 2011; Mustahsan et al., 2023), stem rust (caused by *P. graminis f. sp. tritici*, Turner et al., 2016) and wheat blast (caused by the *Magnaporthe oryzae triticum*, Cruz et al., 2016; Cruppe et al., 2021). Gao et al., (2021) found that the presence of the 2N^vS translocation was associated positively with yield: i) in 17 out of 19 years of trials in a set of advanced breeding lines selected in the Central Great Plains and ii) in cultivars with CIMMYT germplasm evaluated under irrigation and low disease incidence in Ciudad Obregon (Mexico). Aligning with Gao et al. (2021), our study demonstrated that the 2N^vS translocation was associated with the population structure, suggesting that other genetic variants might be associated with the four yield phenotypes besides the 2N^vS from Jagger, as a major parent used in the regional breeding programs.

4.5 Box 1

4.5.1 Genes associated with yield phenotypes

We tested for the association of SNPs with $-\log_{10}(P) > 3$ and annotated genes within the IWGSC CS RefSeq v2.1 (Zhu et al., 2021) to identify putative candidate genes underlying the four yield phenotypes. We set a window size to 20kb centered on each significant SNP.

TraesCS3A03G1184000 associated with yield plasticity, encodes E3 ubiquitin-protein ligase gene. These proteins are well-known for their role in regulating signaling pathways involving jasmonate, salicylic acid, ethylene, gibberellic acid, and auxin in response to various stresses (Vierstra, 2012; Shabek and Zheng, 2014; Kelley, 2018). The specific functions of E3 ubiquitin ligase proteins in response to environmental biotic and abiotic stresses have been characterized in wheat, soybeans and rice (Su et al., 2024). In wheat, the E3 ubiquitin gene *CMPG1-V* overexpression was associated with increased resistance to powdery mildew during both the seedling and adult stages (Zhu et al., 2021). E3 ubiquitin proteins from wheat may either positively or negatively regulate response to salt and drought stress (Zhang et al., 2017; Wu et al., 2020). *TraesCS2B03G1463700* encodes a Protein S-acyltransferase (PAT) 11 gene. *Arabidopsis* mutants lacking *PAT14* gene had premature leaf senescence (Zhao et al., 2016). *TraesCS6A03G0054100* associated with yield plasticity and *TraesCS3B03G1223300* associated with yield in high yielding environments (Table 4.1). These two genes were situated near F-box proteins. This protein family, was identified in rice (Kuroda et al., 2002; Hua et al., 2011), maize (Jia et al., 2013), soybeans (Jia et al., 2017) and *Arabidopsis* (Hua et al., 2011). A major study on F-box genes in wheat identified 409 genes spread across all 21 chromosomes (Li et al., 2020), and were expressed during the formation of spikes, grains, and flag leaves. F-box genes associated with resistance to leaf rust, drought, heat and cold stress (Li et al., 2020). The F-box

protein gene, *TaCFBD*, cloned from wheat, was overexpressed when wheat seedlings were exposed to a temperature of 4°C and overexpressed during the early stages of inflorescence development, suggesting a potential connection to the formation of floral organs (Hong et al., 2012).

Three characterized genes associated with yield in high yielding environments (Table 4.1). *TraesCS5D03G1145000*, encodes a Phospholipase D (PDL), involved in tolerance against freezing, dehydration, heat, and salt stress in wheat, *Arabidopsis*, maize, sorghum and potato (Wang et al., 2021; Wei et al., 2022). *TraesCS7B03G1226200* encodes a GDSL lipase/esterase protein (Glycine – Aspartic acid – Serine – Leucine). GDSL lipase/esterase (GELP) were identified in *Arabidopsis*, maize, soybean and rice (Shen et al., 2022) and are involved in seed germination, coleoptile elongation, lateral root formation, overall root development, plant height, and development of stomata and reproductive structures (Ding et al., 2019). 509 GELP genes were identified in wheat, *TaGELP073*, has a role in the development of anthers and pollen (Yang et al., 2022).

Five characterized candidate genes associated with mean yield (Table 4.1). *TraesCS2D03G0491900* encodes a helicase-conserved C-terminal domain protein. DNA helicases are involved in genetic information processing, including replication, transcription, translation, repair, and recombination (Umate et al., 2010). A genome-wide analysis of an RNA helicase family in wheat showed that certain genes within this family were upregulated in transgenic *Arabidopsis* plants (with ectopic expression of specific wheat helicase genes) under drought, salt, and cold stress conditions (Ru et al., 2021). *TraesCS2D03G0492100* encodes MAIN-LIKE 1 protein. The MAINTENANCE OF MERISTEMS (MAIN) genes play a crucial role in maintaining genome stability, developmental processes, and silencing transposable

elements (Nicolau et al., 2020). In *Arabidopsis*, mutations in the MAIN gene result in premature differentiation and cell death of stem cells, shorter roots, irregularly shaped leaves, reduced fertility, and partial fasciation of stems (Wenig et al., 2013). *TraesCS6B03G1046500* encodes subtilisin-like serine protease (SBT), a subgroup of the serine protease family. In wheat, 255 putative subtilisin-like serine protease (SBT) genes were identified (Zhao et al., 2023) and expression levels of SBT genes varied with fungal and bacterial pathogens, as well as under conditions of drought, heat, and cold, expressed during seedling emergence, tillering, and grain filling period (Zhao et al., 2023). In cotton (*Gossypium hirsutum*), it is hypothesized that the SBT gene *GhSBT27A* enhances drought tolerance by altering the structure of chloroplasts (Dai et al., 2023). *TraesCS6B03G1290400* inhibits pectin methylesterase, its expression in wheat fertile anthers, suggests a potential role in pollen development and fertility (Wang et al., 2023b).

Yield in low yielding environments was primarily a response to drought stress, and associated with six characterized genes (Table 4.1). *TraesCS7D03G0060000*, encodes late embryogenesis abundant (LEA) proteins, its expression in wheat roots, stems, leaves, and seeds varied with environment and associated with drought stress and low-temperature stress (Zan et al., 2020). *TraesCS1A03G0106400* encodes ankyrin repeat (ANK) proteins, which modulate abscisic acid signaling pathways and are associated with tiller number (Dong et al., 2023) and resistance to various fungal diseases, including leaf rust (Kolodziej et al., 2021), stripe rust (Wang et al., 2020), and powdery mildew (Hu et al., 2022). *TraesCS7D03G0060600* encodes a putative β -1,3 glucan synthase (callose synthase 10) gene. Callose plays a crucial role in the transmission of information between cells and regulates growth and development at various stages (Li et al., 2023). Both biotic and abiotic stresses can stimulate the synthesis of callose in plants (Li et al., 2023). Bacterial infections can trigger callose synthesis at the location of the attack, resulting in

thicker cell walls forming a protective physical barrier that aids the plant in defending itself against additional bacterial intrusion (Li et al., 2023).

4.6 Conclusion

In the context of large investments in genome-wide-association studies of quantitative traits including yield and its components (Zhang et al., 2010; Quraishi et al., 2017; Yang et al., 2021), here we show the mismatch between genomic regions associated with mean yield, the most common target of GWAS, yield in high and low yielding environments, and between yield and phenotypic plasticity of yield. Our findings have implications for research, breeding and agronomy. A focus on phenotypic plasticity could be useful to pre-empt GxE. First, to exploit the genetics of yield plasticity, we need to determine whether yield plasticity is agronomically adaptive for the population of genotypes and environments evaluated. Further exploration of data from regional testing networks in major wheat growing regions could be used to answer this context-specific question. Second, selection for yield plasticity may improve selection accuracy and intensity, arising as a potential tool to overcome lower genetic gains partially associated with declining heritability of yield. Third, selection on high yielding environments allows to better detect differences in cultivar-specific phenotypic plasticity. However, maintaining a necessary level of testing in lower yielding environments will capture genomic regions associated with stress adaptation. Fourth, breeders can select semi-independently for yield potential, drought stress tolerance and yield plasticity. Finally, a dual focus on phenotypes with high yield plasticity and enhanced management could further capture breeding and agronomy synergies.

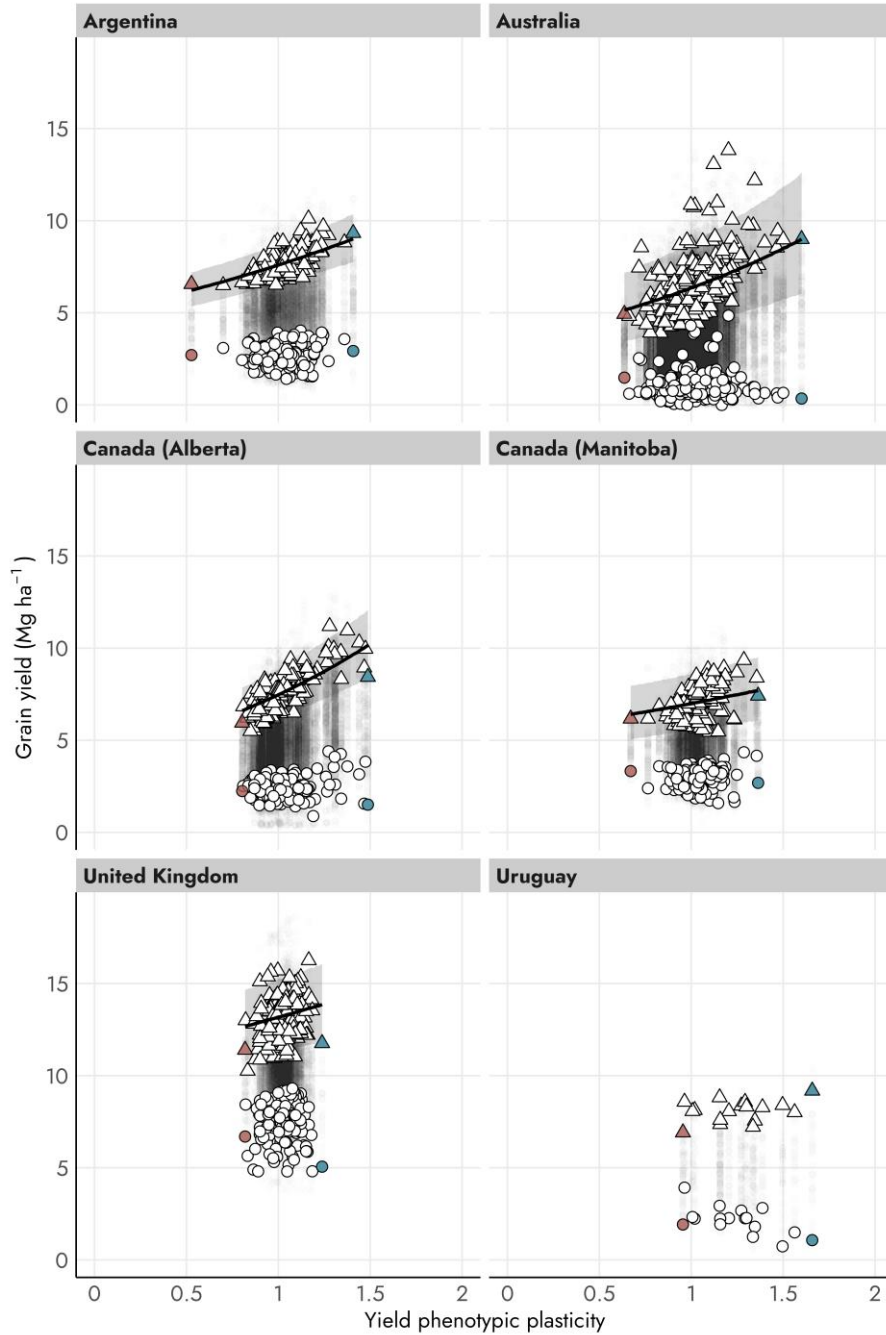


Figure 4.1. Association between genotype-dependent phenotypic plasticity of yield and actual yield in high (triangles, 95th yield percentile) and low (circles, 5th yield percentile) yielding environments in a sample of wheat producing regions. The genotypes with highest (blue) and lowest (red) plasticity are highlighted. Only associations where the slope 95% credible interval does not overlap zero are shown. Model used for quantile regression is in Equation 4. Data were obtained from variety testing networks in each region and reproduced with permission. Additional details on datasets used in this Figure can be found in Appendix Table D.1.

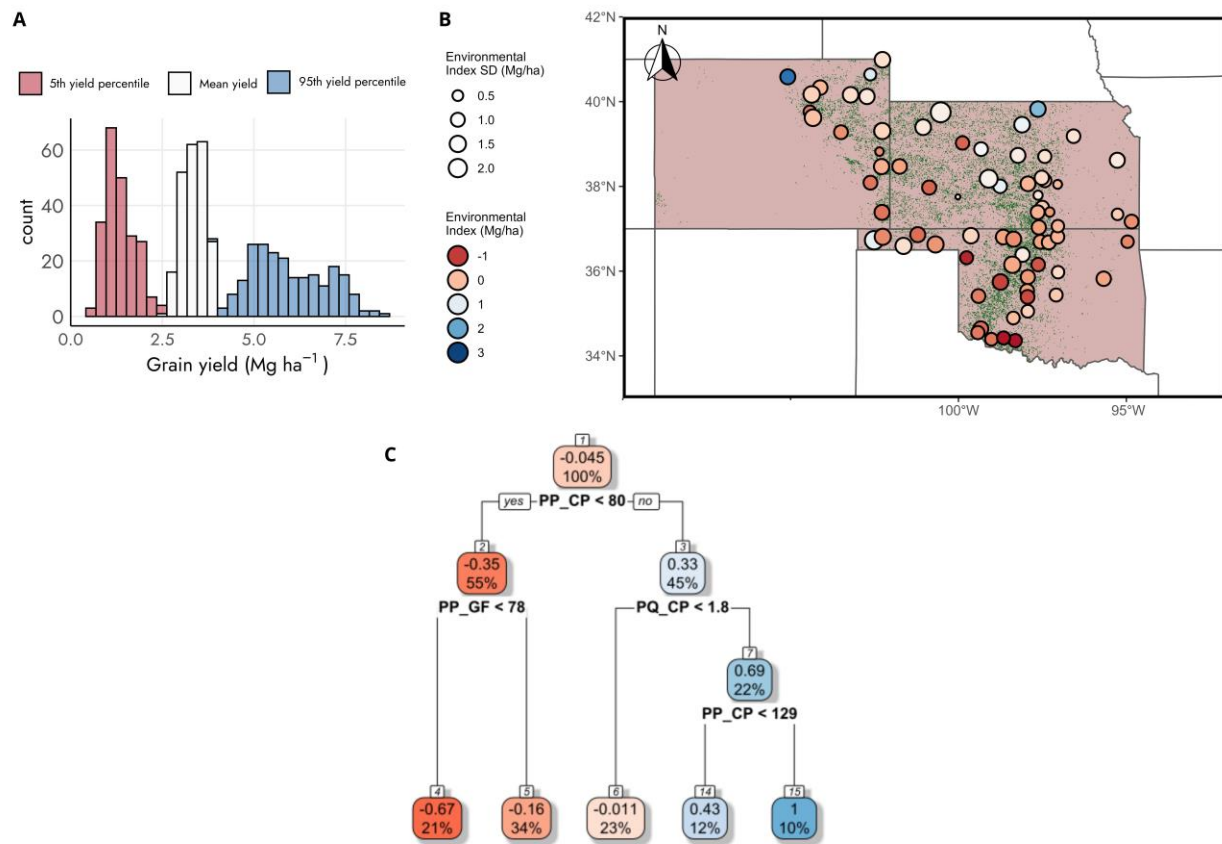


Figure 4.2. (A) Frequency distribution of grain yield in three levels: high yielding environments (blue, 95th percentile), mean yield (white) and low yielding environments (red, 5th percentile). (B) Spatial distribution of experimental sites throughout the states of Colorado, Kansas, and Oklahoma. In (B), each point represents an experimental site, color of the point is relative to the average environmental index of a given location, and their size represents the standard deviation of environmental indexes within a site. (C) Associations between environmental index, e_j , photothermal quotient and the cumulative precipitation from the start of the critical period (-300 °Cd from anthesis) and the end of the grain filling period ($+600$ °Cd from anthesis). Color of nodes/points is relative to the mean environmental yield. In B and C, environmental indexes are expressed as deviations from the overall intercept, μ_0 (mean: 3.4 Mg ha^{-1} , c.i.: $3.3 - 3.5 \text{ Mg ha}^{-1}$), both estimated following Equations 1 and 2. Estimation of levels of the grain yield distribution shown in A are described in Equations 1,2 and 4. Abbreviations: precipitation (PP), photothermal quotient (PQ), critical period (CP), grain filling period (GF).

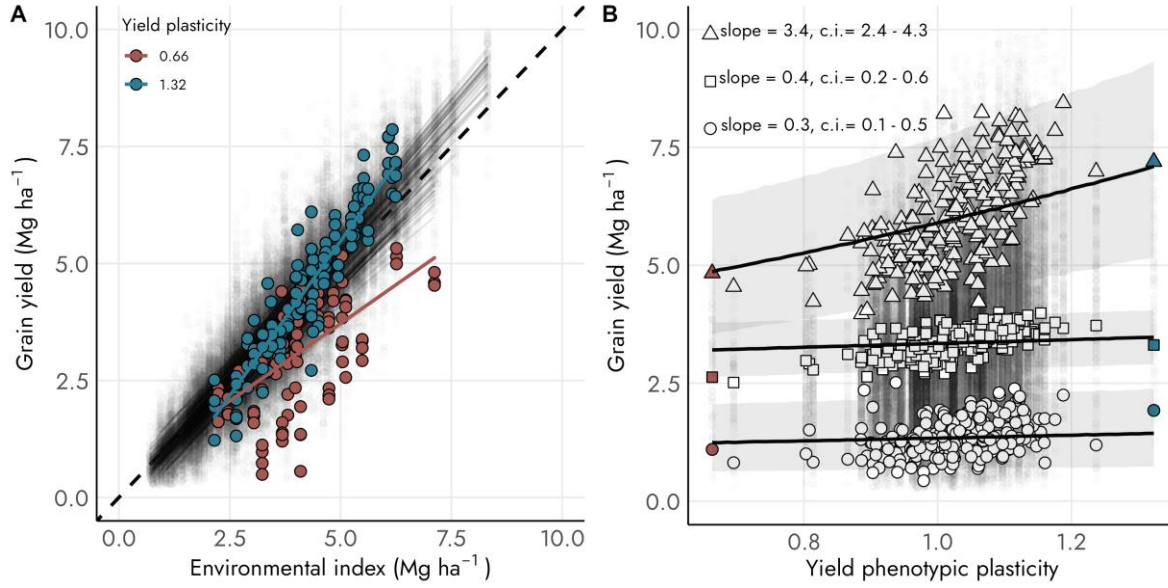


Figure 4.3. Reaction norms relating genotype-dependent yield and environmental index and (B) association of yield and yield plasticity for 234 cultivars grown in at least 25 environments in Central Great Plains. In (A) color lines and symbols are for cultivars with the highest (blue) and lowest (red) yield plasticity, and black lines are the population as a bundle of reaction norms (sensu Van Noordwijk (1989); dashed line is $y = x$). In (B) triangles are high (95th percentile), squares are average, and circles are low (5th percentile) yielding environments. Model used for quantile regression is described in Equation 5. Environmental index is estimated from the sum of μ_0 and e_j (Equation 2). Yield phenotypic plasticity was estimated as $1 + \beta_i$ (Equation 2), i.e., the slope of the reaction norm in panel A.

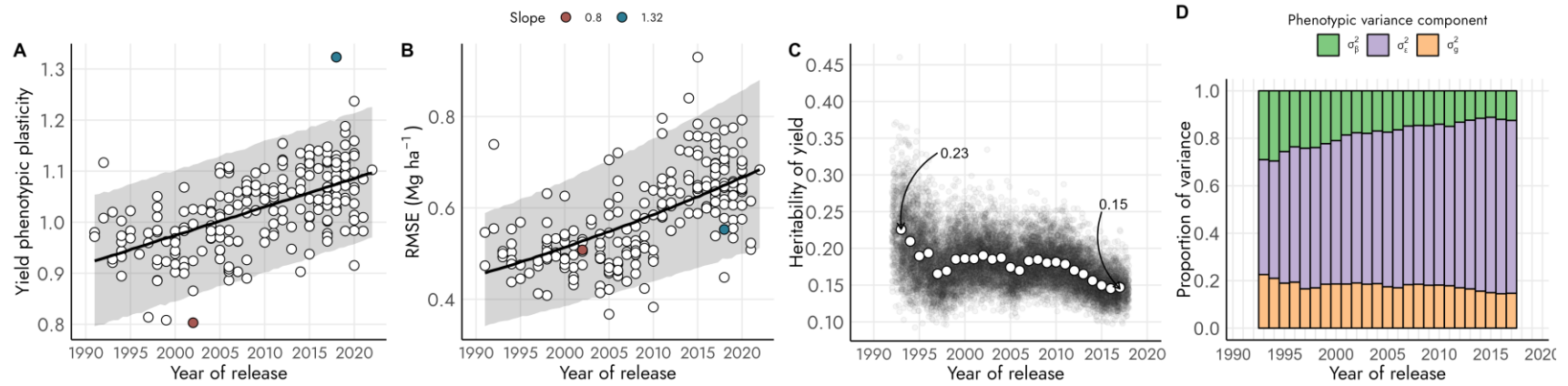


Figure 4.4. Time trends for (A) phenotypic plasticity of yield, (B) root mean squared error (RMSE) from yield-yield environment reaction norm, (C) broad sense heritability of yield and (D) expected value of variance components from broad sense heritability estimation. In A and B, colors show the cultivar with the highest (blue) and lowest (red) yield plasticity. Heritability of yield was estimated using a sliding window of 10 years starting in 1989 until 2022, x-coordinate of open points represents the average heritability for the window sampled. Jitter was added to black points on x, which represent the uncertainty in the estimation of y. Data from cultivars released between 1967-1989, were excluded as only three cultivars were representative of the entire population in that period.

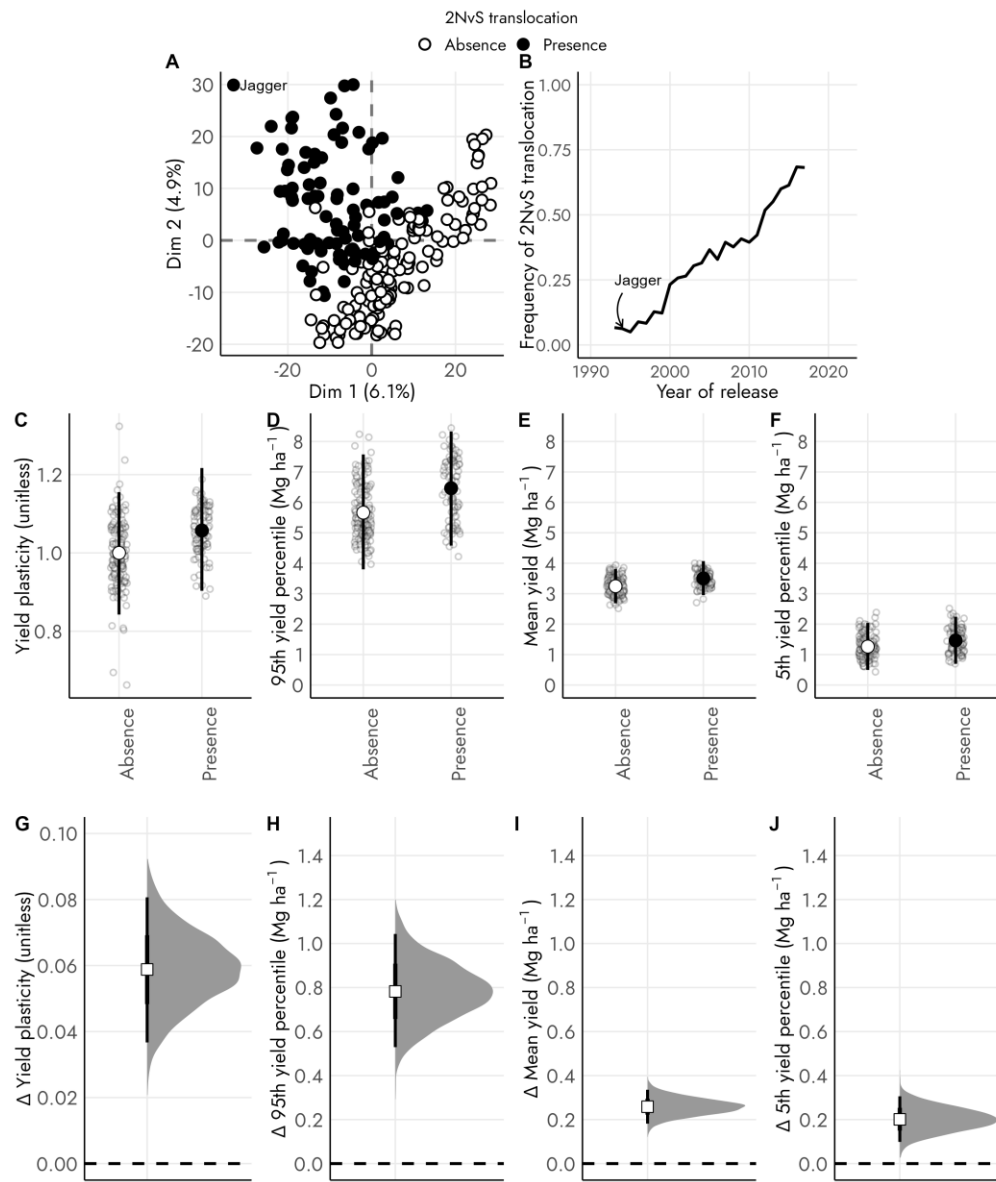


Figure 4.5. Relationship between first two principal components from PCA conducted on the genotypic matrix. Closed symbols represent presence and open symbols represent absence of 2N^vS translocation on chromosome 2A. Jagger is the canonical for the 2N^vS translocation in North American hard winter wheat. (B) Increasing frequency of the 2N^vS translocation with cultivar year of release. Allelic frequency in the population was calculated using a sliding window of 10 years starting in 1989 until 2022; data prior 1989 were scarce, and therefore were excluded. (C-F) Distribution of yield phenotypes for cultivars with presence and absence of the 2N^vS translocation, circles represent the median and whiskers the 95% credible interval of the posterior predictive distribution of yield phenotypes, while open points represent the observed yield phenotypes. (G-J) Posterior distribution of the difference between presence and absence of the 2N^vS translocation, showing magnitude of effect sizes for each yield phenotype, points

represent the mean and whiskers the 95% credible interval. 95% credible interval does not overlap with zero in all four comparisons shown in panels F-I.

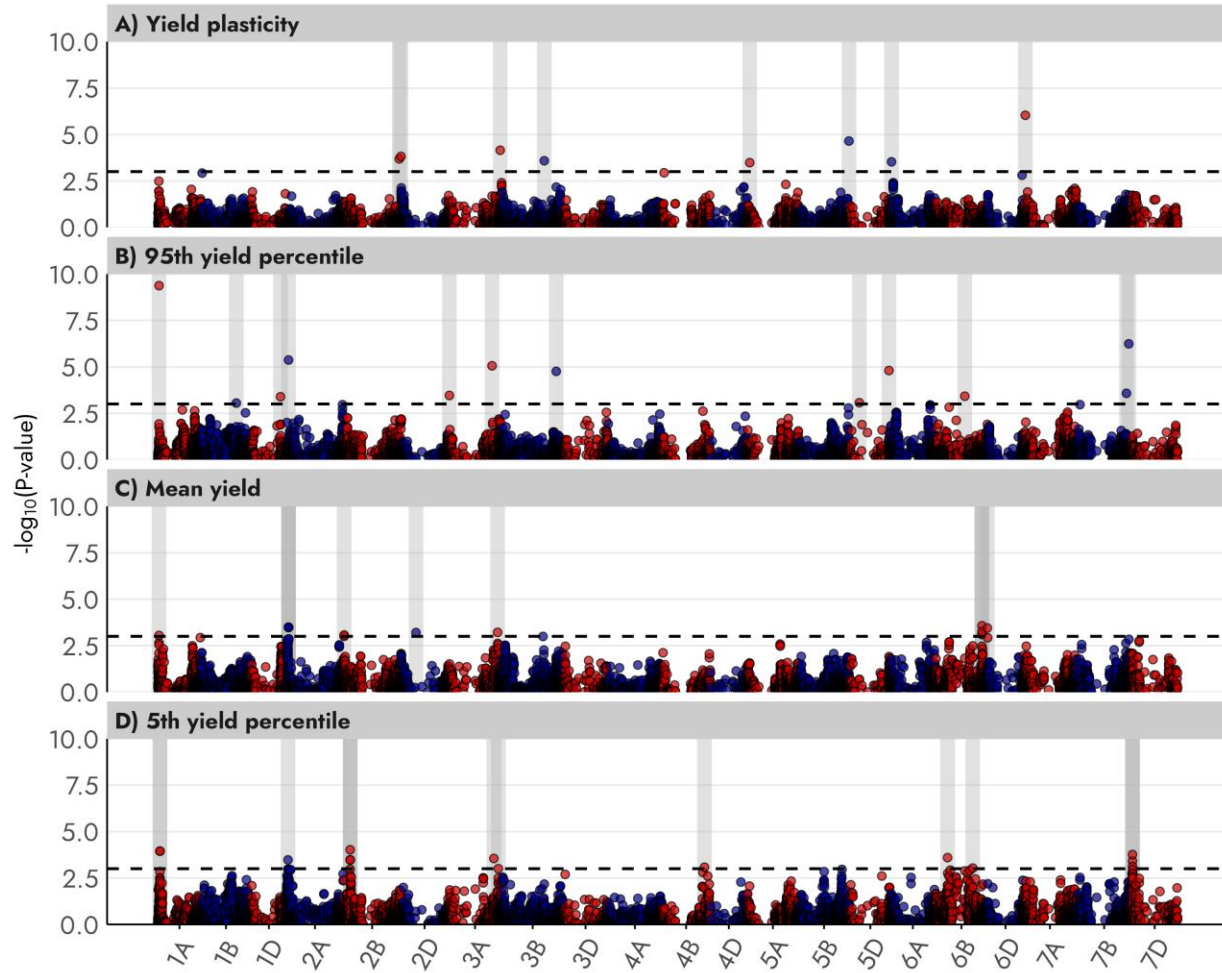


Figure 4.6. Associations of 15,224 SNPs and four yield phenotypes: (A) phenotypic plasticity of yield, (B) yield in high yielding environments (95th yield percentile), (C) mean yield, and (D) yield in low yielding environments (5th yield percentile). Black dashed line is the exploratory threshold of $-\log_{10}(P) = 3.0$, and shaded areas show the position of SNPs above the exploratory threshold.

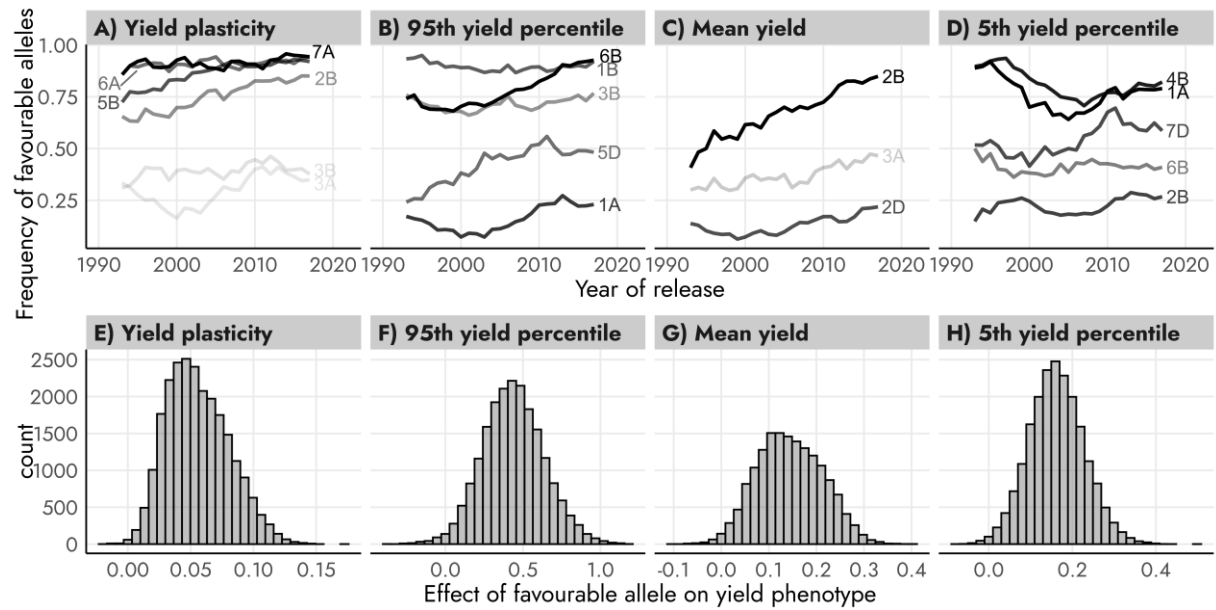


Figure 4.7. (A-D) Variation in the frequency of the favorable alleles associated with four yield phenotypes with cultivar year of release. Allelic frequency in the population was calculated using a sliding window of 10 years starting in 1989 until 2022; data prior 1989 were scarce, and therefore were excluded. Opacity of the allelic frequency lines is relative effect of the favorable allele in each SNP, being the darker colors the SNPs with major effects on traits. (E-H) Distribution of allelic effects for yield traits. Yield plasticity is unitless in E, and units are Mg ha^{-1} for yield phenotypes in F, G and H. Relative effects represent the effect size of a given SNP relative to the maximum effect size for a given trait.

Table 4.1. Genes associated with yield phenotypes in a 20kb window centered on each SNP above the $-\log_{10}(P) = 3.0$ threshold. Genes were described using the Chinese Spring (CS) reference genome RefSeq v2.1 (Zhu et al., 2021). Abbreviations: chromosome (Chr.), base pairs (bp).

Trait	Chr.	Physical location (bp)	Gene Name	Description
Yield plasticity	2B	781222236	TraesCS2B03G1463700	Protein S-acyltransferase 11
	3A	726890110	TraesCS3A03G1184000	E3 ubiquitin-protein ligase RGLG3
	3B	587824478	TraesCS3B03G0914100	Uncharacterized protein
	3B	587824478	TraesCS3B03G0914200	Basic-leucine zipper domain;
	5B	704099016	TraesCS5B03G1336800	Uncharacterized protein
	6A	13708715	TraesCS6A03G0054100	F-box domain
95th yield percentile	1B	493165543	TraesCS1B03G0773600	Uncharacterized protein
	3B	754137029	TraesCS3B03G1223300	F-box domain
	5D	134802435	TraesCS5D03G0270200	Uncharacterized protein
	5D	547030857	TraesCS5D03G1145000	Phospholipase D delta
	5D	547030857	TraesCS5D03G1145100	Uncharacterized protein
	7B	724961593	TraesCS7B03G1226200	GDSL lipase/esterase
Mean yield	2D	206645004	TraesCS2D03G0491900	Helicase conserved C-terminal domain
	2D	206645004	TraesCS2D03G0492100	Protein MAIN-LIKE 1
	6B	649190074	TraesCS6B03G1038400	Serine-threonine/tyrosine-protein kinase, catalytic domain RIPK
	6B	651828250	TraesCS6B03G1046400	Uncharacterized protein
	6B	651828250	TraesCS6B03G1046500	Subtilisin-like protease SBT1.4
	6B	726368246	TraesCS6B03G1290400	Pectinesterase inhibitor domain
	6B	726368246	TraesCS6B03G1290500	Uncharacterized protein
5th yield percentile	1A	27594591	TraesCS1A03G0106400	Ankyrin repeats
	1A	27594593	TraesCS1A03G0106400	Ankyrin repeats
	3A	701725274	TraesCS3A03G1092300	Uncharacterized protein
	7D	13070614	TraesCS7D03G0060000	Late embryogenesis abundant protein, LEA-25/LEA-D113
	7D	13070644	TraesCS7D03G0060000	Late embryogenesis abundant protein, LEA-25/LEA-D113
	7D	13415400	TraesCS7D03G0060600	1,3-beta-glucan synthase subunit FKS1, domain-1/Callose synthase 10

Chapter 5 - High yield stability and susceptibility to stripe rust

associate with large yield gaps in rainfed winter wheat

Abstract

Narrowing yield gaps, *i.e.* the difference between water-limited yield potential and actual yield, is fundamental for food security. Phenotypic plasticity of grain yield and resistance to stripe rust (*Puccinia striiformis* f. *sp. tritici*) have been analyzed independently, but their combined contribution to yield gaps in wheat (*Triticum aestivum* L.) is uncertain. This study tested three hypotheses. First, yield gap increases with decreasing yield plasticity, *i.e.* there is a tradeoff between yield stability and yield gap. Second, resistant phenotypes have smaller yield gaps under conditions favoring stripe rust development. Third, absent of conditions favorable to disease development or presence of crop protection, responses to stripe rust resistance would depend on whether there is or not a metabolic cost of stripe rust resistance. By exploring these hypotheses, we aim to understand trade-offs and synergies between stripe rust resistance and yield phenotypic plasticity under varying management and environment. Grain yield, and stripe rust ratings were obtained from a factorial experiment comparing 20-55 cultivars under two management intensities, one reflecting standard grower practices in the region (*i.e.*, enough N for a yield goal of 4 Mg ha⁻¹ and no fungicide applied), and a second with a reasonable level of management intensification (*i.e.*, an additional 45 kg N ha⁻¹, one fungicide application at jointing and a second at heading) in 21 location-years in the southern Great Plains of the US. We estimated cultivar-specific yield phenotypic plasticity (*i.e.*, the inverse of yield stability) as the ratio between the yield variance of a given genotype and the total yield variance in the dataset. Water-limited yield potential was estimated using quantile regression, and used to derive yield gaps. Cultivars with high yield phenotypic plasticity (less stable yield) had smaller yield gaps in

environments with high water-limited yield potential. Combining the addition of N and fungicide with cultivars with high yield plasticity could narrow yield gap regardless of environmental potential. Under conditions favorable for disease, stripe rust resistance narrowed yield gaps, particularly where disease chemical control was absent or ineffective. The null yield difference between stripe rust resistant and susceptible phenotypes when protected with foliar fungicides reflects there is no cost of disease resistance. Both yield stability and stripe rust susceptibility increase the magnitude of yield gaps in winter wheat regardless of environment yield potential and conditions conducive to stripe rust development. When disease is absent, stripe rust resistance does not have a yield penalty, suggesting that breeders can develop cultivars with high yield plasticity and stripe rust resistance adapted to environments where stripe rust is present but uncommon, such as western Great Plains. Developing forecasting models to quantify the economic benefits of crop protection under varying environments and disease resistance can contribute to: (i) target crop protection to conditions where positive economic benefits are more likely and (ii) reduce environmental footprint from fungicide use.

5.1 Introduction

‘Feeding 9.7 billion’ by 2050 (United Nations, 2024) requires either expanding cultivated area or narrowing yield gaps, defined as the difference between water-limited yield potential (Y_w) and actual yield for rainfed crops (van Ittersum et al., 2013; van Wart et al., 2013; Patrignani et al., 2014; Lollato et al., 2019). Expansion of cultivated area comes at expense of environment (IPCC, 2022), which goes against the United Nations Sustainable Development Goals (United Nations General Assembly, 2015). Thus, narrowing yield gaps is the most sustainable alternative to ensure food security.

Here we focus on wheat, which provides approx. 20% of calories and 11% of protein in the human diet (Shewry, 2007; Shewry and Hey, 2015). During the last decade, the US southern Great Plains have produced an annual average of 43 Mt of bread wheat (USDA-NASS, 2024) representing approximately 6% of the global wheat production (FAO, 2024; USDA-NASS, 2024). The wheat yield gap for the region averages 36% (Patrignani et al., 2014; Lollato et al., 2017, 2019; Jaenisch et al., 2021). Hence, there is an opportunity to reduce the wheat yield gap to the economic threshold of about 20-25% via improved management (Lobell et al., 2009).

Since the inception of agriculture in the Neolithic era, agricultural systems sought stable yield to ensure food security, as excess yield could not be stored over the long term or transported elsewhere (Abbo et al., 2022). Modern agricultural systems, in contrast, generally seek economic profit; crop management and cultivar selection decisions for cereal grains are targeted to capture, in the form of grain yield, favorable growing conditions while mitigating negative impacts under stress (Abbo et al., 2022). Yield stability is a value-laden concept, and the dual improvement of actual yield and yield stability is a common, often uncritically held aim of agronomic and breeding research (Mahmodi et al., 2011; Raseduzzaman and Jensen, 2017). However, the proposition of improving actual yield and yield stability overlooks an implicit tradeoff (Calderini and Slafer, 1999; Raj et al., 2023). For example, the addition of nitrogen and fungicide on top of a standard grower practice results in less stable yields, and associates with responsiveness to improved yielding environment (see Figure 2A in Raj et al., 2023). Here, we examine yield stability from the complementary lens of phenotypic plasticity, *i.e.* the ability of an organism to produce multiple phenotypes in response to environmental conditions (Bradshaw, 1965; Dewitt and Scheiner, 2004). Stability, or reduced plasticity, is the ‘tendency of a characteristic of a physiological or morphological system to be held constant’ (Bradshaw, 1965).

Yield phenotypic plasticity is an adaptive trait in the US central Great Plains (Grogan et al., 2016; Lollato et al., 2020b; Giordano et al., 2024a; b), where high plasticity cultivars outyield low plasticity (more stable) cultivars in high-yielding environments, without tradeoffs under stressful, low-yielding environments.

Stripe rust (also known as “yellow rust”, caused by *Puccinia striiformis* f. sp. *tritici*), was first observed in North America in 1915 (Carleton, 1915). It became a yield-limiting factor in the US southern Great Plains since early 2000s (Chen et al., 2002; Chen, 2005) as a result of increasingly virulent pathogens better adapted to warmer climates (Chen, 2005; Markell and Milus, 2008). Eighty seven stripe rust resistance genes have been reported that associate with resistance to multiple stripe rust races in wheat (Boden et al., 2023). However, the genetic diversity of stripe rust races and the co-evolution with crops challenge durable resistance (Qayoum and Line, 1985; Chen and Line, R.F, 1995). Worldwide, 14% of yield gap in wheat can be attributed to fungal and bacterial diseases (Oerke, 2006). Environmental drivers of stripe rust epidemics are widely reported (Grabow et al., 2016; De Wolf et al., 2023) and crop protection practices have the potential to increase actual yield and narrow yield gaps in the Central Plains (Thompson et al., 2014; Jaenisch et al., 2019, 2021, 2022; Lollato et al., 2019; Cruppe et al., 2021).

There is long-standing evidence on metabolic costs of disease resistance (Van der Plank, 1963; Bergelson and Purrington, 1996; Brown, 2002; Walters and Heil, 2007; Brown and Rant, 2013). Vanderplank’s (1963) early work, characterizing the behavior of potato (*Solanum tuberosum* L.) cultivar ‘Vertifolia’ to late blight, caused by *Phytophthora infestans* (Mont.) de Bary, set the stage to an era of plant breeding that aimed to minimize detrimental effects of disease resistance on economically valuable traits such as grain yield and quality (Brown and

Rant, 2013). A successful example of resistance genes with no yield penalty when compared to susceptible near-isogenic line, apply to barley (*Hordeum vulgare* L.) lines resistant to powdery mildew (Kølster et al., 1986; Kølster and Stølen, 1987; Jørgensen and Jensen, 1990), caused by *Erysiphe graminis* DC. f. sp. *hordei* Em. Marchal. A contrasting example related to the costs of disease resistance is the presence of hypersensitive, pathogen-induced reactions that increase respiration rate and associate with lower yield in barley infected with powdery mildew (Smedegaard-Petersen and Stølen, 1981).

We lack a combined approach to study the trade-off between two traits, *i.e.*, stripe rust resistance and grain yield stability under varying environments and crop protection. In addition to this biological tradeoff, there is a tradeoff whereby breeding efforts are divided between improvement of Y_w and maintenance breeding, including disease resistance (Grassini et al., 2025). By exploring these trade-offs, we aim to identify management and environment combinations where allocation of breeding efforts to yield stability and stripe rust resistance can contribute to narrowing yield gaps.

This study quantifies the relationships of yield plasticity and stripe rust resistance with yield gaps in rainfed winter wheat under two management intensities. We advance three working hypotheses:

- (i) There is a tradeoff between yield and yield stability. As outlined in Figure 5.1A, high yield stability (low plasticity) comes at the expense of larger yield gaps in high-yielding environments.
- (ii) Resistant phenotypes have smaller yield gaps under conditions favoring stripe rust development (Figure 5.1B). However, absent of conditions favorable to disease development, we could expect two scenarios, shown in Figure 5.1B: (i) the solid line

- where, disease resistance has a metabolic cost and stripe rust susceptible phenotypes outyield resistant phenotypes and; (ii) the dashed line, where there is no yield difference between stripe rust resistance and susceptible phenotypes.
- (iii) Absent chemical disease protection, resistant phenotypes will outyield susceptible counterparts (Figure 5.1C). In contrast, in protected crops, two scenarios shown in Figure 5.1C: (i) the solid line where higher yields and smaller yield gaps will associate with high plasticity and stripe rust susceptible phenotypes and, (ii) the dashed line where, there is no yield difference between stripe rust resistant and susceptible phenotypes.

5.2 Material and methods

5.2.1 Field experiments

Rainfed experiments were conducted in 21 environments resulting from the combination of locations and years in the states of Kansas, Oklahoma, and Texas. Trials started in 2013-14 and were conducted until 2020-21 (Figure 5.2, Appendix Table E.1). A factorial experiment was conducted in each location-season combining 20 to 55 winter wheat cultivars and two management intensities: (i) standard grower practice, which includes a single nitrogen (N) application as granulated urea at GS 25 (Zadoks et al., 1974) after winter dormancy with a N rate aiming at 4.0 Mg ha⁻¹ yield after subtracting available soil N at sowing in the 0-60 cm profile, and (ii) an “intensive management” treatment that consisted of the same N regime as that in the standard plus an additional 45 kg N ha⁻¹ at GS 31, coupled with two fungicide applications, the first at GS 32 and the second between GS 39 and GS 60 (Supplementary Table 2). This treatment reflected a reasonable level of management intensification, focusing on two of the leading variables causing wheat yield gaps in the region (Jaenisch et al., 2021) rather than full kitchen-

sink approach (Jaenisch et al., 2019, 2022). Treatments were based on established cultivar performance trials in the region and were replicated three or four times depending on location-season. In Kansas, treatments were arranged on a strip-plot design where cultivars were randomized within blocks and neighboring strips represented management intensities. In Texas, treatments were established in a split-plot design with management assigned to the whole plot and cultivars to sub-plots. In Oklahoma, a neighboring intensively-managed block was established adjacent to the original variety trial managed under standard grower practices. To deal with heterogeneous experimental designs in this dataset, we developed Bayesian models, where all model parameters and considered as random quantities, to establish associations of grain yield with yield stability and stripe rust resistance (see section 5.2.3). The size of the experimental unit ranged from 1.5 m (7 rows, 0.21 m row spacing) x 3.0 m in Kansas, to 1.7 m (8 rows, 0.21 m row spacing) x 9.0 m in Oklahoma.

Sowing date, previous crop, and tillage practices aimed at recommended practice for each location-season (Munaro et al., 2020). Seeding rates were 101 kg ha⁻¹ for Kansas and 67 kg ha⁻¹ for Oklahoma and Texas, and all plots were sown with 55 kg of diammonium phosphate per hectare applied in furrow with the seed. Supplementary Table 1 shows soil chemical properties, and details on crop husbandry and treatment applications are in Supplementary Table 2.

Stripe rust resistance phenotypes were retrieved for each cultivar × year combination. The stripe rust resistance ratings ranged from 1 to 9, with 1 being resistant and 9 being susceptible. Ratings 1-3 were classified as resistant, ratings 4-6 were classified as intermediate and ratings 7-9 as susceptible. We note that resistance ratings of a given cultivar may have changed over time due to loss of genetic resistance (Kolmer, 1996). Plots were harvested with self-propelled small plot combines. Grain weight and moisture were measured on-site during

harvest with a monitor incorporated in the combine, and yield adjusted to dry matter accounting for the plot area plus borders.

5.2.2 Environment

Daily weather data were retrieved from Daymet (Thornton et al., 2014) using the *daymetr* package available in R (Hufkens et al., 2018). Daymet provides daily weather gridded estimates of 1 km × 1km spatial resolution from ground based meteorological stations (<https://daymet.ornl.gov/overview>). Weather data were summarized for (i) the critical period for yield determination between -300°Cd and 100°Cd centered on anthesis using a base temperature of 4.5°C (Fischer, 1985; Dreccer et al., 2007; Cossani and Sadras, 2021), (ii) grain fill, from 100 °Cd to 600 °Cd after anthesis using a base temperature of 0°C (Dupont et al., 2006), (iii) the entire season from sowing to harvest and (iv) monthly estimates. Crop anthesis date was estimated with a locally calibrated model (Lollato et al., 2020a) in two out of 21 environments where anthesis dates were not available.

5.2.3 Statistical analysis

5.2.3.1 Yield plasticity and yield gap

Because not all cultivars were tested in all site-years, we created a subdataset where we filtered cultivars that were tested in at least 16 location-seasons, which accounts for 32 environment × management combinations, establishing a sufficiently large sample to obtain reliable estimates of grain yield phenotypic plasticity (Appendix Figure E.1). For each cultivar (i : 1,2, ..., 16) tested in at least 16 location-seasons, we calculated grain yield phenotypic plasticity (α_i) as the variance ratio (Dingemanse et al., 2010; Sadras and Richards, 2014; Giordano et al., 2024a),

$$\mathbf{x}_i = \frac{\sigma_{g_i}^2}{\sigma_E^2}, \quad (1)$$

where $\sigma_{g_i}^2$ is the variance of the i^{th} cultivar and σ_E^2 the pooled variance for the population of cultivars across all sources of variation. Thus, we assumed $\mathbf{x}_i$ is the true value of yield phenotypic plasticity for a given cultivar.

Grain yield at the i^{th} observation ($i: 1, 2, \dots, n$) in the j^{th} environment ($j: 1, 2, \dots, 20$) and the k^{th} management ($k: 1 - intensive, 2 - standard$) was modeled following a hierarchical Bayesian approach. The model assumes observed grain yield y_{ijk} follows a Gamma distribution, with expectation equal to μ_{ijk} and dispersion ϕ (Eq. 2). The process behind μ_{ijk} is a linear model where $\mathbf{x}_i$ represents a vector of yield phenotypic plasticities (Eq. 3). β_{0jk} is a vector of parameters representing the intercept at each environment $\times$ management combination. β_{1jk} is a vector of coefficients that represents the effect of yield phenotypic plasticity on grain yield at each combination of environment $\times$ management.

$$y_{ijk} \sim SN(\mu_{ijk}, \sigma^2, \xi), \quad (2)$$

$$\mu_{ijk} = \beta_{0jk} + \beta_{1jk}\mathbf{x}_i. \quad (3)$$

Water-limited yield potential at the j^{th} environment, Yw_j , was estimated with Eq. 4. Estimation of Y_w from rainfed field experiments under non-limiting resources is a valid approach if crops are grown with best available management (Supplementary Table 2, Fischer, 2015). Briefly, to estimate Y_w , we retrieved at the j^{th} environment the posterior predictive distribution of μ_{ij1} for the intensive management treatment ($k = 1$). Thus, Yw_j derives from calculating the 0.99 quantile of $\mu_{ij1}|\mathbf{y}$:

$$Yw_j = Q_{0.99}(\mu_{ij1}|\mathbf{y}). \quad (4)$$

Consequently, the yield gap, Yg_{ijk} , was expressed in percentage as:

$$Yg_{ijk} = \frac{Ya_{ijk} - Yw_j}{Yw_j} * 100, \quad (5)$$

where, Ya_{ijk} is the actual yield at i^{th} phenotypic plasticity under the j^{th} environment $\times k^{th}$ management combination.

5.2.3.2 Stripe rust resistance and yield gap

To estimate the effect of stripe rust resistance on Yg we included environments where at least two different phenotypes occurred simultaneously. Intermediate stripe rust resistance phenotypes were considered as: (i) susceptible, in environments where intermediate and resistant phenotypes were recorded, (ii) resistant, in environments where susceptible and intermediate cultivars were recorded, and (iii) not considered for analysis, in environments where the three stripe rust resistance phenotypes were recorded.

Let y_{ijkl} be the i^{th} grain yield at the j^{th} environment ($j: 1, 2, \dots, 9$), for k^{th} management ($k: 1 = intensive, 2 = standard$) and l^{th} stripe rust phenotype ($l: 1 = resistant, 2 = susceptible$); it follows a skewed normal distribution with expected value μ_{ijk} , variance σ^2 , and skewness ξ . The process behind μ_{ijk} is an intercept only model (Eq. 8).

$$y_{ijkl} \sim SN(\mu_{jkl}, \sigma^2, \xi). \quad (6)$$

We estimated the yield response to stripe rust resistance (ΔYa_{jk}) as difference between the posterior predictive distribution of resistant ($\mu_{jk1}|\mathbf{y}$) and susceptible ($\mu_{jk2}|\mathbf{y}$) phenotypes:

$$\Delta Ya_{jk} = \mu_{jk1}|\mathbf{y} - \mu_{jk2}|\mathbf{y}. \quad (7)$$

To explore environmental drivers of ΔYa_{jk} we included two environment-specific covariates between GS 25 and GS 31 (Zadoks et al., 1974) that are associated with stripe rust

epidemics (Grabow et al., 2016): the number of days with rainfall ($DWRF_j$) and the number of days with mean temperatures between 7 °C and 12 °C ($T712_j$).

$$\Delta Y a_{jk} = \theta_{0k} + \theta_{1k} DWRF_j + \theta_{2k} T712_j + \theta_{3k} (DWRF_j \times T712_j). \quad (8)$$

5.2.3.3 Model fitting and validation

Bayesian hierarchical models were fitted using weakly informative priors (Supplementary Table 4) with the exception of priors for parameters β_{0jk} , β_{1jk} and μ_{jkl} for which we selected a truncated normal distribution with an upper bound equal to a grain yield of 12.9 Mg ha⁻¹, which represents the theoretical biological limit based on radiation use efficiency and transpiration use efficiency (Sinclair, 2013). A Hamiltonian Monte Carlo sampling algorithm implemented using brms-Stan (Bürkner, 2017) allowed to obtain 20,000 posterior draws on 4 chains of which we discarded the first 10,000 as burn-in interval and kept the later 10,000 for inference. In total we generated 40,000 posterior draws used for statistical inference. For better model convergence we set *adapt_delta* parameter to 0.95. Scripts for reproducible analysis of models used are available in <https://github.com/giordanon/PLASTICITY-YIELD-GAP>.

5.3 Results

5.3.1 Environments

Across sources of variation, grain yield ranged from 0.7 Mg ha⁻¹ to 9.5 Mg ha⁻¹, Y_w ranged from 4.2 Mg ha⁻¹ to 10.2 Mg ha⁻¹ (Appendix Figure E.2), and the yield gap ranged from 9 % to 65 % (Appendix Figure E.3). Grain yield associated positively with the photothermal quotient and duration of the critical period, and with the number of days with daily mean temperature between 7 and 12 °C during the GS 25 – GS 31 period (Figure 5.3A). Grain yield was negatively related to vapor pressure deficit and mean temperature during the critical period (Figure 5.3A). The duration of critical period varied 1.9-fold and ranged from 25 to 47 days, and

the mean temperature in the critical period ranged from 10.4 to 19.8 °C (Appendix Table E.4). The photothermal quotient during the critical period varied 1.9-fold, from 1.1 MJ °Cd⁻¹ to 2.1 MJ °Cd⁻¹ (Appendix Table E.4). Vapor pressure deficit during critical period varied from 378 to 1535 Pa (Appendix Table E.4). Water supply varied 3.1-fold, from 302 to 940 mm, and was the major contributor to the second principal component (17%, Figure 5.3B).

5.3.2 Relationship between yield plasticity and yield gap

Grain yield plasticity ranged from 0.42 to 1.45 among the 16 cultivars evaluated in at least 32 environments (Appendix Table E.2, Figure 5.4). The slope of the relationship of grain yield and yield plasticity (β_{1jk} , Eq. 3) ranged from -1.8 Mg ha⁻¹ to 3.4 Mg ha⁻¹ per unit plasticity (Figure 5.4). Across management intensities, yield plasticity associated with higher yield in 13 environments (posterior probability > 0.95), was unrelated to grain yield in 5 environments, and associated negatively with yield in one environment (posterior probability > 0.95). A tradeoff was apparent in one environment, OK19, where higher yield plasticity associated with higher yield under intensive management at the expense of lower yield with standard management (Figure 5.4G).

Figure 5.5A demonstrates how a cultivar with high phenotypic plasticity for yield ('WB4303', plasticity = 1.45) was better able to capture favorable environmental conditions than a less plastic cultivar ('Double Stop CL+', plasticity = 0.42). Yield gaps ranged from 50% in high Y_w environments with low plasticity cultivars and standard management, to 8% in high Y_w environments with high plasticity cultivars and intensive management (Figure 5.5C). Under standard management, the benefit of the plastic cultivar was more apparent (posterior probability = 0.90) in $Y_w > 8.5$ Mg ha⁻¹ (Figure 5.5B). Under intensive management, the benefit from the plastic cultivar was apparent (posterior probability = 0.90) in $Y_w > 5.2$ Mg ha⁻¹ (Figure 5.5B).

Under $Y_w = 10.1 \text{ Mg ha}^{-1}$, yield gaps were 25% larger under standard and 31% larger under intensive management with low plasticity (high stability) cultivars (Figure 5.5C).

5.3.3 Association between stripe rust resistance and yield gaps

Environment and management modulated the yield difference between stripe rust resistant and susceptible phenotypes (Figure 5.6 , Appendix Figure E.4). In unresponsive environments to stripe rust resistance, yield gap was similar for resistant and susceptible stripe rust phenotypes and averaged 35% under standard and 23% under intensive management (Figure 5.6). In responsive environments, the yield gap was 15% larger under standard management and 12% larger under intensive management with susceptible cultivars (Figure 5.6). In responsive environments, the largest yield gap, averaging 53%, was under standard management and susceptible phenotypes and the lowest gaps, averaging 29%, were under intensive management and resistant phenotypes (Figure 5.6).

Stripe rust resistant and susceptible phenotypes yielded similarly in 31 out of 38 environment $\times$ management combinations, while resistant phenotypes yielded more than susceptible in 7 environment $\times$ management combinations. Responsiveness to the stripe rust resistance was associated with greater number of rainfall days and number of days with temperature between 7 and 12 °C, both between GS 25 and GS 31 (Figure 5.7). Predictions at regional scales from the model presented in Equations 7 and 8 suggest that the likelihood of a resistant phenotype to outyield a susceptible counterpart decreases from east to west (Figure 5.7D, Figure 5.7E).

5.3.4 Interactions between yield plasticity and stripe rust resistance

Higher yields related with high yield plasticity phenotypes in 35 out of 38 combinations of environment and management sampled (Figure 5.8). Pooling across 35 environment $\times$

management combinations where yield plasticity was a positive trait, there was no yield difference between stripe rust resistant and susceptible phenotypes regardless of crop protection (posterior probability = 0.48, Figure 5.8).

5.4 Discussion

The US southern Great Plains is a drought-prone region and environmental variation of yield in our dataset associated primarily with duration of the critical period for yield, which is shortened with warmer temperature (Sadras et al., 2022) and lower seasonal water supply (Figure 5.3). Couëdel et al. (2021) highlighted the co-occurrence of drought and heat stress and quantified the spatial and temporal variation of these stresses for the US wheat growing regions, which are often compounded by windy events (Zhao et al., 2022). Grain yields explored in this study were similar to those reported in previous studies evaluating maximum wheat grain yields in rainfed experiments within the study region (range: 1.2-9.3 Mg ha⁻¹ in Lollato et al., 2017). Similarly, Y_w estimated using Bayesian quantile regression, was within the 1.2-10.9 Mg ha⁻¹ range estimated by Jaenisch et al., (2021) using a calibrated crop simulation model in the study region. Consequently, the average yield gap of 31% in our study compared to an average 35% estimated using a boundary function method from grower-reported data in the study region (Jaenisch et al., 2021) and with 36% calculated using yield data from USDA-NASS for the State of Kansas (Fischer et al., 2014).

5.4.1 Hypothesis 1: Yield plasticity related negatively with yield gap in high yielding environments

Less stable, highly plastic phenotypes generally returned lower yield gaps (Figure 5.5A). This highlights the limitations of the common proposition to improve both yield and yield stability, and supports the notion that yield stability comes at the expense of large yield gaps. We

note that there are multiple proposed definitions for crop yield stability in literature (*e.g.*, Eberhart and Russell, 1966), and our conclusions are tied to the definition of yield stability outlined in this article and by Bradshaw (1965). Our finding aligns with field trials in the region where higher plasticity cultivars were more responsive to nitrogen supply (Giordano et al., 2024a). Raj et al., (2023) also suggested a greater wheat yield response to the combined addition of nitrogen and fungicide in higher-yielding environments. A physiological approach revealed that grain yield response to management intensification in the study region was driven by increased grain number, resulting from greater biomass accumulation and nitrogen uptake without changes in harvest index (de Oliveira Silva et al., 2020). This study builds upon these previous reports by providing insights from the combined interactions between yield plasticity, management intensification, and environment.

In the first eight decades of the 20th century, breeding for yield and agronomic adaptation reduced yield stability, quantified as the slope of the regression between yield *per se* and environmental mean yield (Wolterreck, 1909) of wheat in the US Great Plains, Argentina, Australia, Italy, and the UK (Calderini and Slafer, 1999; Giordano et al., 2024b). Other cases of tradeoff between yield gap and yield stability include sunflower and long-season spring wheat in Argentina (Sadras et al., 2009; Curin et al., 2021), chickpea in Australia (Sadras et al., 2016), and spring wheat in Finland (Peltonen-Sainio et al., 2011). In common with our findings, the tradeoff between yield gap and yield stability resulted from the association between yield plasticity and yield in high yielding environments. The tradeoff is common but not universal; a collection of 169 wheat lines grown in six environments in Mexico returned an association between low plasticity of yield and smaller yield gaps because phenotypes performed similarly in high-

yielding environments, and high plasticity was associated with low yield under drought (Sadras et al., 2009).

5.4.2 Hypothesis 2: Yield gaps are larger with cultivars susceptible to stripe rust in unprotected crops under conducive conditions for disease development

Stripe rust resistance reduced yield gaps under conditions conducive for disease, particularly for unprotected crops (which in this study is confounded with low nitrogen supply since the treatment structure does not allow for isolating the effects of nutrients *versus* foliar fungicide). Previous studies in the region reported that foliar fungicides can economically narrow yield gaps (Jaenisch et al., 2019, 2022; Lollato et al., 2019), even on stripe rust-resistant phenotypes (Cruppe et al., 2021). Thus, foliar fungicides can mitigate the lack of differences between stripe rust resistant and susceptible phenotypes under most environmental conditions explored in this analysis (Figure 5.7A). Yield responses to stripe rust resistance are unique to our combination of genotypes and environments and their extrapolation to future scenarios must account for plant-pathogen co-evolution (McIntosh et al., 2018), where breeding efforts are allocated to introduce new genetics for stripe rust resistance. Within this context, ‘maintenance breeding’ termed by Grassini et al., (2025) is defined as the loss of ‘agronomic fitness’ of a cultivar over time due to evolving environments including pests, and can explain up to 47% of the genetic progress.

The yield difference between stripe rust resistant and stripe rust susceptible phenotypes was associated with the number of days with rainfall and the number of days with temperature between 7 °C and 12 °C between GS 25 and GS 31. These conditions are related to critical stages of the pathogen life cycle, *e.g.* urediniospores germination is promoted by high relative humidity as it favors the growth of the germ tube over condensation droplets (Rapilly, 1979; Grabow et

al., 2016; Carmona et al., 2020). While early studies found a wider range of temperatures favoring disease development (e.g., Sharp 1965) found that the optimal range for appressorium development was between 2 °C and 15 °C), we used the temperatures and developmental window developed recently associated with epidemics during the last century within the US southern Great Plains are a consequence of the pathogen adaptation to warmer environments (Chen, 2005; Markell and Milus, 2008).

Evidence in the study region (Jaenisch et al., 2019) suggests that adding a fungicide application in environments conducive to both high yield and disease can economically reduce winter wheat yield gap to the economic threshold of about 20-25% (Lobell et al., 2009). Our study expands on environmental predictors of yield response to crop protection and disease resistance, as means of reducing net income uncertainty to intensified management practices. Intensified management practices result in higher financial risk exposure (Jaenisch et al., 2019), which associates with lower levels of technology adoption (Spiegel et al., 2021). Assuming equal costs to grow stripe rust resistant and susceptible cultivars, under current standard farmer practices and disease conducive environments, adoption of stripe rust resistant cultivars could narrow yield gaps up to 15% of Y_w without higher financial risk exposure. Using a subset of the database used in the current study comprised of five Kansas site-years (out of the 21 total site-years here reported), de Oliveira Silva et al. (2020) postulated two potential strategies for farmers in the region to manage the risk associated with management intensification: a risky approach seeking to maximize yield where farmers select cultivars with high responsiveness to management and high yield response variability; and a more conservative approach selecting cultivars with high mean response but stable yields in response to management.

5.4.3 Hypothesis 3: Greater frequency of smaller yield gaps when combining high plasticity-resistant stripe rust phenotypes

Higher yields were more frequently associated with high plasticity, low stability phenotypes (*i.e.*, right two quadrants on Figure 5.8). The null yield difference between stripe rust resistant and susceptible phenotypes when protected with foliar fungicides (Figure 5.8) reflects there is no cost of disease resistance supporting the ‘dashed lines’ hypothesis presented in Figure 5.1B and Figure 5.1C. Contrasting evidence to our findings suggest costs of rust resistance genes in wheat exists but is not common (The et al., 1988; Singh and Huerta-Espino, 1997; Brevis et al., 2008). In a set of 22 advanced spring wheat near isogenic lines, presence of gene *Lr34* associated with 5.9 % yield drag in protected plots and 43-84% yield advantage in unprotected plots against leaf rust (Singh and Huerta-Espino, 1997). The et al., (1988) found that presence of stem rust resistance gene *Sr36* associated with 9% yield drag under absence of disease, even though *Sr36* is present in widely grown cultivars in Australia (Singh et al., 2016).

In western wheat growing region of Kansas and Oklahoma, susceptible phenotypes outyielded resistant counterparts (Figure 5.7D, Figure 5.7E). This phenomenon is expected, and associated with the lack of environmental conditions for stripe rust development in this subregion, primarily driven by a decline in rainfall from east to west (Couëdel et al., 2021). Because stripe rust is not a prevalent wheat yield limiting factor in this subregion, breeders select for locally adapted cultivars that do not frequently carry stripe rust resistance. Incorporating stripe rust resistance into adapted cultivars to western Great Plains, can contribute to narrow wheat yield gaps under years conducive for disease with no yield penalty in years when disease is absent.

5.5 Conclusion

We advanced a framework to quantify the association of yield gap with yield phenotypic plasticity and stripe rust resistance. We showed that high yield stability and susceptibility to stripe rust increase the magnitude of yield gaps. When disease is absent, stripe rust resistance does not have a yield penalty, suggesting that breeders can develop cultivars with high yield plasticity and stripe rust resistance adapted to environments where stripe rust is uncommon, such as western Great Plains. Developing forecasting models to quantify the economic benefits of crop protection under varying environments and disease resistance can contribute to: (i) target crop protection to conditions where positive economic benefits are more likely and (ii) reduce environmental footprint from fungicide use.

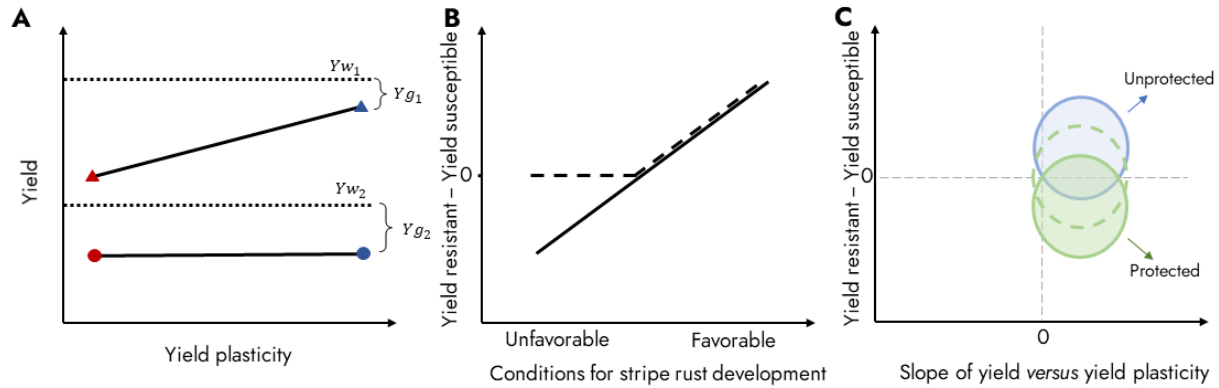


Figure 5.1. Conceptual framework and working hypotheses. (A) Hypothesis 1: Relationship between yield and yield plasticity in environments with high (Y_{w1}) and low (Y_{w2}) water-limited yield potential (dashed lines). We hypothesize that high yield stability (low plasticity) correlates with larger yield gaps in high yielding environments. Solid lines are the actual yield for high (blue) and low (red) yield plasticity cultivars. (B) Hypothesis 2: resistant (+R) phenotypes have smaller yield gaps under conditions favoring stripe rust development and larger gaps under absence of disease conditions than susceptible (-R) phenotypes. (C) Hypothesis 3: Distributions of the slope of yield versus yield plasticity (see panel A) and the yield difference between resistant (+R) and susceptible (-R) phenotypes to stripe rust (also shown in panel B), with (green) and without (blue) fungicide application. In C, stripe rust-resistant phenotypes will have smaller yield gap compared to susceptible counterparts when unprotected (blue) and *vice versa* when protected (green) with foliar fungicide.

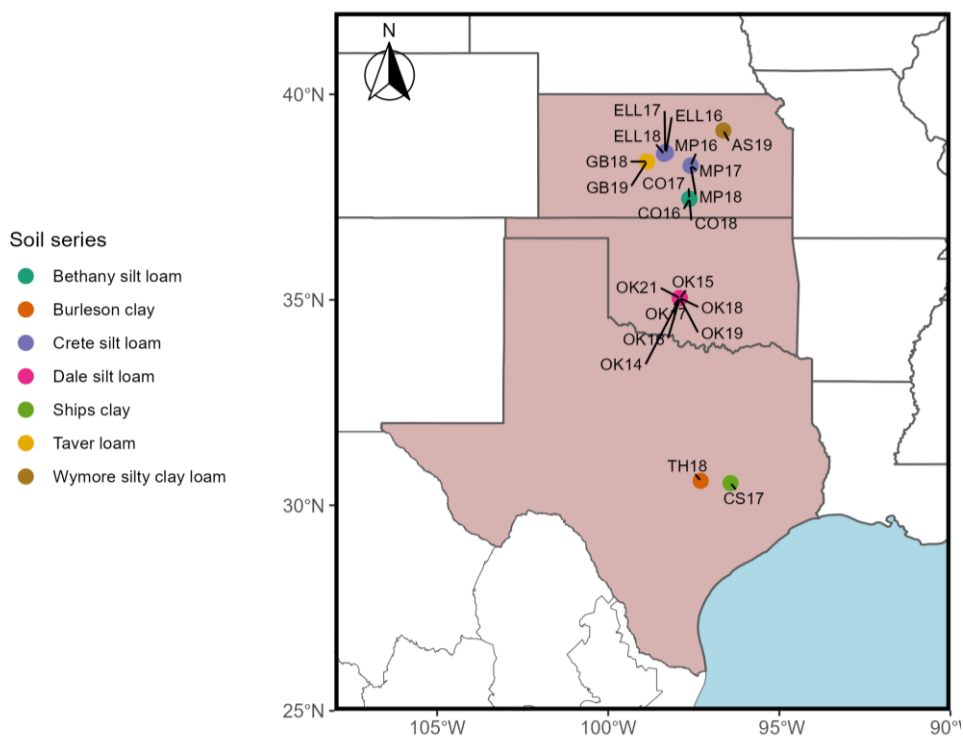


Figure 5.2. Spatial distribution of the factorial trials combining 20-55 winter wheat cultivars and two management intensities. Experiments were replicated in 21 location-seasons with some locations hosting trials during more than one season; location-season codes are explained in Appendix Table E.1. Color codes indicate soil series.

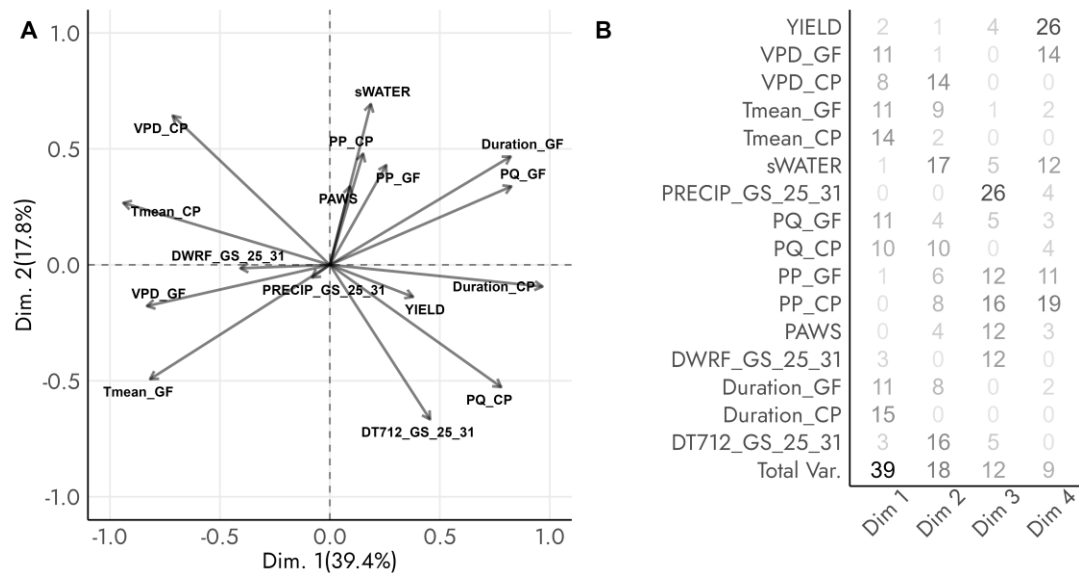


Figure 5.3. Principal component analysis for environmental variables: biplot (A) and variance contribution within dimension (B) in experiments carried out in the Great Plains between 2014 and 2021. Abbreviations: Mean temperature (Tmean), vapor pressure deficit (VPD), photothermal quotient (PQ), incident solar radiation (SR), plant available water at sowing (PAWS), total seasonal water supply including seasonal rainfall and PAWS (WATER), precipitation (PP), number of days with temperatures between 7 and 12 °C between GS 25 and GS 31 (DT712_GS_25_31), number of days with rainfall between GS 25 and GS 31 (DWRF_GS_25_31), accumulated rainfall between GS 25 and GS 31 (PRECIP_GS_25_31), critical period (CP) and grain filling period (GF). Prefix “s” indicates seasonal averages of environmental variables.

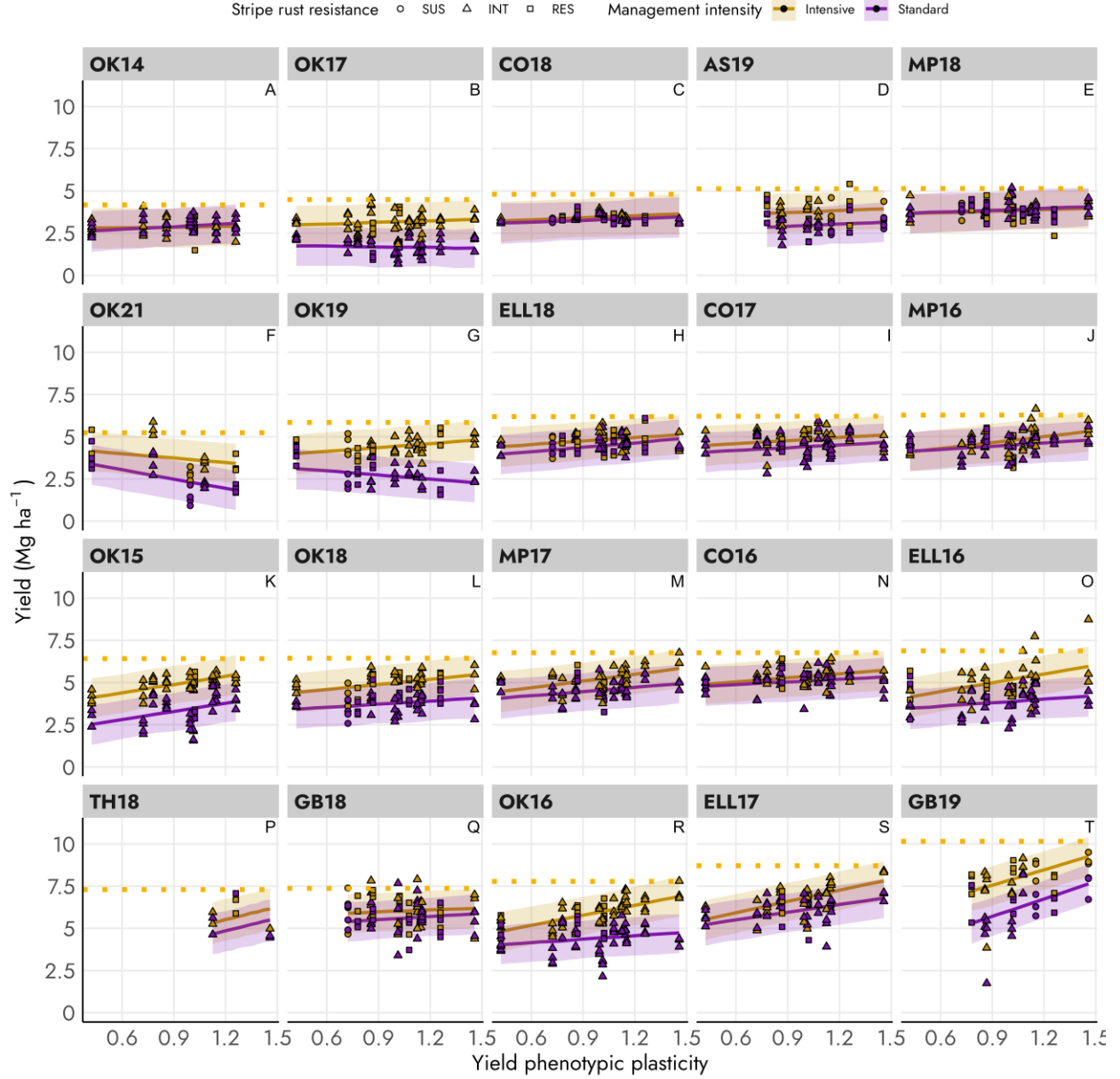


Figure 5.4. Relationship between grain yield and yield phenotypic plasticity (unitless) for winter wheat grown in 20 location-seasons in the Great Plains under intensive (yellow) and standard (purple) management intensity. Dashed line represents the water-limited yield potential Y_w (Eq. 4) in each location-year. Solid lines represent the mean and ribbons the 95% credible interval of the posterior predictive distribution of grain yield, presented in Equations 2 and 3. The slope of the relationship between yield-yield plasticity represents parameter β_{1jk} in Eq. 3.6. Panels are ordered from top left to bottom right according to Y_w .

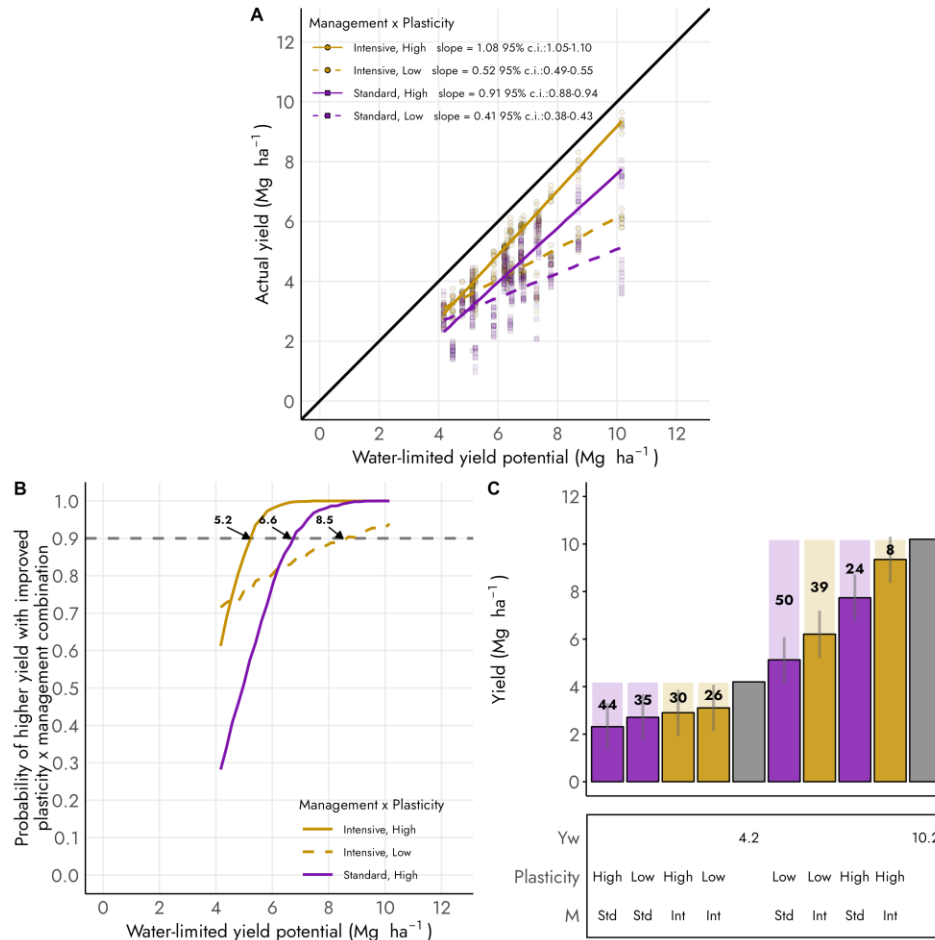


Figure 5.5. (A) Relationship between water-limited yield potential and actual yield for cultivars with high (solid lines; cultivar: `WB4303`; plasticity = 1.45) and low (dashed lines; cultivar: `Double Stop CL+`; plasticity = 0.42) yield phenotypic plasticity under intensive (yellow lines, circles) and standard (purple lines, squares) management. (B) Relationship between the probability of an improved plasticity x management combination yielding more than the baseline (low plasticity, standard management). In B, dashed line is the threshold of 0.9 probability of greater yield with improved plasticity x management combination, while arrows indicate the Y_w at the intersection with posterior probability = 0.9. (C) Comparison of water-limited yield potential (Y_w , grey bars expressed in $Mg\ ha^{-1}$) and actual yield for cultivars with contrasting yield plasticity (cultivars are `WB4303`, high plasticity and `Double Stop CL+`, low plasticity) and management. In A, lines represent the mean of the actual yield; points are a 10-draw sample of $\mu_{ijk|y}$; inset legend show the mean and the 95% credible interval of the slope of the relationship between Y_w and $\mu_{ijk|y}$; solid black line represents the 1:1 line. In B, Y_w is expressed in $Mg\ ha^{-1}$ and labels in shaded areas are the expected yield gap for a given $G \times E \times M$ management combination, whiskers are the 95% credible intervals around the mean. Abbreviations: water-limited yield potential (Y_w), management intensity (M), standard (Std) and intensive management (Int).

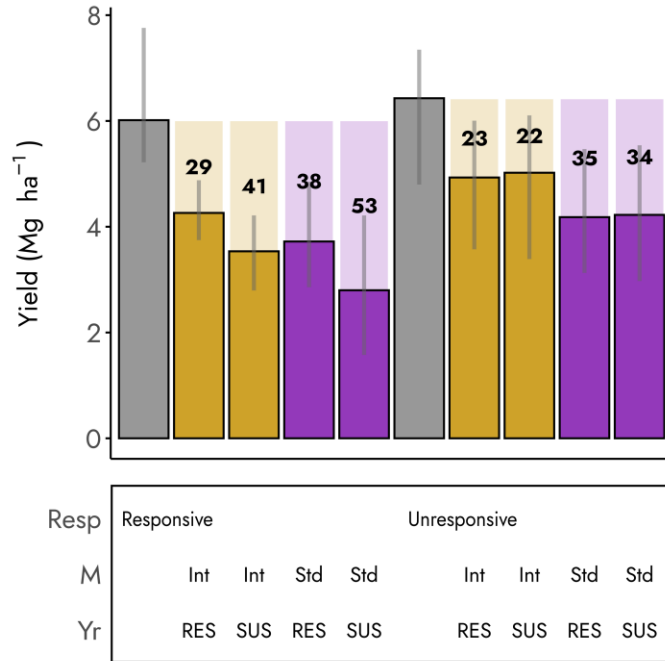


Figure 5.6. Contributions of management intensification and stripe rust resistance to yield gap under responsive (left) and unresponsive (right) environments to stripe rust resistance. Colored bars represent the mean and whiskers the standard deviations for each combination of environment, management and stripe rust resistance. Grey bars are the mean Y_w , while whiskers are the standard deviations of Y_w . The numbers on top of the bars shows the average yield gap, expressed in percentage units. Abbreviations: management (M), intensive (Int), standard (Std), stripe rust resistance (Yr), resistant phenotype (RES), susceptible phenotype (SUS).

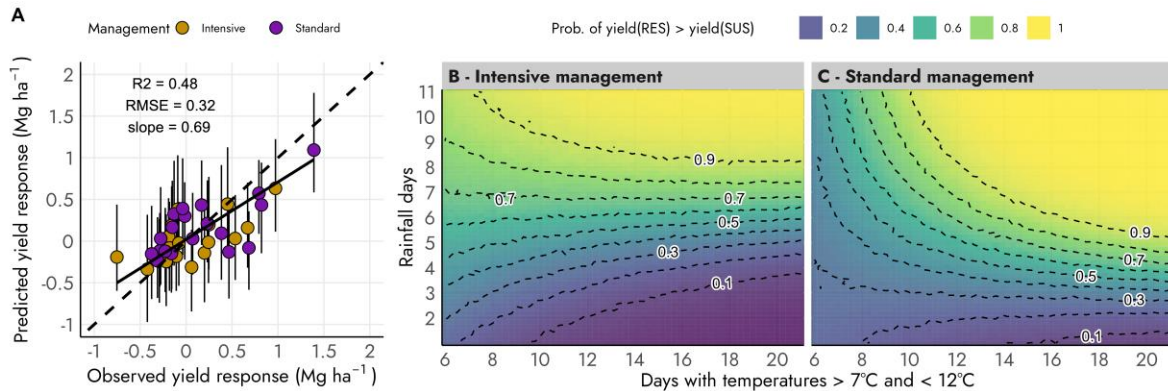


Figure 5.7. (A) Comparison of observed yield response to stripe rust resistance and response predicted with model. Model assumes that the yield response to stripe rust resistance (i.e., yield difference between resistant and susceptible cultivars) is associated with management and environmental factors described in Equation 8. Contour plots show the probability of greater yields with resistant (RES) vs susceptible (SUS) phenotypes under varying rainfall days and days with daily mean temperatures between 7°C and 12°C between GS 25 and GS 31 under intensive (B) and standard (C) management intensity. Dashed lines in B and C represent the iso-probability lines.

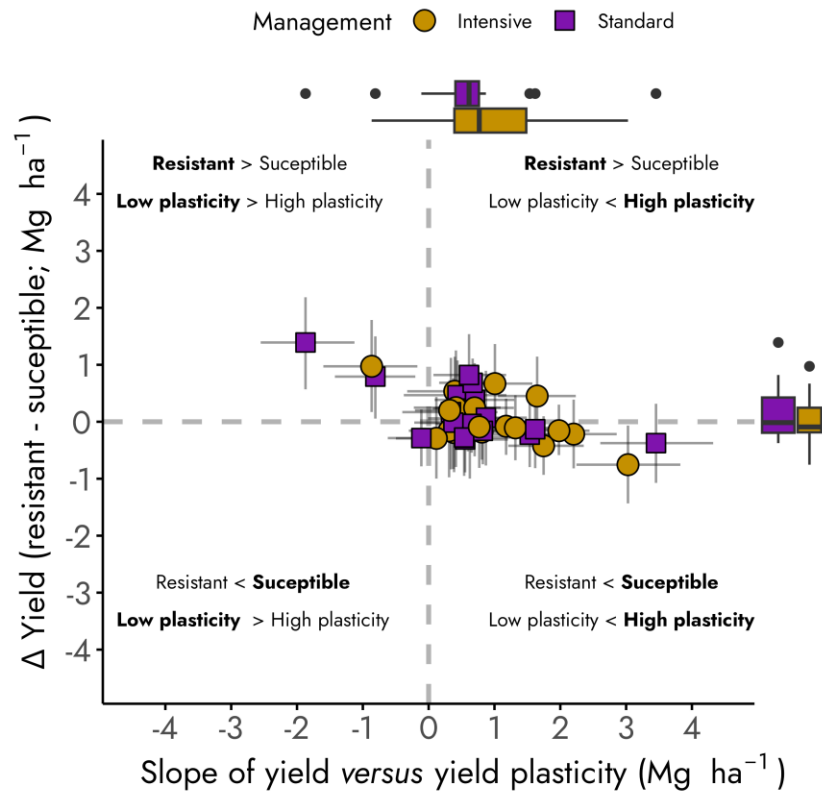


Figure 5.8. Relationship between the slope of yield versus yield plasticity and yield difference between resistant and susceptible phenotypes to stripe rust. Each point represents the expected value for an E x M combination and whiskers are the 95% credible interval. Management combinations were a grower standard practice (purple) and intensive management (brown) adding of N and fungicide. Bold labels in each quadrant indicates the combination of yield plasticity x stripe rust resistance that produced the highest yield in each E x M combination. Side boxplots show the distribution of the responses to plasticity (top), and to stripe rust resistance (right).

Chapter 6 - From value chain to network – implications for sustainability

Abstract

We propose a three-step process to advance food systems sustainability, using wheat as a case study. This process is informed by data collected during a two-day expert elicitation workshop involving 46 stakeholders from the wheat industry. First, we move toward an operational definition of sustainability grounded in the views of wheat value chain stakeholders. Second, we propose a framework for identifying both common and diverging priorities across sectors of the value chain. Third, we suggest collaboration strategies to develop an agreed upon sustainability stamp for loaves of bread, that embodies and is consistent with the conceptual definition of sustainability. We show that there is *a priori* consensus across the wheat industry as to how sustainability should be defined. The ranking of sustainability priorities, was not associated to the level of agreement of a given sustainability indicator across the wheat industry, revealing each sector has its own unique sustainability goals. Defining a sustainability stamp on a loaf of bread would require, i) spreading of economic incentives throughout industry sectors, ii) implementation of a sustainability framework across the industry, iii) defining the role of university and third-party audit institution on guiding framework implementation.

6.1 Introduction

Science and society do not simply interact but are co-constructed (Kampourakis, 2022). This is partially because science deals with things and phenomena that are often outside our daily experience, hence the alternatives: inventing new languages or using metaphors (Reynolds, 2022). Metaphors are widespread in science (*e.g.*, “black hole”), and reflect our culture and are

value-laden; the role of glial cells shifted from “housekeeping” and “nursemaid” supporting the executive functions of the neurons to “architects of memory”, reflecting the more highly esteemed occupations associated with traditionally male-dominated professions (Reynolds, 2022). In biological science, we are used to thinking of a hierarchy of scales (William, 1976); genes are at the lowest level and scale to cell, tissue, organism, individual, society, and so forth (Noble, 2012). The reductionist causal chain is then represented with upward-pointing arrows; “up” and “down” are unhelpful metaphors (Noble, 2012). Uni-directional cause-and-effect arrows in the “pipeline” from genotype to phenotype is inconsistent with the molecular evidence (Noble, 2012; Sadras and Hayman, 2025).

Value chain is a common metaphor to refer to a series of concatenated activities performed by multiple individual business units to transform inputs into outputs of greater economic value generating profit (*i.e.*, “value”) during the transformation process (Porter, 2008). In a context of sustainability, the conceptual definition of “value chain” does not fully account for interdependency among sectors on a “chain”, which are required to progress towards sustainability goals (Klerkx et al., 2010). It was shown that we are cognitively better at drawing cause-and-effect arrows, from A to B, than we are at thinking of loops from A to B, B to C, and C to A (Levy et al., 2018). For wine grape growers, the concept of sustainability conforms to a network with common abstract goals and regional specific strategies (Hoffman et al., 2014).

The evolving nature behind the definition of sustainability, is tied to dimensions of sustainability and driven by changing society demands throughout time. The number of dimensions evolve, as if it were an antibody-antigen model, where the expectation of society and industries (antibody) change over time forcing the evolution of sustainability definitions and dimensions (antigen, Figure antibodies Sadras). Schaller (1993) proposed an early definition to

agricultural sustainability centered in four dimensions being environmentally sound, productive, economically viable and socially desirable. For Schaller (1993) the evolving nature of the concept is apparent, '*people's beliefs and values will continue to mold public understanding of the concept*', which highlights the need of a sustainability definition grounded on contemporary, industry-specific demands.

The evolution of the definition of agricultural sustainability becomes elusive, for example, when dealing with solutions and unintended consequences from the use of fertilizer inputs in crop production (Zhang et al., 2015). As an example, over 800% increase in nitrogen use during the last century (Frink et al., 1999), associated with greater productivity and coping with global food demand during the second part of the 20th century (Dobermann and Cassman, 2005). However, in recent decades science and society became aware of negative externalities from greater use of nitrogen in major crop producing regions, which are associated with negative impacts on human health (*e.g.*, blue baby syndrome, Majumdar, 2003), tropospheric ozone pollution (Galloway et al., 2003), eutrophication of water (Conley et al., 2009), increased nitrous oxide emissions and consequently climate change (Reay et al., 2012).

Recent efforts focused on sustainability frameworks in systems-specific sectors, such as agricultural systems (Mouratiadou et al., 2021; Cano et al., 2023). However, the approach of advancing sustainability science by observing individual sectors of the food system overlooks an implicit challenge that limits practice adoption and decision-making towards sustainability goals (Grabs et al., 2024): the mismatch (*i.e.*, differences in quality or quantity between the supply and demand) of stakeholders' priorities on sustainability dimensions and indicators (Geijzendorffer et al., 2015).

Wheat is crucial to food security at global scales, as it provides 20% of the calories and 11% of proteins in the human diet (Shewry, 2009; Shewry and Hey, 2015). Here, we use the wheat industry as a case study to show that the linear flow of matter implicit in a “chain” from seed-to-bread (Figure 6.1A) overlooks the multiple flows of information in a “network” (Figure 6.1B). The “value chain” framework fails to identify interactions among stakeholders, which are relevant to advance wheat sustainability. During two days we interviewed a diverse group of experts representing different sectors of the wheat industry. We show that a network perspective – rather than a chain perspective – reveals common themes across stakeholders, from wheat breeders and farmers to millers, bakers and consumers, that could help to build a consensual, operational definition of sustainability. We hypothesize that common and abstract goals for sustainability exist across stakeholders. From an industry network perspective, we advance on a sustainability framework identifying both common and fragmented sustainability indicators. Here, we hypothesize that most important sustainability indicators would be common across sectors of the wheat industry, with less common indicators being sector-specific. Finally, we conclude suggesting network collaboration strategies to advance the industry towards a unified sustainably produced loaf of bread, that agrees with the conceptual definition of sustainability.

6.2 Methods

6.2.1 Study region

The U.S. Great Plains is one of the largest contiguous wheat producing region in the world (Fischer et al., 2014). During the last decade, an annual average of 13 million hectares were planted to wheat (USDA-NASS, 2024), totaling an average of 32 million tons, 62% of U.S. wheat production (USDA-NASS, 2024). During the last 10 years, 8% of wheat traded

internationally was sourced from the U.S. Great Plains and primarily imported into developing countries (Mottaleb et al., 2022).

6.2.2 Expert elicitation

A two-day expert elicitation workshop took place in Manhattan, Kansas, USA during March 26th and 27th, 2024. Prior to the workshop (20-22 February 2024), invitations were sent to 83 potential participants representing 56 independent institutions involved in the wheat industry (Appendix Table F.1). Forty-six wheat industry network experts agreed to participate in this workshop, representing major public and private institutions of six major, equally distributed, sectors: i) wheat breeding, ii) wheat agronomy, iii) input supply, iv) wheat growers, v) milling and baking industries, and vi) retail and consumers (Appendix Figure F.1). Experts were selected based on their domain knowledge, extensive experience on the wheat industry, and a proven track record in the specific area of interest. The diverse group of participants represented institutions with regional (e.g., farmers, local industry, and breeding programs), to national (i.e., Wheat Foods Council), and international footprint (e.g., Bayer Crop Science, Bimbo Bakers, ADM Milling, Grain Craft, John Deere, etc.; Appendix Table F.1)

Data was collected from the selected experts using guided discussions divided in modules targeted to: i) define sustainability, ii) identify and rank sustainability indicators, iii) identify technologies and practices with potential to advance sustainability in each sector, and iv) combine value chain efforts to advance in a unified sustainability stamp on a loaf of bread. The tools deployed across exercises were developed in close collaboration with professional facilitators of expert discussions and community vitality specialists. Participants were divided in groups of seven to nine experts representing the same sector for modules i—iii (deployed in day one) and different sectors for module iv (sections i-iv), deployed in day two (Appendix Figure

F.2). In each group, discussions were moderated by one trained facilitator. During the entire expert elicitation workshop, two scribes were assigned to each group for keeping detailed record of experts' discussions. See Appendix for further details on the surveying instruments used and timing of each of the tasks conducted.

6.2.3 Definition of sustainability

Upon participant's arrival to the workshop we drew an unbiased baseline on the definition of sustainability by asking each participant for a written, open-ended answer to "what does sustainability mean to you?". We collected 39 useful (*i.e.*, with at least one concept within the sentence) definitions. The unbiased baseline was compared against a biased answer of the same question that participants provided at the end of the workshop after two days of discussion among peers. We collected 34 useful definitions.

6.2.4 Listing and ranking of sustainability indicators

An expert talk at the beginning of the elicitation provided the conceptual framework for sustainability assessment. The presentation centered on five sustainability dimensions, which served as a framework for the upcoming tasks. Dimensions were: economic, production, environmental, social and human, as detailed in Smith et al., (2017). Participants were given a handout with definitions of the five sustainability dimensions (see Appendix F).

The second task was divided into five steps, one for each sustainability dimension. Participants were given 90 minutes to go through structured discussions and provide a list of sustainability indicators within each of the five dimensions. Across tables and dimensions, participants originated 154 sustainability indicators which then subjected to a paired comparisons matrix ranking based on participants opinions (Green and Haines, 2015, see Appendix F for details).

Participants were presented with five paired comparisons matrices, one for each sustainability dimension. Briefly, each matrix comprises a series of binary choices between pairs of sustainability indicators, where participants must select the preferred indicator in each comparison (Appendix Figure F.3). The results are recorded in a matrix, where each element represents a comparison between two indicators. For instance, if the participant prefers indicator “profitability” over indicator “risk management”, the matrix entry corresponding to that pair is marked with a 1 for “profitability” and a 0 for “risk management”, and vice-versa. After completing all comparisons, the rankings of the sustainability indicators can be derived by counting the number of votes in each row for each indicator. The indicator with the highest score is ranked the highest, with subsequent rankings based on the number of votes each indicator accumulates.

6.2.5 Relevance and adoption of technologies to improve sustainability indicators

Next, we deployed a quadrant analysis (Bens, 2017) to identify technologies with potential to improve sustainability indicators and assess their current level of adoption within each sector of the wheat industry. The goal of this exercise was to identify technologies of high relevance and low adoption, which can provide means to progress on sustainability indicators and their associated metrics. Participants were presented to a two-dimensional chart, with “level of adoption” on the horizontal axis and “relevance to sustainability indicator” on the vertical axis. The chart was divided in a four-quadrant grid: high adoption-more relevant, high adoption-less relevant, low adoption-less relevant, low adoption-more relevant. Using color-coded sticky notes, with colors referring to sustainability dimensions, participants filled out the chart with possible technologies impacting the top three ranked sustainability indicators during the paired comparisons exercise (Appendix Figure F.4).

6.2.6 Industry network innovation strategies with “now-how-wow” structure

During the second day of the workshop, participants were re-arranged in six groups of seven or eight members. Groups were constituted by participants with different expertise backgrounds representing different sectors of the wheat industry. Participants had the chance to join efforts across the value chain to identify innovation strategies with the goal of advancing on a unified sustainability stamp on a loaf of bread. We utilized the “now-how-wow” structure to achieve this goal (Ericson and Törlind, 2013). The exercise lasted two hours, which were subdivided in three stages. The first 30 minutes were intended for participants to brainstorm about the “wow” scenario, or ideal scenario they will encounter under implementation of a unified sustainability stamp on a loaf of bread. During the next 30 minutes, participants brainstormed about the current situation on the industry network or “now” scenario. Finally, participants spent one hour discussing strategies to collaborate throughout the industry aiming to establish clear steps needed to bridge the two previously established scenarios (*i.e.*, the “now” and the “wow”), on a “how” exercise (Appendix Figure F.5). At the end of each stage the table facilitator, pointed a group leader who summarized the group discussion in an easel pad. At the end of the exercise, one participant per table summarized the findings to the entire group of experts.

6.2.7 Data analysis

Definitions of sustainability were compiled on a spreadsheet, and two independent coders extracted concepts from the definitions (Appendix Table F.2). The coding process was revised twice to unify vocabulary. From 59 unique concepts, 23 concepts were the same among coders and retained for further analysis, reflecting a 39% agreement between independent coders (Appendix Table F.2). A matrix of concepts was generated, where each definition had one to five

associated concepts. The matrix was introduced within a network analysis conformed by nodes and ties. Node weights were relative to the number of times each concept appeared relative to the total number of concepts. For example, out of 79 total concepts, “economic viability” appeared 8 times, thus that concept received a node weight of 8. Tie weights were relative to the number of times two concepts appeared together in the same definition. For instance, the concept “environmental responsibility” and “economic viability” appeared together in the same definition 4 times, and assigned a tie weight of 4. Using the network of sustainability definitions, we tested for power law behavior by exploring the exponential slope parameter of relation between the number of concepts *versus* tie weights. To quantify the degree of consensus on the definition of sustainability across stakeholders, we compared the slope parameters between networks of unbiased (definitions written before workshop) and biased definitions (written after two days of discussions) of sustainability.

Sustainability indicators were filtered to the top five indicators in each sector $\times$ domain combination. Experts provided 127 sustainability indicators; however, the terminology was inconsistent. To standardize the vocabulary, we identified common indicators and consolidated them into a unified framework. To achieve this, a designated leader met with table facilitators to ensure consistency in classification and terminology. Additionally, we refined the classification based on scribe notes capturing discussions around sustainability indicators. For example, terms such as “profit stability”, “profitability”, and “return on investment” were grouped under the category "Profitability".

Ranking scores of sustainability indicators were scaled to a range 0-1 using a min-max normalization, and expressed as ‘Importance’ in percentage (%) units.

$$y' = \frac{y - \min(y)}{\max(y) - \min(y)} * 100. \quad \text{Eq. 1}$$

In Eq. 1, y' is the scaled vector of importance of sustainability indicators, while y is the vector of rankings from the paired comparisons matrix.

Sustainability indicators were classified into dimensions and their commonality across sectors. These sustainability dimensions (economic, production, environmental, social, and human) were defined prior to the workshop (Smith et al., 2017). When an indicator was assigned to multiple dimensions, the final classification was determined based on the most frequently assigned dimension across sectors. Additionally, indicators were grouped based on their commonality into five categories: sector-specific, agreement across two, three, or four sectors, and agreement across sectors—with the latter assumed when an indicator was raised as important in at least five of the six sectors.

We modeled the association of ranking of indicators and their commonality across sectors as follows:

$$\begin{aligned} \frac{y'_{ij}}{100} &\sim \text{Beta}(\mu_j, \phi_j), \\ \mu_j &= \text{logit}^{-1}(\beta_0 + \beta_{1j}z_{ij}). \end{aligned} \quad \text{Eq. 2}$$

In Eq. 2 y'_{ij} is the importance of sustainability indicators, and follows a Beta distribution, which has support between zero and one. The expected value, μ_j , and dispersion, ϕ_j , are both a function of z_{ij} , a vector containing the classification of sustainability indicators according to their commonality across industry sectors (j^{th} : sector-specific, two sectors, three sectors, four sectors, across sectors). Parameters β_0 and β_{1j} are the linear predictors of μ_j .

Technologies were categorized based on their relevance to sustainability and level of adoption (see Appendix F for details). Using `Web Plot Digitizer`

(<https://apps.automeris.io/wpd>), we extracted the x- and y-coordinates corresponding to adoption and relevance, assigning each technology accordingly. To standardize terminology, we identified common technologies and grouped them into unified categories. The data from the Now-How-Wow exercise was summarized by extracting key discussion points from the easel pads and reviewing scribe notes.

6.3 Results

6.3.1 A priori consensus across stakeholders on sustainability definitions

Stakeholders shared a priori consensus on the definition of sustainability. The most common concepts were: “environmental responsibility”, “continue into future”, “productivity” and “economic viability” (Figure 6.2A). Highly connected concepts were common across the industry network (Figure 6.2A). The network of concepts behind definitions of sustainability conformed to a power-law, where few concepts were highly connected (Figure 6.2B). A priori consensus on concepts behind sustainability was highlighted by the lack of difference in the exponential slope of the power-law relationship between number of concepts and tie weight ($p=0.15$, Figure 6.2B). Definitions of sustainability did not vary between answers written prior to discussions compared to answers written after two days of workshop (Figure 6.2, Appendix Figure F.6, Appendix Figure F.7).

6.3.2 Relevant sustainability indicators are not necessarily common across sectors

Out of 27 sustainability indicators included in the framework, only six were common across the industry: “technology adoption”, “consumer education & preferences”, “productivity”, “capacity building”, “water”, and “profitability” (Figure 6.3). The importance of common sustainability indicators varied greatly with sectors (Figure 6.3).

When looking across sectors of the industry network, the highest ranked sustainability indicators in at least more than one sector were “grain quality”, “food security”, “quality of foodstuff produced” and “profitability” (Figure 6.3, Figure 6.4). The ranking of sustainability indicators was not associated with the number of sectors in which the indicator was highlighted as relevant (Figure 6.4).

6.3.3 Network collaboration to advance in a sustainability stamp on a loaf of bread

Stakeholders identified major challenges across the industry network that currently prevent advancing on a sustainability stamp on a loaf of bread (Figure 6.5A): (i) the lack of a sustainability definition and consensus metrics, (ii) the lack of incentives for input source traceability, (iii) the fact that sustainability is considered as a marketing strategy and, (iv) the international demand for sustainable wheat grain is minimal as major US wheat importer countries are not willing to pay premiums for sustainably-produced wheat.

Major priorities for sustainability are improving “grain quality” and “quality of foodstuff produced” (Figure 6.3, Figure 6.4). The lack of grain segregation in elevators and mills determines that ‘all wheat goes in the same batch’ which means that there are no economic incentives for growers to produce high-quality wheat, leading sometimes to situations where high-quality wheat is destined to animal feed. Moreover, wheat breeders highlighted that there are no incentives to develop wheat cultivars with high nutrition profile. The lack of consumer education on understanding the labels in wheat-based products is highlighted as the primary cause for the absence of economic incentives. Multiple labels with different meanings contrasts with the use of a standardized nutritional label, confusing the consumer and potentially misleading customer preference towards sustainably produced bread.

Stakeholders agreed on potential features on a sustainable bread label (Figure 6.5B). First, label has two levels (*e.g.*, gold and silver) allowing to explore demand curves for customer willingness-to-pay differential amounts for sustainable bread. Second, the label requires traceability and identity protection of individuals involved in producing and processing wheat. Third, packaging of sustainable product aligns with ‘circular economy’ principles (*e.g.*, recyclable packaging, limiting the use of plastic). Finally, stakeholders suggested that the product behind the label be whole grain bread, meeting the human domain of sustainability. Wheat industry stakeholders agreed upon three aspects that interact towards advancing on a sustainability stamp on a loaf of bread (Figure 6.5B): (i) the need for economic incentives throughout the value chain to compensate for sustainability efforts, (ii) implementing a sustainability assessment framework with clearly established sustainability priorities and metrics and, (iii) defining the role of universities on the science for continued development and updating of the sustainability framework. Finally, stakeholders agreed on the need of a third-party auditor to ensure rigorous compliance to the framework.

Investment of incentives in label marketing and advertisement would help customers to better understand the label and consequently lead to greater preference for sustainably produced bread. One of the crucial aspects to advance on the implementation of the framework we propose is to incorporate infrastructure and operational changes needed for grain segregation at elevators and mills. This aspect, combined with sustained demand for sustainable bread, would allow to distribute premiums for high-quality sustainable wheat grain across players, and consequently drive breeding incentives to develop high nutritious profile wheat cultivars and demand for sustainable farm input sources.

A third-party stakeholder should lead on audits of the process of sustainable wheat production and processing, based on standards provided on sustainability framework. The framework in Figure 6.3 results from the co-interaction of university researchers and industry stakeholders in its development. Continued research efforts by involved universities would allow the framework to stay up to date with changing society expectations.

6.4 Discussion

6.4.1 Implications of a priori consensus on the definition of sustainability

The emergence of strong and connected nodes of sustainability concepts suggests that the network is scale-free. Non-linear systems are characterized by strong interaction among its components and its interpretation cannot be addressed from reductionist approaches (Wimsatt, 2007). Thus, addressing sustainability challenges from an industry network perspective aligns with stakeholders perception of sustainability and theory (Wimsatt, 2007). Strong and connected nodes such as: “economic viability”, “environmental responsibility”, and “productivity” can be a starting point to build an operational definition of sustainability across value chain. Wheat industry stakeholders showed that common sustainability goals are abstract and remain the same across varying contexts. A group of wine grape growers in California agreed on common sustainability goals across regions (Hoffman et al., 2014). Here, we show that regardless of the sector in the wheat industry, sustainability goals are alike.

Aligned to our initial hypothesis, sectors of the wheat industry have different strategies (i.e., common sustainability indicators across all sectors were only three) to reach common and abstract sustainability goals. Thus, it is crucial to identify causes of misalignments in sector-specific strategies to achieve sustainability goals. The sustainability indicator ‘grain quality’, a critical aim of agronomic and breeding research (Giordano et al., 2023, 2024), is at the center of

the discussion among wheat industry sectors. For the breeding sector, minimum grain quality standards exist to ensure market access to varieties developed. For millers, grain quality relates to reducing waste and energy used in the milling process, and providing uniform quality product for bakers. However, for the midstream grower sector, grain quality is not relevant as they are not compensated economically for managing for it. Local markets may develop (e.g., workshop participant Farm Strategy created a marketing platform connecting growers with high quality grain and storage capacity with buyers willing to compensate monetarily for such grain; workshop participants Amber Wave and PureField Ingredients market wheat protein and/or vital wheat gluten and compensate growers based on minimum standards), but the reality is that most of the crop is still marketed as a commodity. Further development of sustainability frameworks should focus on identifying strategies that align with common goals across industry sectors.

6.4.2 Cooperation across sectors to advance on wheat industry sustainability

Consumers and producers are spread in space and time (Sundkvist et al., 2005), which results in asymmetric information flow (*i.e.*, price transmission) among them (Vavra and Goodwin, 2005). In recent decades, asymmetric price transmission worsened, a consequence of globalization of the wheat market, emergence of new export markets, and more homogeneous wheat consumption patterns (Vavra and Goodwin, 2005). Therefore, producers cannot adapt to changing society expectations over sustainably produced bread. Strategies to advance towards sustainability proposed by industry stakeholders aimed to facilitate information flows among sectors in the form of price signals. A positive feedback loop is apparent, where investment of economic incentives on clear marketing and advertising can help build consumer trust on sustainability stamp, increasing product demand, leading to greater economic benefits from sustainable stamp products.

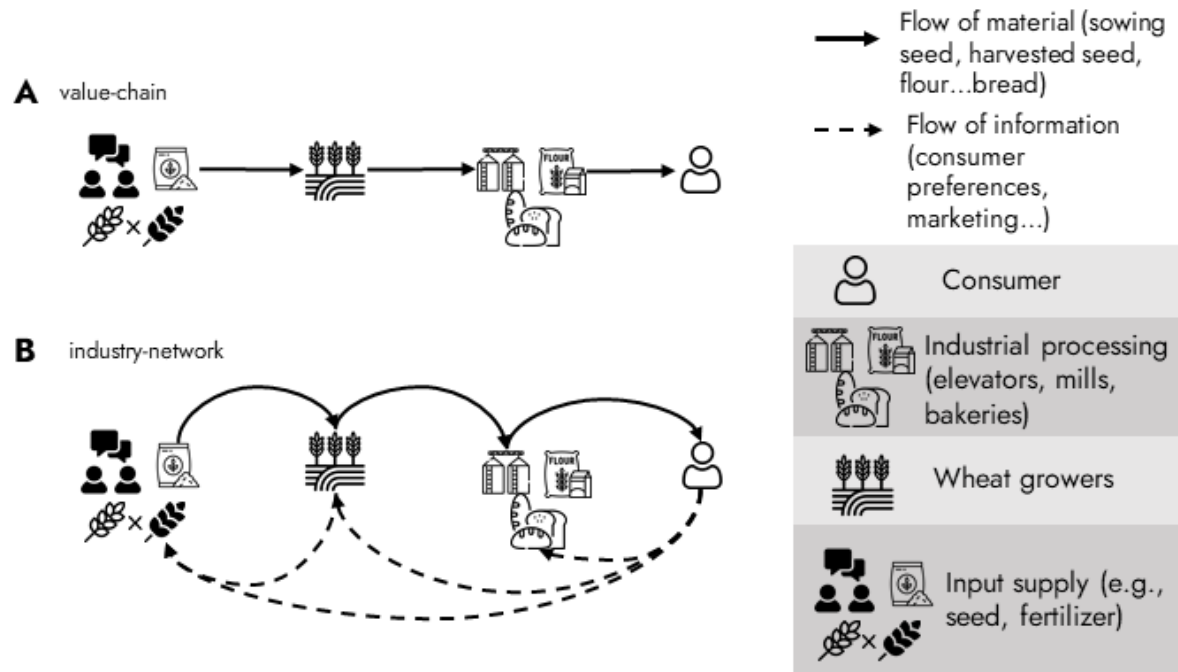
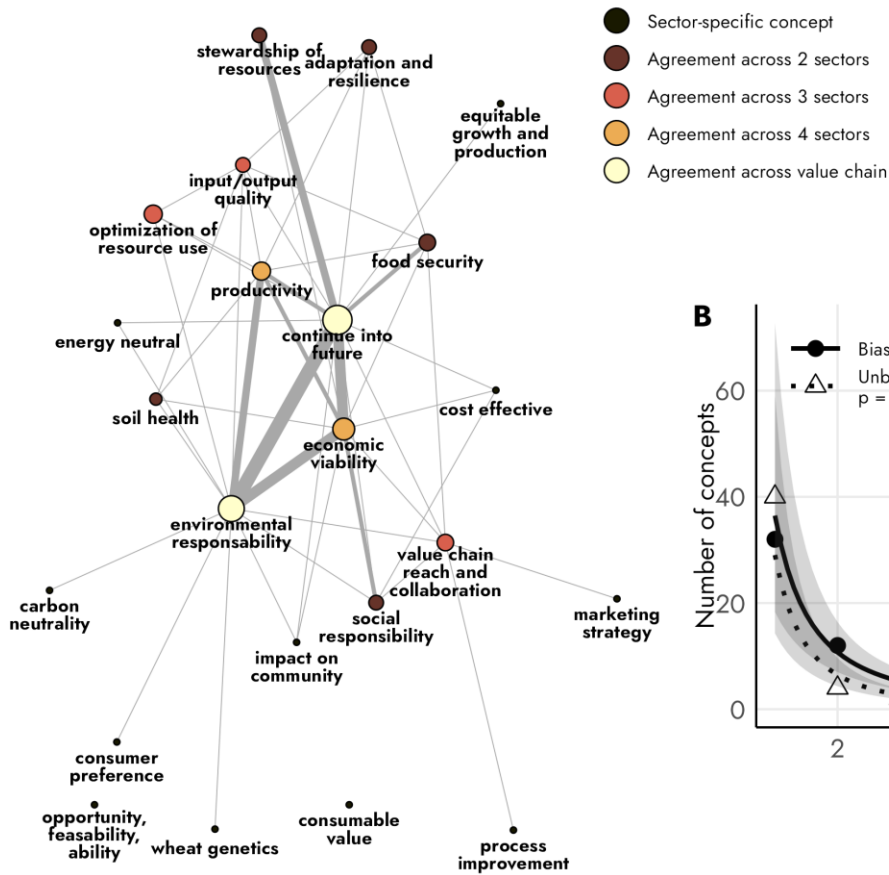


Figure 6.1. Hypothetical relations across sectors on the wheat industry. Top panel A is business as usual, where limited information flow across sectors exists. Bottom panel B is the scenario under enhanced collaboration towards common sustainability goals across sectors.

A



B

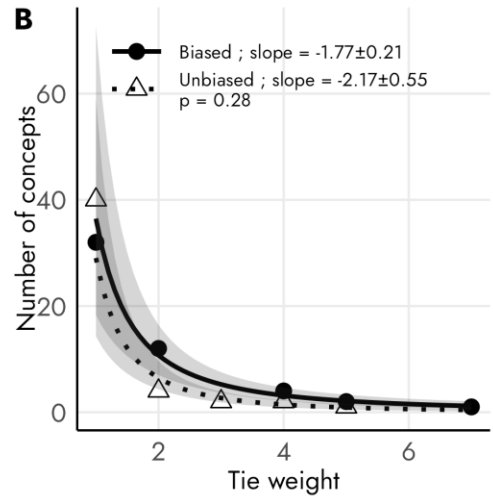


Figure 6.2. A) Network reflecting common and unique elements in the definitions of sustainability across stakeholders in the wheat network industry. Node sizes are relative to the number of times a concept appeared while tie weights are relative to the number of times two concepts appeared together in a definition. Colors indicate the number of sector where the same concept appeared, a sector was counted if at least one participant included the concept within the definition. Agreement across sectors (yellow) was assumed when the concept was included in at least five or six industry sectors. Sectors are: i) wheat breeding, ii) wheat agronomy, iii) input supply, iv) wheat growers, v) milling and baking industries and vi) retail and consumers. B) Association between tie weights and number of concepts conforms to a power law. Open symbols represent the association resulting from analysis of the unbiased answers, written by participants before they interact in table discussions, upon arrival at expert elicitation. Closed symbols represent the association resulting from biased answers written at the end of the two-day expert elicitation. P-value represents the significance of the comparison of the exponential slope of biased and unbiased sustainability definitions.

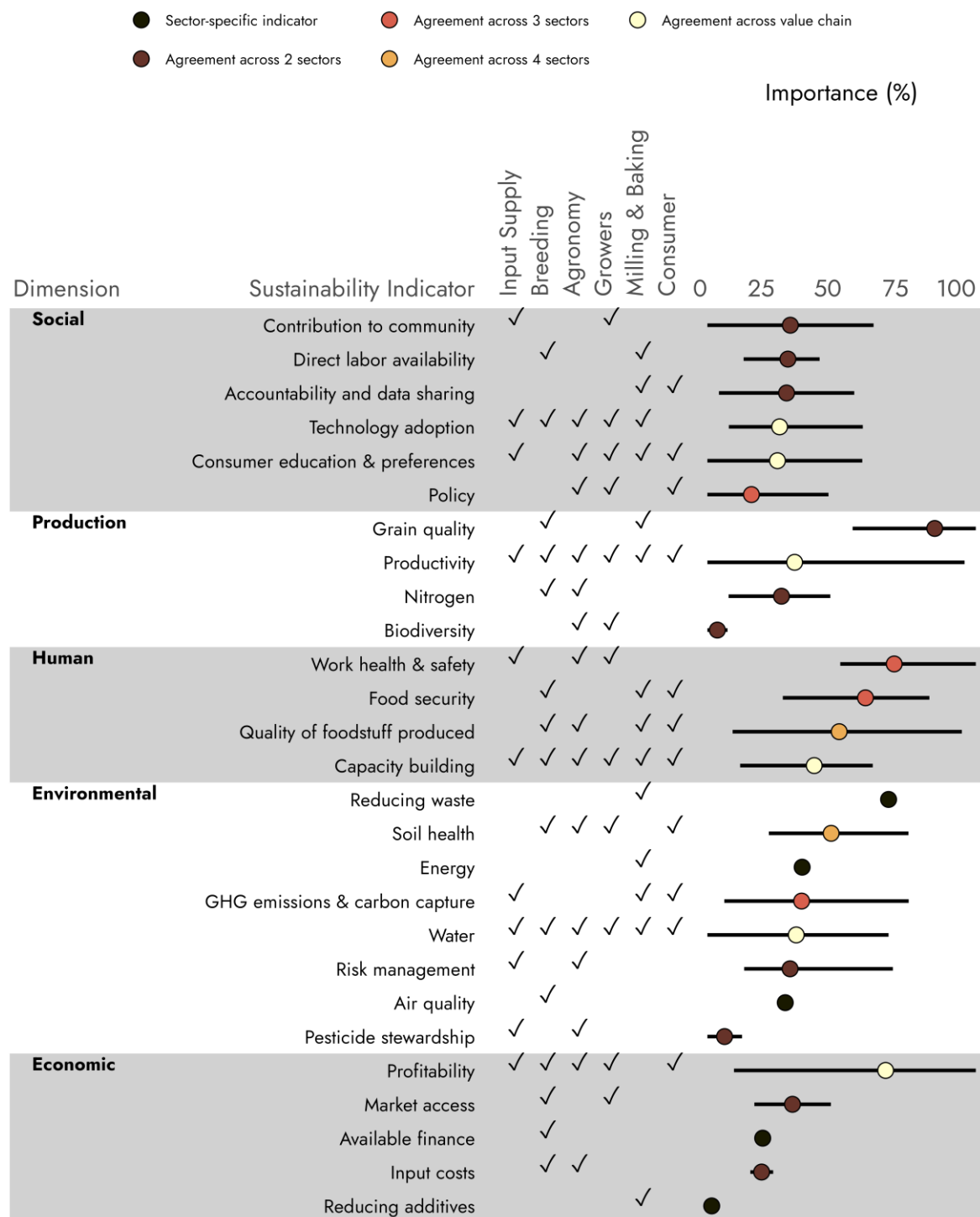


Figure 6.3. Sustainability assessment framework resulting from surveying a group of 46 wheat industry network experts. Sustainability indicators were filtered to the top five from the raking exercise on paired comparisons in each sector x dimension combination. Checkmark indicates that a specific sector within the network selected the indicator as relevant. Points represent percent votes of that given indicator compared to others indicators within each sector x dimension combination.

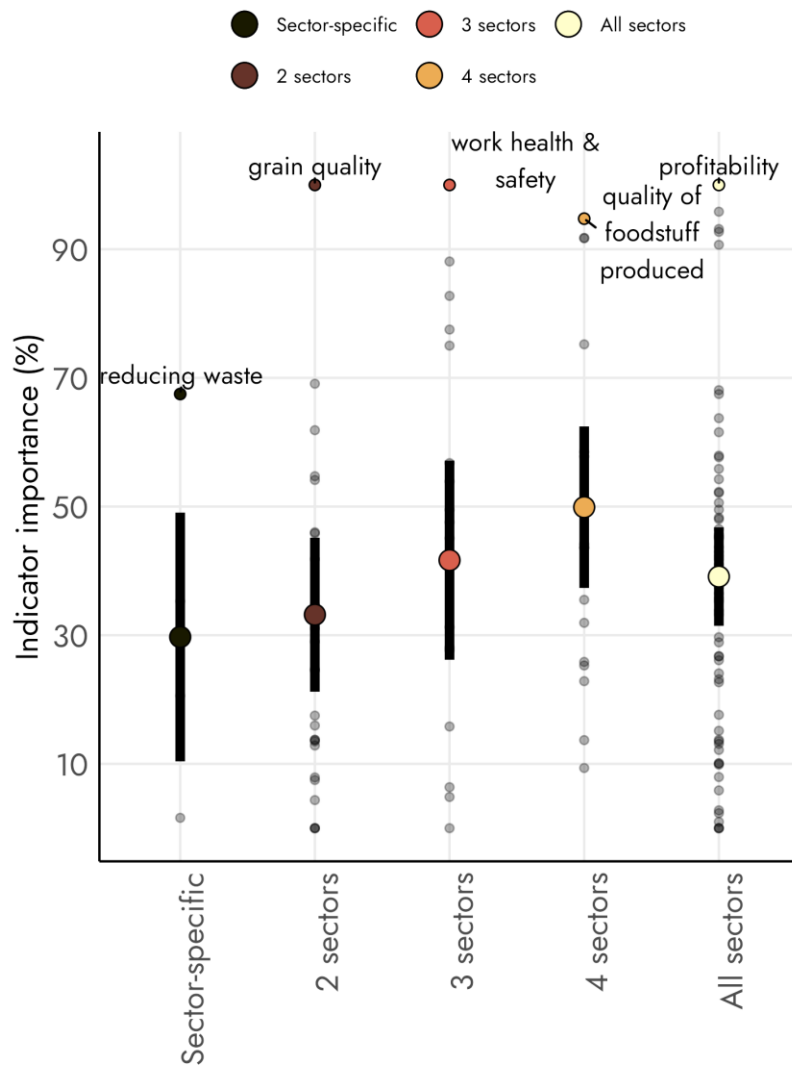


Figure 6.4. Distribution of rankings of sustainability indicators for sector agreement clusters. Colors indicate the number of sector where an indicator appeared. When an indicator was raised by five or six sectors it was classified as “all sectors”. Sectors are: i) wheat breeding, ii) wheat agronomy, iii) input supply, iv) wheat growers, v) milling and baking industries and vi) retail and consumers.

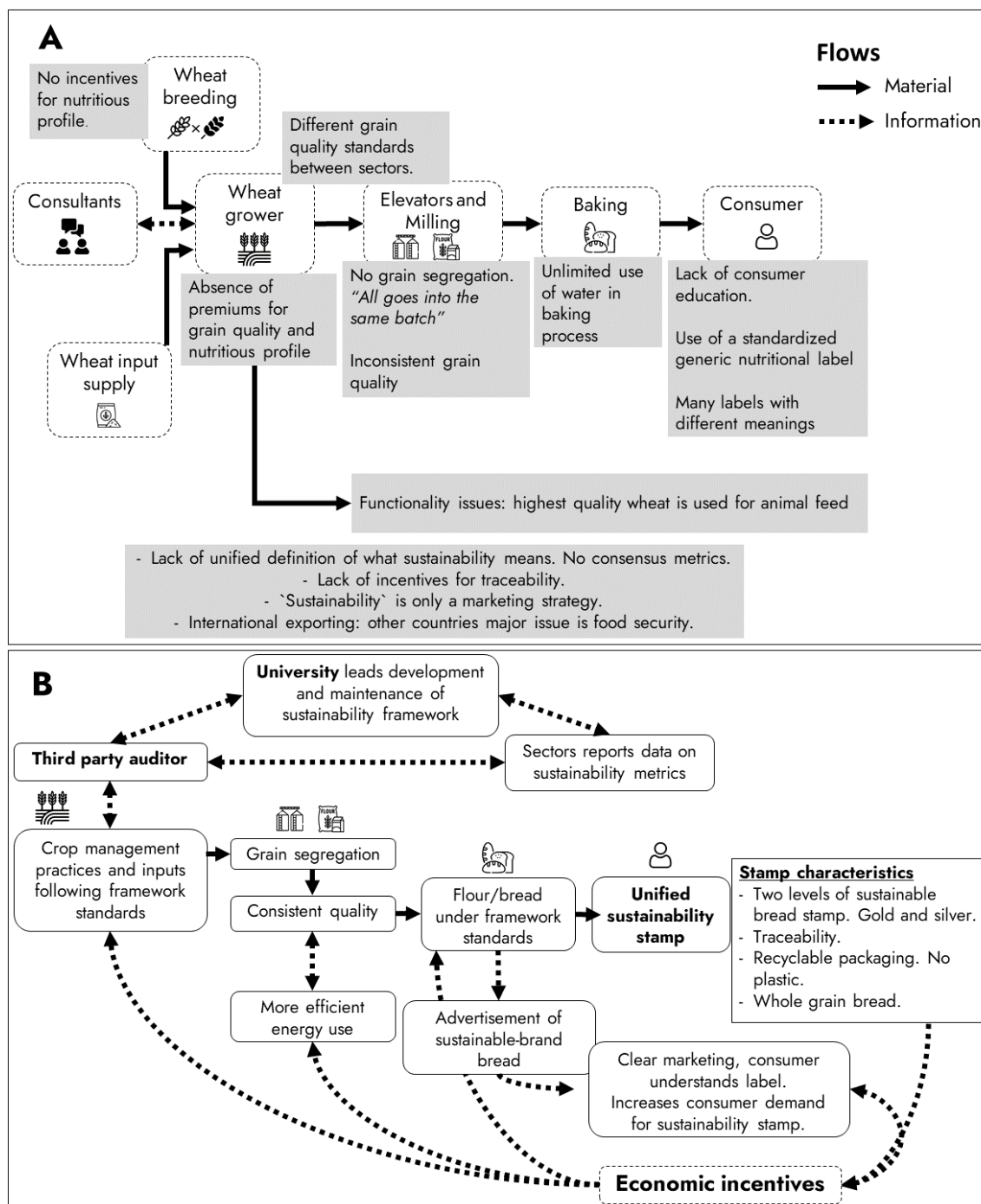


Figure 6.5. A) Current challenges in the wheat industry network limiting development of sustainable brand bread. B) Network of associations among wheat industry stakeholders under implementation of strategies for bread with sustainability stamp.

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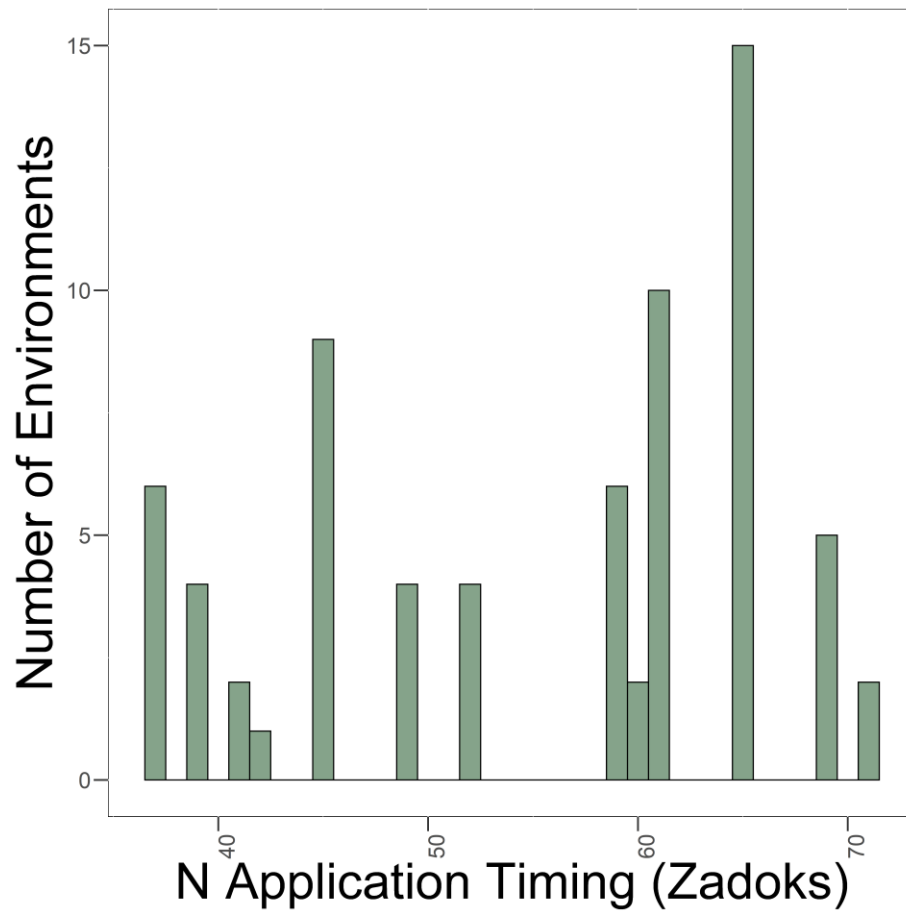
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Appendix A - Chapter 1 Supplementary Material



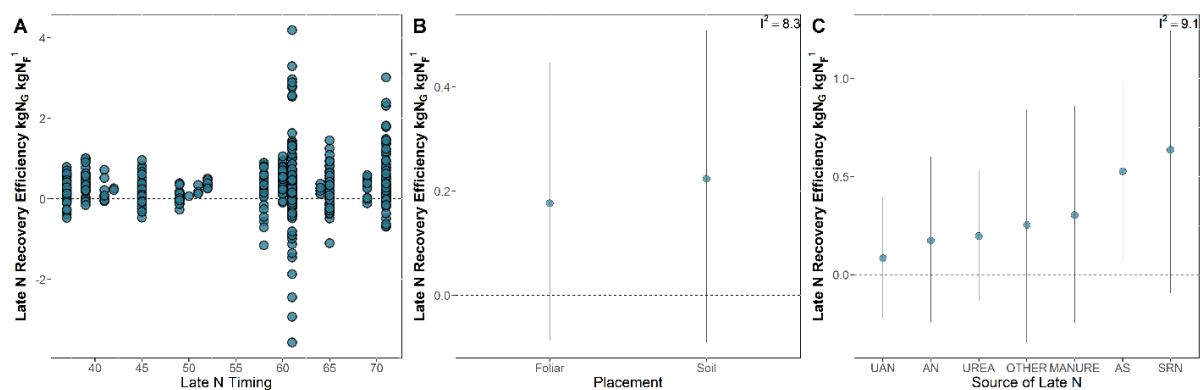
Appendix Figure A.1. Timing of application distribution for the subset of studies used for evaluating the effects of environmental attributes on GPC response to late-season N.

Appendix Table A.1. Mean values for each of the clusters generated using K-means algorithm, for the two evaluated periods: critical period (CP) and grain filling period (GF). Abbreviations: precipitation (PP), photothermal quotient (PQ), mean temperature (TMEAN).

PERIOD	Variable	unit	Cluster Mean		Cluster relative difference (%)	Omnibus test of means comparisons
			Low	High	(High Low ⁻¹) x100	Bootstrapped p-value
CP	Duration	days	30.9	51.3	66	0.056
CP	PP	mm	72.6	285.8	293.7	0.182
CP	PQ	MJ °C ⁻¹	1.6	2.2	37.5	0.142
CP	Tmean	°C	18	24.5	36.1	0.134
GF	Duration	days	27.8	37.4	34.5	0.325
GF	PP	mm	57.5	143.9	150.3	0.271
GF	PQ	MJ °C ⁻¹	1	1.3	30	0.139
GF	Tmean	°C	24.7	30	21.5	0.293

Appendix Table A.2. Association between GPC response ratio and grain yield and protein environments. Pearson's *r* represents the mean and bootstrapped 95% confidence interval. The *p*-values represents the 97.5% quantile of the distribution of bootstrapped *p*-values. Grain yield and grain protein concentration environment were defined by the average value of basal N treatment in each environment.

		Grain Yield Environment	Grain Protein Environment
ln (GPC Response Ratio)	Pearson's <i>r</i>	0.19 (0.09; 0.28)	-0.43 (-0.50; -0.37)
	<i>p</i> -value	0.016	<0.001



Appendix Figure A.2. Impact of late nitrogen management practices on late N recovery efficiency: (A) Late N recovery efficiency was unrelated to late N timing. Effect of different late N fertiliser placement (B) and sources (C) on the Late N recovery efficiency. I^2 = I-squared statistic. In panels B and C: points represent the mean effect and whiskers correspond to the bootstrapped CI; grey whiskers indicate non-significant effects corresponding to the 97.5% quantile of the bootstrapped *p*-values. Key: AN (ammonium nitrate), AS, (ammonium sulphate), SRN (slow-release nitrogen), UAN (urea ammonium nitrate), UREA (granulated urea).

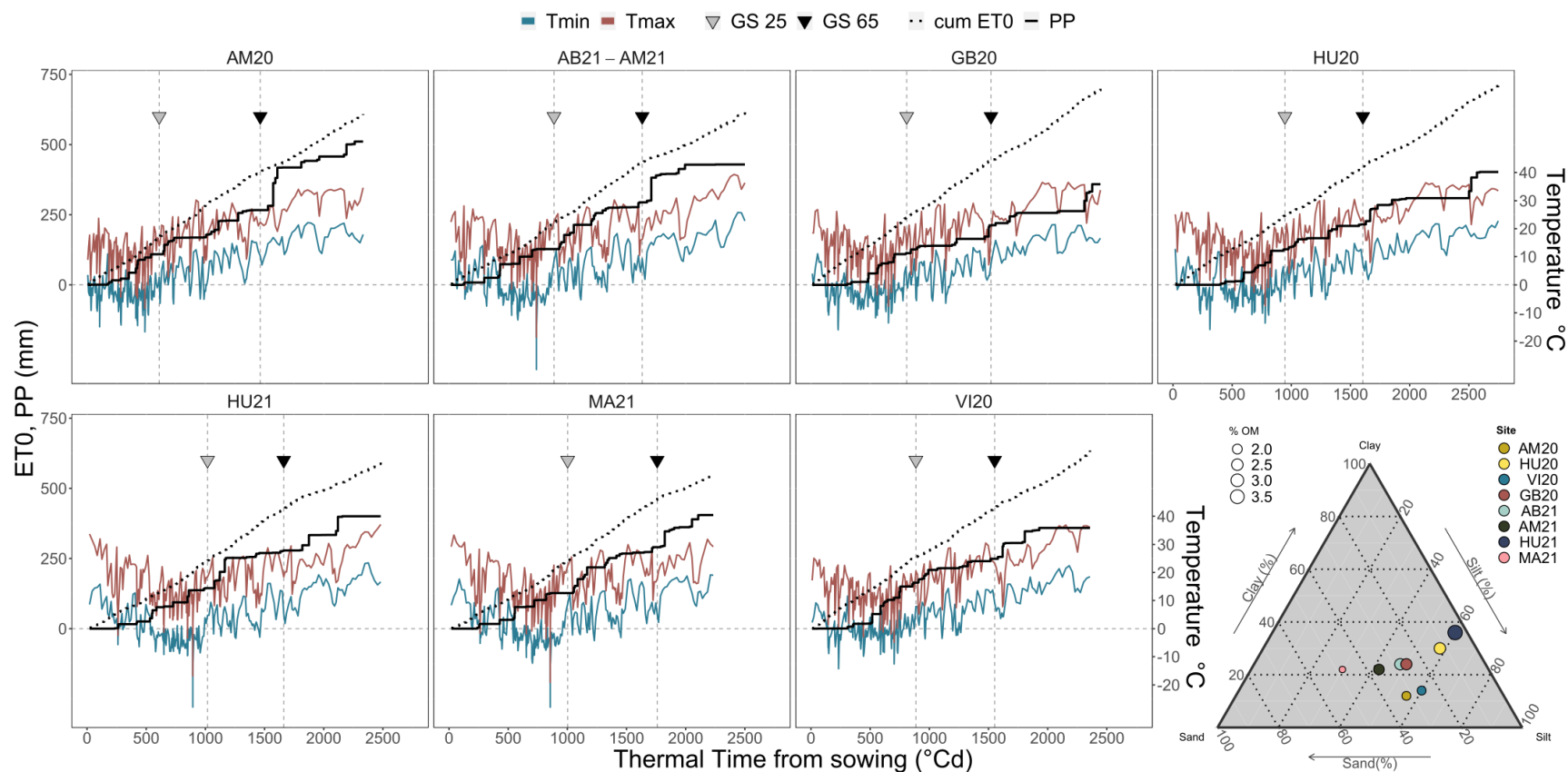
Appendix B - Chapter 2 Supplementary Material

Appendix Table B.1. Texture and soil chemical properties at each 0-15 and 15-60 cm soil depth. * P extractable with Mehlich III method.

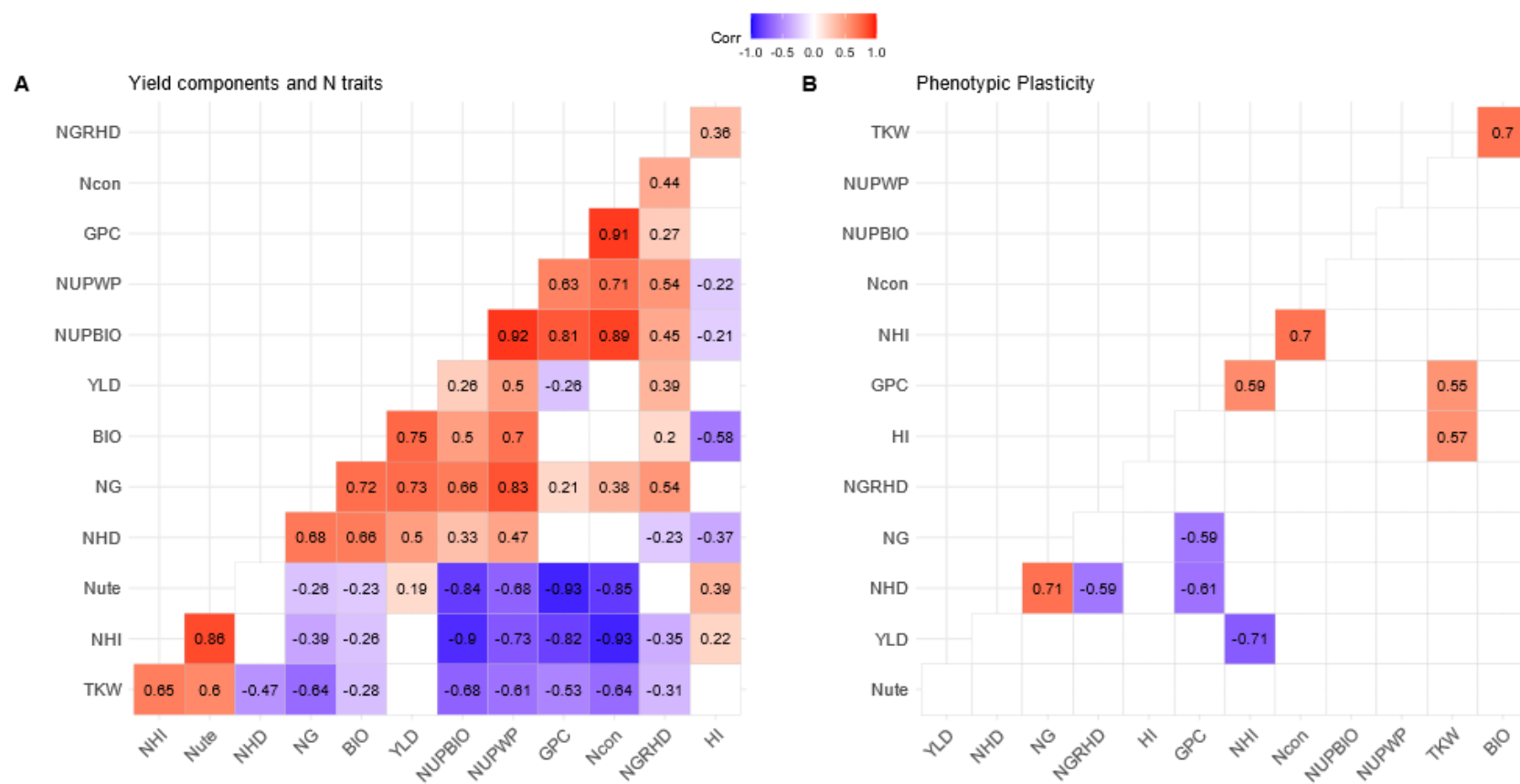
Location	depth	san d	silt	clay	OM	pH	CEC	Ca	Cu	Mg	Mn	Na	P*	K	Zn	Fe	S	Cl
	cm	%					$\frac{meq}{100g}$	ppm										
Ashland	0_15	32	56	12	1.8	5.9	11.35	1119.8	0.5	122.9	8.7	10.9	59.3	216.6	0.6	47.4	0.9	3.1
Ashland	15_60	38	50	12	1.1	7.2	8.91	1495.9	0.4	117.4	4.6	9.4	38.2	159.5	0.4	27.5	0.8	2.2
Hutchinson	0_15	28	48	24	2.42	5.48	23	2222.3	1.5	185.7	36	15	68.7	334.5	0.8	81.7	23	6.7
Hutchinson	15_60	26	48	26	2.3	6.71	19	3315.1	1.6	201.5	22.9	17.4	50.6	273.6	0.7	69.4	19	5.3
Viola	0_15	48	30	22	1.6	5.1	19.92	890.5	0.8	265.7	28.3	16.4	62	157.1	0.4	70.1	2	4.6
Viola	15_60	NA	NA	NA	1.6	5.4	18.99	1151.9	0.8	337	21.7	30	48.2	139.9	0.4	65	2	6.7
Great Bend	0_15	26	50	24	2.4	5.5	21.96	1517.3	2.5	391.4	22.6	50.3	208	622	3.2	132.1	6.2	7
Great Bend	15_60	20	50	30	2.3	6.4	22.52	2075.5	1.9	535.7	20.1	111.7	147	558.3	2.1	124.6	6.2	7.3

Appendix Table B.2. Grain yield and protein concentration for each environment. Anthesis date, precipitation, mean temperature, duration and photothermal quotient across 14 wheat cultivars for the critical period (CP) and grain filling period (GF). Values are means $\pm$ standard error.

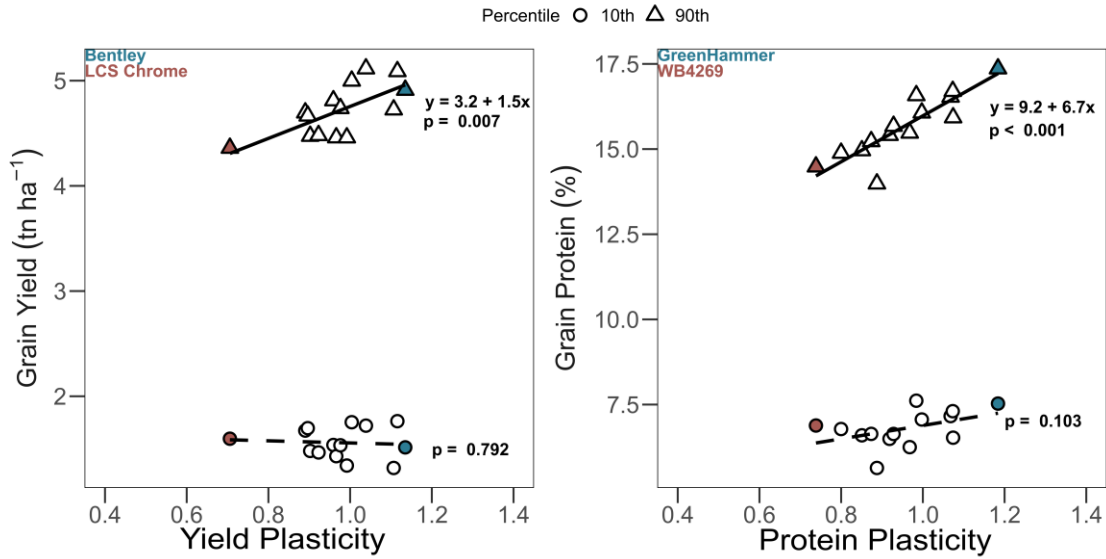
Env	Yield	Grain protein concentration	Anthesis date	Precipitation (mm)		Mean Temperature ($^{\circ}\text{C}$)		Duration (days)		Photothermal quotient ($^{\circ}\text{C MJ}^{-1}$)
	Mg ha^{-1}	%	DOY	CP	GF	CP	GF	CP	GF	CP
AB20	2.65 $\pm$ 0.7	12.70 $\pm$ 1.5	143 $\pm$ 3.6	185 $\pm$ 27.4	114 $\pm$ 31.1	15.6 $\pm$ 0.7	24.3 $\pm$ 0.5	34 $\pm$ 2.1	25 $\pm$ 0.7	1.7 $\pm$ 0.10
AB21	4.04 $\pm$ 0.8	8.07 $\pm$ 1.1	135 $\pm$ 3.6	145 $\pm$ 16.2	37 $\pm$ 3.7	14.2 $\pm$ 1.4	22.2 $\pm$ 0.6	38 $\pm$ 4.2	28 $\pm$ 1.0	1.8 $\pm$ 0.20
AM21	3.75 $\pm$ 0.9	8.34 $\pm$ 1.0	133 $\pm$ 3.6	147 $\pm$ 21.9	46 $\pm$ 23.5	13.5 $\pm$ 0.8	21.9 $\pm$ 0.6	40 $\pm$ 2.4	29 $\pm$ 0.7	1.9 $\pm$ 0.13
GB20	2.55 $\pm$ 0.4	14.88 $\pm$ 1.5	138 $\pm$ 3.6	94 $\pm$ 12.4	61 $\pm$ 18.8	14.1 $\pm$ 1.1	23.2 $\pm$ 0.8	38 $\pm$ 2.4	27 $\pm$ 1.4	2.0 $\pm$ 0.14
HU20	4.17 $\pm$ 0.4	14.38 $\pm$ 1.3	130 $\pm$ 3.6	117 $\pm$ 3.7	25 $\pm$ 3.8	13.4 $\pm$ 0.3	22.3 $\pm$ 0.6	40 $\pm$ 1.0	28 $\pm$ 0.7	2.0 $\pm$ 0.03
HU21	3.40 $\pm$ 0.7	7.48 $\pm$ 1.2	128 $\pm$ 3.6	50 $\pm$ 24.1	98 $\pm$ 24.3	12.5 $\pm$ 0.3	21.2 $\pm$ 0.6	43 $\pm$ 1.2	30 $\pm$ 1.7	2.1 $\pm$ 0.09
MA21	2.35 $\pm$ 0.8	10.05 $\pm$ 1.3	136 $\pm$ 3.6	108 $\pm$ 10.8	48 $\pm$ 5.2	14.5 $\pm$ 1.8	19.2 $\pm$ 0.3	37 $\pm$ 4.5	16 $\pm$ 2.9	1.8 $\pm$ 0.25
VI20	2.38 $\pm$ 0.7	10.10 $\pm$ 1.7	130 $\pm$ 3.6	86 $\pm$ 12.8	57 $\pm$ 12.8	13.8 $\pm$ 0.3	22.6 $\pm$ 0.8	38 $\pm$ 0.6	28 $\pm$ 1.5	1.9 $\pm$ 0.04



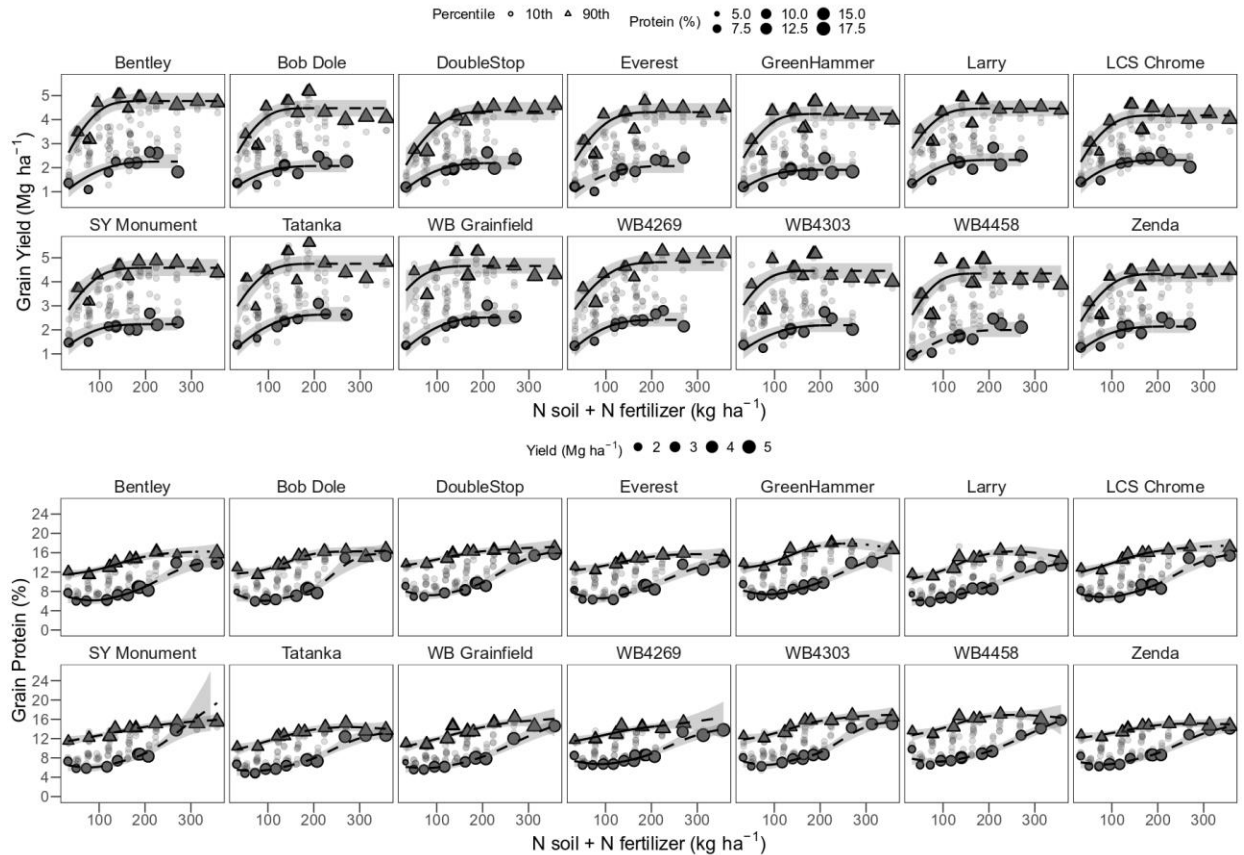
Appendix Figure B.1. Cumulative reference evapotranspiration (ET0; black dotted line), rainfall (PP; solid black line), and minimum (Tmin; blue) and maximum (Tmax; red) temperature for winter wheat in seven location-seasons in Kansas. In 2021, the trial near Ashland Bottoms was conducted in two nearby fields with contrasting soil texture; thus, only one weather pattern is shown for both fields. Grey arrowheads show the timing of N fertilization (GS 25) and black arrowheads show timing of fungicide application (GS 65). Top soil (0-15 cm) texture triangle and organic matter content in eight soils-seasons is also shown. Abbreviations: Ashland Bottoms 2A2 field (AB), Ashland Bottoms M3 field (AM), Great Bend (GB), Hutchinson (HU), Manhattan (MA), Viola (VI), season 2019-2020 (20), season 2020-2021 (21), top soil 0-15 cm organic matter percentage (%OM).



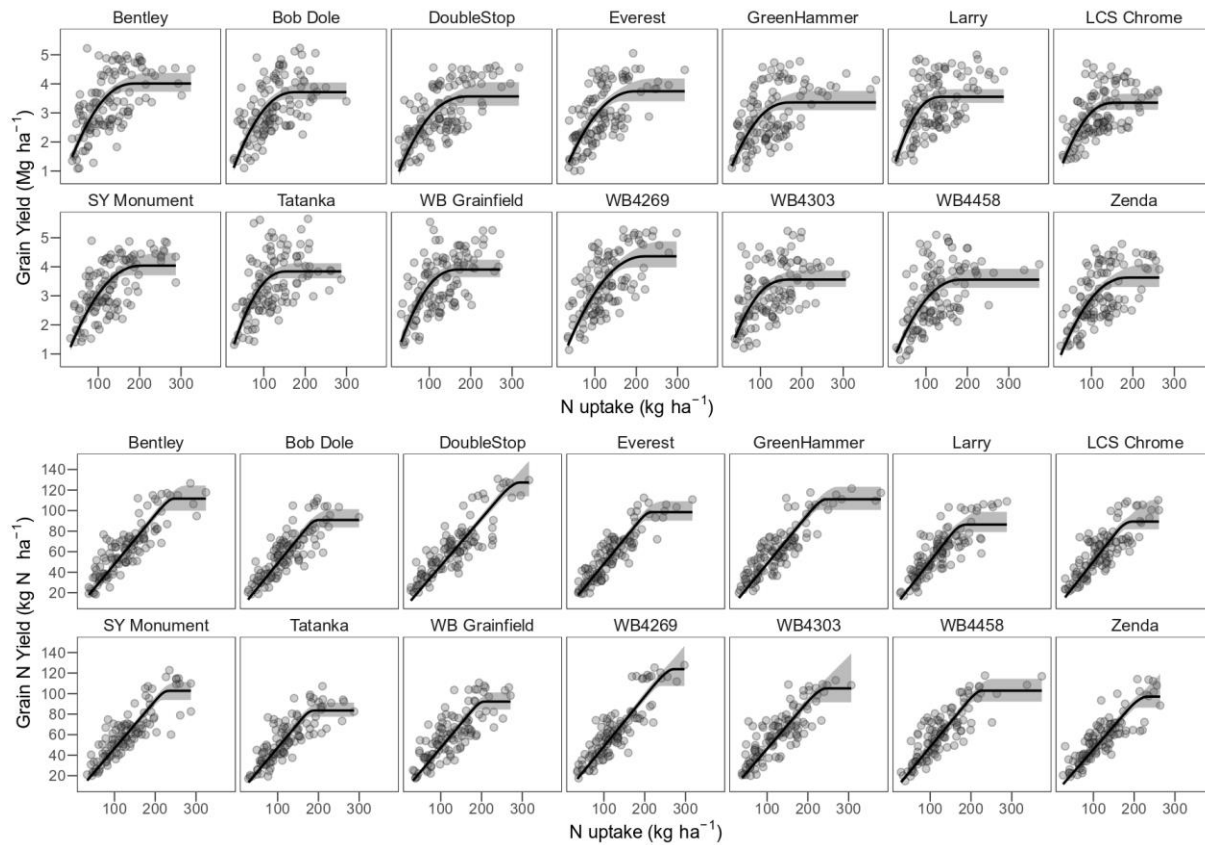
Appendix Figure B.2. Correlation matrix showing the associations among yield components, crop nitrogen traits and their respective phenotypic plasticity (PP). Red colors indicate positive association while blue colors negative association among variables. White slots are non-significant correlations ($p > 0.05$). Traits are grain yield (YLD), grain protein concentration (GPC), stover biomass at maturity (BIO), harvest index (HI), aboveground nitrogen uptake at maturity (NUPWP), stover N uptake at maturity (NUPBIO), stover N concentration at maturity (Ncon), nitrogen harvest index (NHI) and nitrogen utilization efficiency (Nute).



Appendix Figure B.3. Association of grain yield phenotypic plasticity and yield high (90th percentile) and low (10th percentile) yield and protein environments. P-value represent the significance of the slope estimated by adjusting an ordinary least squares loss function. Colors highlight the least (red) and the most plastic (blue) cultivars for yield and protein.



Appendix Figure B.4. Wheat grain yield (top) and protein (bottom) response to N supply under conditions conducive to high (90th percentile, triangles) and low (10th percentile, circles) trait expression for all 14 cultivars included in the study. Linetype indicates the phases conceptualized in Figure 2.2: solid (phase I), dashed (phase II), dotted (phase III). Lines represent the posterior medians and ribbons the 95% estimation credible interval for model predictions. The size of the symbol shows protein concentration in the yield panels (top) and yield in the protein panels (bottom).



Appendix Figure B.5. Wheat grain yield (top) and N yield (bottom) response to N uptake across environments for all 14 cultivars included in the study. Solid lines represent the posterior medians and ribbons the 95% estimation credible interval for model predictions.

Appendix Table B.3. Models metrics comparison between a model in which parameters of grain yield and protein concentration response to nitrogen supply are estimated across cultivars (Pooled) against a model that includes cultivar x nitrogen interaction, for which parameters were estimated for each of the cultivars.

Trait	Quantile	Model	WAIC	R2	RMSE
Yield	90th	Cultivars	163.0	0.85	0.64
Yield	10th	Cultivars	198.4	0.88	0.76
Yield	90th	Pooled	203.8	0.65	1.09
Yield	10th	Pooled	173.3	0.89	0.80
Protein	90th	Cultivars	91.5	0.62	0.42
Protein	10th	Cultivars	144.6	0.31	0.65
Protein	90th	Pooled	100.9	0.50	0.50
Protein	10th	Pooled	45.4	0.56	0.34

Appendix Table B.4. Priors used in bayesian linear models to describe associations of plasticity of grain yield and protein and crop traits. Abbreviations: uniform distribution (U), normal distribution (N), Cauchy distribution (C), half student t distribution (HST), agronomic optimum nitrogen (AON), nitrogen use efficiency (NUE), critical N uptake (NC), harvest index (HI), nitrogen harvest index (NHI).

Fig.	Response Variable	Predictor Variable	Intercept (β_0) prior	Slope (β_1) prior	σ_i^2 prior
5A	Yield	Yield Plasticity	$\beta_0 \sim U(0, 10.21)$	$\beta_1 \sim N(0, 50)$	$\sigma_i^2 \sim HST(3, 0, 2.5)$
5B	Grain Protein	Protein Plasticity	$\beta_0 \sim U(0, 17.8)$		
5C	Protein Plasticity	Yield Plasticity	$\beta_0 \sim N(0, 10)$		
7A	Yield at phase I		$\beta_0 \sim U(0, 10.21)$		
7E	Yield at phase II				
7C	Protein at phase I				
7G	Protein at phase II				
7I	Protein at phase III				
7B	Yield at phase I	Protein Plasticity			
7F	Yield at phase II				
7D	Protein at phase I				
7H	Protein at phase II				
7J	Protein at phase III				
9A	Yield at NC	Yield Plasticity	$\beta_0 \sim HST(3, 3.7, 2.5)$	$\beta_1 \sim C(0, 1)$	
9C	NC		$\beta_0 \sim HST(3, 174, 23.9)$		
9F	NUtE		$\sigma_i^2 \sim HST(3, 0, 2.5)$		
9H	N Yield		$\beta_0 \sim HST(3, 82.1, 11.6)$		
9B	Yield at NC	Protein Plasticity	$\beta_0 \sim HST(3, 3.7, 2.5)$		

9D	NC		$\beta_0 \sim HST(3, 174, 23.9)$		
9G	NUtE		$\beta_0 \sim HST(3, 0, 2.5)$		
9I	N Yield		$\beta_0 \sim HST(3, 82.1, 11.6)$		
10A	Grain Protein	Yield Plasticity	$\beta_0 \sim U(0, 17.8)$	$\beta_1 \sim N(0, 10)$	$\sigma_i^2 \sim HST(3, 0, 2.5)$
10C	HI		$\beta_0 \sim U(0, 1)$		
10F	Shoot biomass		$\beta_0 \sim U(0, 3000)$	$\beta_1 \sim N(0, 100)$	$\sigma_i^2 \sim HST(3, 0, 45.8)$
10H	Grains m ⁻²		$\beta_0 \sim U(0, 44594)$	$\beta_1 \sim N(0, 10^5)$	$\sigma_i^2 \sim HST(3, 0, 1032)$
10J	1000 kernel weight		$\beta_0 \sim U(0, 40)$	$\beta_1 \sim N(0, 10)$	$\sigma_i^2 \sim HST(3, 0, 2.5)$
10L	Heads m ⁻²		$\beta_0 \sim U(0, 1848)$	$\beta_1 \sim N(0, 10^4)$	$\sigma_i^2 \sim HST(3, 0, 39.2)$
10N	Grains head ⁻¹		$\beta_0 \sim U(0, 49)$		
10B	Grain Yield	Protein Plasticity	$\beta_0 \sim U(0, 10.21)$	$\beta_1 \sim N(0, 10)$	$\sigma_i^2 \sim HST(3, 0, 2.5)$
10D	HI		$\beta_0 \sim U(0, 1)$		
10G	Shoot biomass		$\beta_0 \sim U(0, 3000)$	$\beta_1 \sim N(0, 100)$	$\sigma_i^2 \sim HST(3, 0, 45.8)$
10I	Grains m ⁻²		$\beta_0 \sim U(0, 44594)$	$\beta_1 \sim N(0, 10^5)$	$\sigma_i^2 \sim HST(3, 0, 1032)$
10K	1000 kernel weight		$\beta_0 \sim U(0, 40)$	$\beta_1 \sim N(0, 10)$	$\sigma_i^2 \sim HST(3, 0, 2.5)$
10M	Heads m ⁻²		$\beta_0 \sim U(0, 1848)$	$\beta_1 \sim N(0, 10^4)$	$\sigma_i^2 \sim HST(3, 0, 39.2)$
10O	Grains head ⁻¹		$\beta_0 \sim U(0, 49)$		$\sigma_i^2 \sim HST(3, 0, 2.6)$
11C	Slope (HI NHI ⁻¹)	Yield Plasticity	$\beta_0 \sim N(0, 10)$	$\beta_1 \sim N(0, 10)$	$\sigma_i^2 \sim HST(3, 0, 2.5)$
11D	Slope (HI NHI ⁻¹)	Protein Plasticity			

Appendix C - Chapter 3 Supplementary Material

Flat priors for the Canada dataset

Non-informative priors were used to fit out model to the Canadian Prairies dataset. We defined priors hyper parameters to allow a reasonable range of values for our five parameters of interest.

$$\beta_{1j} \sim U(0.001, 0.20), \quad (1)$$

$$AOPD_j \sim U(10, 400), \quad (2)$$

$$\alpha_{1j} \sim U(0, 0.05), \quad (3)$$

$$\max VPD_j \sim TN(10, 250), \quad (4)$$

$$\min RPD_j \sim TN(10, 00). \quad (5)$$

Model Fitting

Our model was fit to data with program R using two Manhattan-Hastings algorithms nested within a Gibbs sampler. The fitting process can be summarized as follows:

1. Select a suitably high number of iterations of our Gibbs sampler, K .
2. Pick initial values for β_{1j} , $AOPD_j$, α_{1j} , $\max VPD_j$, $\min RPD_j$.
3. Generate proposals β_{1j}^{prop} and $AOPD_j^{prop}$ with two normal proposal distributions centered at $\beta_{1j}^{(k-1)}$ and $AOPD_j^{(k-1)}$, respectively.
4. Evaluate the Metropolis-Hastings ratio:

$$MH_{\mu} = \frac{[\beta_{1j}^{prop}, AOPD_j^{prop} | \cdot]}{[\beta_{1j}^{(k-1)}, AOPD_j^{(k-1)} | \cdot]}.$$

5. With probability $\min(MH_\mu, 1)$, accept β_{1j}^{prop} , $AOPD_j^{prop}$ as the k^{th} samples of the posteriors of β_{1j} and $AOPD_j$. Otherwise, set the k^{th} sample of each posterior to be equal to the $k - 1^{th}$ sample.

$$\beta_{1j}^{(k)}, AOPD_j^{(k)} = \begin{cases} \beta_{1j}^{prop}, AOPD_j^{prop} & MH > u \\ \beta_{1j}^{(k-1)}, AOPD_j^{(k-1)} & otherwise. \end{cases}$$

Where $u \sim U(0,1)$.

6. Generate proposals α_{1j}^{prop} , $maxVPD_j^{prop}$, and $minRPD_j^{prop}$, with three normal proposal distributions centered at $\alpha_{1j}^{(k-1)}$, $maxVPD_j^{(k-1)}$, and $minRPD_j^{(k-1)}$, respectively.

7. Evaluate the Metropolis-Hastings ratio:

$$MH_{\sigma^2} = \frac{[\alpha_{1j}^{prop}, maxVPD_j^{prop}, minRPD_j^{prop} | \cdot]}{[\alpha_{1j}^{(k-1)}, maxVPD_j^{(k-1)}, minRPD_j^{(k-1)} | \cdot]}.$$

8. With probability $\min(MH_{\sigma^2}, 1)$, accept α_{1j}^{prop} , $maxVPD_j^{prop}$, and $minRPD_j^{prop}$ as the k^{th} samples of the posteriors of α_{1j} , $maxVPD_j$, and $minRPD_j$. Otherwise, set the k^{th} samples of each posterior to be equal to their respective $k - 1^{th}$ samples.

$$\alpha_{1j}^{(k)}, maxVPD_j^{(k)}, minRPD_j^{(k)} = \begin{cases} \alpha_{1j}^{prop}, maxVPD_j^{prop}, minRPD_j^{prop} & MH > u \\ \alpha_{1j}^{(k-1)}, maxVPD_j^{(k-1)}, minRPD_j^{(k-1)} & otherwise. \end{cases}$$

Where $u \sim U(0,1)$

9. Repeat steps 3 through 8 until K samples for each parameter have been obtained.

We used a normal distribution with a random walk to generate our proposals. At each iteration, each proposal was generated from a normal distribution with a mean equal to the value of the $k - 1^{th}$ sample of its associated posterior. The variance of these proposal distributions was tuned empirically to result in a suitable acceptance rate. Our updates were blocked such that those parameters relating to the expected yield, β_{1j} and $AOPD_j$, were updated at the same time.

Likewise, terms relating to the variance, α_{1j} , $maxVPD_j$, $minRPD_j$, were updated together. Note that the value of each MH-ratio at each iteration is equal to the likelihood function evaluated at the proposed samples divided by the likelihood function evaluated at the most recent samples, adjusted by a set of indicator functions to account for our uniform priors.

$$MH_{\mu} = \frac{[\beta_{1j}^{prop}, AOPD_j^{prop} | \cdot]}{[\beta_{1j}^{(k-1)}, AOPD_j^{(k-1)} | \cdot]}$$

$$= \frac{L(\beta_{1j}^{prop}, AOPD_j^{prop}, \alpha_{1j}^{(k-1)}, maxVPD_j^{(k-1)}, minRPD_j^{(k-1)}) * I(\beta_{1j}^{prop}, AOPD_j^{prop})}{L(\beta_{1j}^{(k-1)}, AOPD_j^{(k-1)}, \alpha_{1j}^{(k-1)}, maxVPD_j^{(k-1)}, minRPD_j^{(k-1)})}$$

With,

$$I(\beta_{1j}^{prop}, AOPD_j^{prop}) = \begin{cases} 1 & 0.001 < \beta_{1j}^{prop} < 0.2 \text{ and } 50 < AOPD_j^{prop} < 400 \\ 0 & \text{otherwise.} \end{cases}$$

Likewise,

$$MH_{\sigma^2} = \frac{[\alpha_{1j}^{prop}, maxVPD_j^{prop}, minRPD_j^{prop} | \cdot]}{[\alpha_{1j}^{(k-1)}, maxVPD_j^{(k-1)}, minRPD_j^{(k-1)} | \cdot]}$$

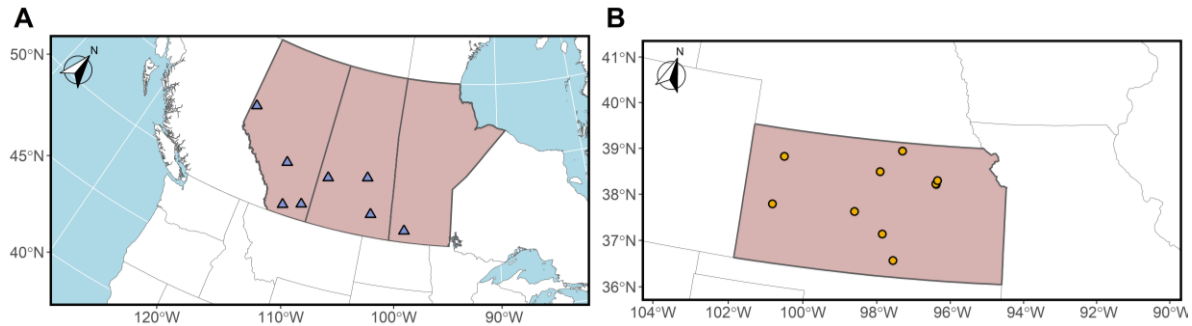
$$= \frac{L(\beta_{1j}^{(k-1)}, AOPD_j^{(k-1)}, \alpha_{1j}^{prop}, maxVPD_j^{prop}, minRPD_j^{prop}) * I(\alpha_{1j}^{prop}, maxVPD_j^{prop}, minRPD_j^{prop})}{L(\beta_{1j}^{(k-1)}, AOPD_j^{(k-1)}, \alpha_{1j}^{(k-1)}, maxVPD_j^{(k-1)}, minRPD_j^{(k-1)})}$$

Where $I(\alpha_{1j}^{prop}, maxVPD_j^{prop}, minRPD_j^{prop})$ similarly equals 1 if all proposals fall in the support of their respective priors and 0 otherwise.

The algorithm was implemented using program R with 2,000,000 iterations, discarding the first 400,000 as burn-in interval. The final MCMC chain was thinned by taking 1 every 4 samples in order to reduce autocorrelation between successive samples within the chain. We implemented the “*divide and conquer*” approach which allowed us to split the data by yield environment, fungicide treatment., and seed size. As such, the results of our model fitting process, and the

subject of our analysis, were 12 posterior distributions, corresponding to each combination of seed treatment, seed size and yield environment, for each of our 5 parameters.

Supplementary Figures and Tables



Appendix Figure C.1. Spatial distribution of the field trials evaluating grain yield response to plant density as affected by seeding management in (A) the Canadian Prairies and (B) Central Great Plains in Kansas, United States. Trials were conducted during more than one year in certain locations accounting for a total of 45 site-year combinations.

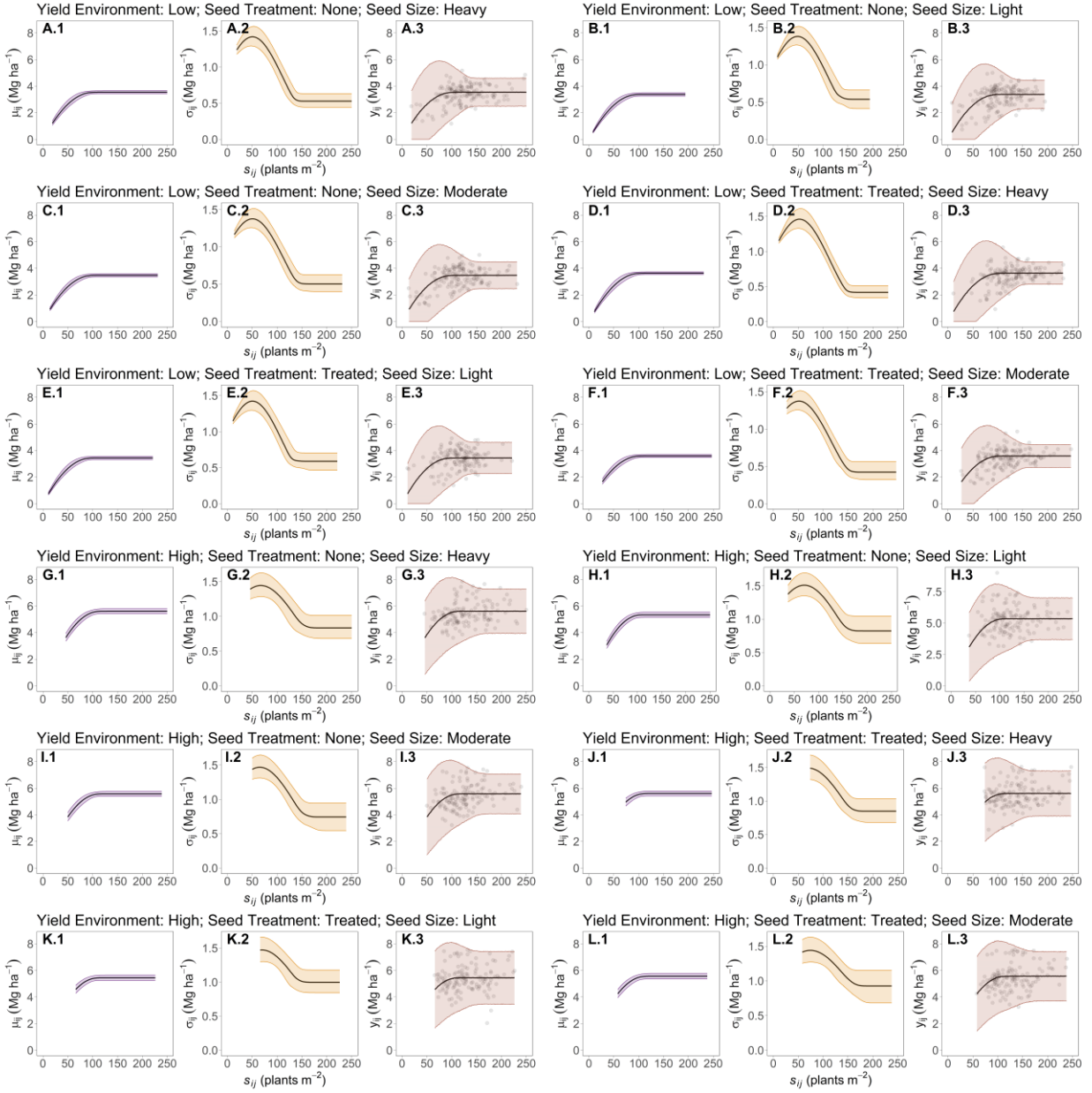
Appendix Table C.1. Geographic reference, planting and stand count dates on 25 environments across Kansas.

Environment	Longitude	Latitude	Planting Date	Stand Count Date
ABA21	-96.6203	39.13253	10/13/2020	12/15/2020
ABM21	-96.6326	39.14316	10/14/2020	12/15/2020
ASH19	-96.6326	39.14316	11/1/2018	1/9/2019
ASH20	-96.6326	39.14316	10/25/2019	NA
BEL19	-97.6717	39.81375	10/3/2018	11/7/2019
BEL20	-97.6717	39.81375	9/27/2019	10/16/2019
BLC21	-97.6717	39.81375	9/29/2020	12/15/2020
BLS21	-97.6717	39.81375	10/5/2020	12/15/2020
COL20	-101.057	39.38508	NA	NA
COL21	-101.057	39.38508	NA	12/15/2020
GRETB20	-98.8695	38.36257	10/18/2020	NA
HUE21	-98.0268	37.92968	9/17/2020	12/15/2020
HUO21	-98.0268	37.92968	9/29/2020	12/15/2020
HUT19	-98.0268	37.92968	10/22/2018	11/14/2019
HUT20	-98.0268	37.92968	10/10/2019	NA
HUTSOY20	-98.0268	37.92968	10/28/2019	10/28/2019
LEO19	-101.201	38.29822	9/27/2018	11/5/2019
LEO20	-101.201	38.29822	9/25/2020	10/23/2019
LEO21	-101.201	38.29822	9/25/2020	12/15/2020
MAN19	-96.5902	39.21819	10/23/2018	12/10/2019
MAN20	-96.5902	39.21819	10/26/2019	NA
MAN21	-96.5902	39.21819	10/7/2020	12/15/2020
MIT19	-98.262	39.30544	11/4/2018	NA
MIT20	-98.262	39.30544	NA	NA
SUM20	-97.6602	37.36659	10/17/2019	NA

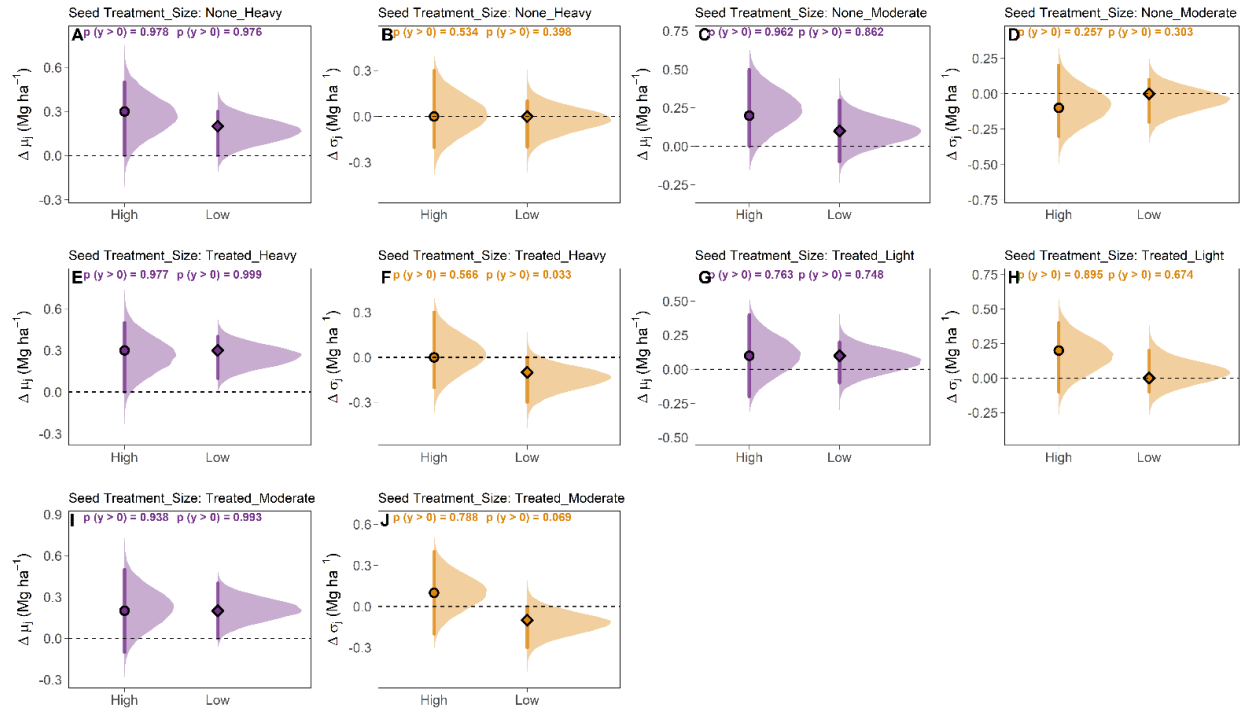
Appendix Table C.2. Texture and soil chemical properties at each 0-15 and 15-60 cm soil depth. Soil analysis was not available for sites: MIT19, MIT20, COL20 and COL21. * P extractable with Mehlich III method.

Site	Year	Depth (cm)	CEC S meq/100g	Ca ppm	Mg ppm	Na ppm	OM LOI %	P-M ppm	pH	NO ₃ -N ppm	NH ₄ -N ppm	K ppm	S ppm	Sand %	Silt %	Clay %
ABA	21	0-15	23.17	2,524.1	266.3	10.0	2.5	32.8	6.1	6.8	6.9	345.2	6.0	12	58	30
ABA	21	15-60	23.45	2,834.0	299.1	12.4	2.3	20.0	6.4	5.0	6.3	314.9	6.2	8	60	32
ABM	21	0-15	14.63	1,313.0	145.1	9.8	1.8	30.2	5.5	11	5.6	224.4	5.8	26	60	14
ABM	21	15-60	11.83	1,465.1	150.5	10.2	1.3	13.4	6.3	4.2	3.9	175.7	3.2	26	60	14
BLC	21	0-15	26.46	1,597.7	226.6	17.5	2.9	92.7	4.7	50.1	9.6	549.5	17.6	10	64	26
BLC	21	15-60	26.32	2,084.4	285.2	20.3	2.7	44.4	5.2	33.4	7.2	421.2	14.8	8	62	30
BLS	21	0-15	24.76	1,371.3	193.2	13.8	2.9	50.6	4.8	14.6	8.4	402.8	12.3	12	64	24
BLS	21	15-60	24.52	2,033.1	267.8	24.6	2.6	20.6	5.4	7.8	6.2	319.3	9.2	10	60	30
HUE, HUEO	21	0-15	25.8	4,720.9	122.3	11.1	3	27.7	7.3	54.8	9.6	352.2	7.3	26	46	28
HUE, HUEO	21	15-60	28.65	5,405.3	100	13.1	2.6	11.8	7.7	36.9	7.7	284.3	6.5	26	42	32
MAN	21	0-15	34.05	6,064.7	229.9	14	3.9	16.2	7.4	7.5	11.6	347.4	8.2	4	60	36
MAN	21	15-60	34.89	6,227.2	225.1	15.1	3.7	12.7	7.4	8.3	9.5	328.9	7.3	4	60	36
LEO	21	0-15	20.88	2,497.2	324.5	13.5	2.1	118.6	6.8	16.2	5.9	793.2	7.1	18	54	28
LEO	21	15-60	22.81	2,858.4	497.9	20	1.9	40.2	7	12.5	7.9	716.8	6.3	16	48	36
ASH	20	0-15	11.35	1,119.8	122.9	10.9	1.8	59.3	5.9	4.7	2.5	216.6	0.9	32	56	12
ASH	20	15-60	8.91	1,495.9	117.4	9.4	1.1	38.2	7.2	3.2	2.4	159.5	0.8	38	50	12
MAN	20	0-15	27.38	4,885.3	251.4	15.3	4	12.1	7	7.5	7.3	309.3	2.7	12	56	32
MAN	20	15-60	34.35	6,234.4	281.4	13.4	3.7	7	7.3	6.8	6.1	301.3	2.5	8	56	36
HUTSOY	20	0-15	24.18	1,958.8	348.3	8.8	2.8	88.6	5.4	7.8	4.1	425.5	4.2	28	44	28
HUTSOY	20	15-60	25.99	2,778.9	505.7	14.5	2.2	45.5	6.2	5.8	4.9	368.9	4.9	26	40	34
HUT	20	0-15	23.0	2,222.3	185.7	15.0	2.4	68.7	5.5	34.5	6.1	334.5	23.0	28	48	24
HUT	20	15-60	19.0	3,315.1	201.5	17.4	2.3	50.6	6.7	20.4	5.4	273.6	19.0	26	48	26
GRETB20	20	0-15	21.96	1,517.3	391.4	50.3	2.4	208	5.5	22.8	1.5	622	6.2	26	50	24
GRETB20	20	15-60	22.52	2,075.5	535.7	111.7	2.3	147	6.4	12.9	1.3	558.3	6.2	20	50	30

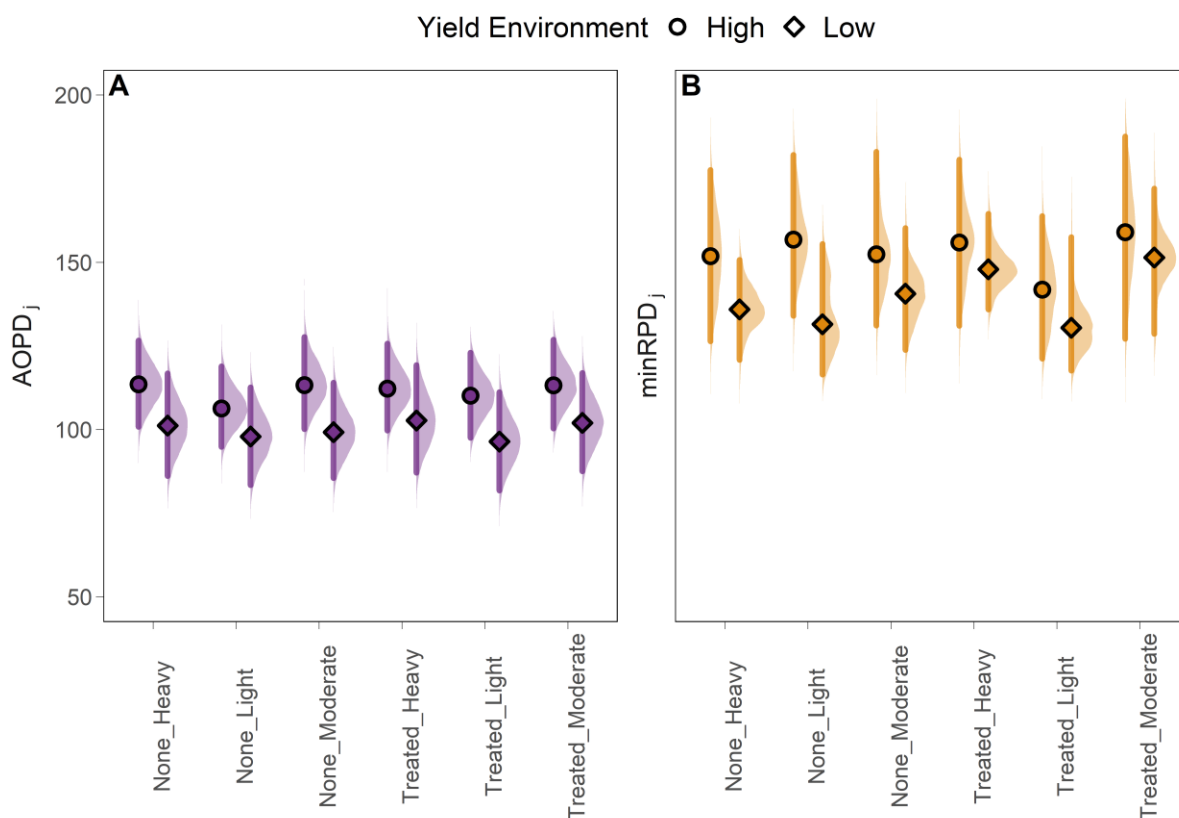
SUM	20	0-15	19.92	890.5	265.7	16.4	1.6	62	5.1	2.9	1.4	157.1	2	48	30	22
SUM	20	15-60	18.99	1,151.9	337	30	1.6	48.2	5.4	3.5	2.4	139.9	2			
LEO	20	0-15	18.3	2,433.9	460.3	19.2	2.9	155	6.6	30.9	3.7	864	4.9	16	58	26
LEO	20	15-60	31.09	4,845.7	582.2	21.9	1.9	67.2	7.6	15.6	7.8	747.4	3.8	14	52	34
BEL	20	0-15	23.93	1,617.4	209.9	22.5	2.9	53.2	4.7	46.3	5	392	7.9	16	60	24
BEL	20	15-60	27.84	2,597.3	342.3	46.8	2.7	31.3	5.5	29.4	5.3	358.4	5.8	8	62	30
ASH	19	0-15	22.1	3,329.0	550.0	21.0	3.0	8.4	6.5	3.0	6.5	304.0	2.6	12	50	38
ASH	19	15-60	25.3	3,604.0	760.0	36.0	2.2	3.7	6.7	1.7	7.9	309.0	2.2	6	50	44
LEO	19	0-15	20.8	2,401.0	399.0	28.0	2.4	91.5	6.2	36.4	3.5	826.0	4.8	34	40	26
LEO	19	15-60	30.7	4,876.0	558.0	24.0	1.6	17.8	7.9	2.6	3.3	604.0	3.6	24	46	30
MAN	19	0-15	26.3	2,977.0	357.0	17.0	3.5	22.3	6.2	3.2	7.3	162.0	2.5	16	58	26
MAN	19	15-60	26.5	4,477.0	411.0	26.0	2.8	8.9	7.0	2.6	5.9	217.0	3.5	14	56	30
HUT	19	0-15	26.1	4,746.0	163.0	35.0	2.9	27.2	8.0	16.7	3.2	315.0	3.3	28	42	30
HUT	19	15-60	28.4	5,202.0	162.0	128.0	2.2	4.0	8.1	13.2	4.5	194.0	12.5	22	42	36
BEL	19	0-15	28.0	2,056.0	296.0	17.0	3.1	52.4	5.4	0.4	3.0	437.0	3.4	16	54	30
BEL	19	15-60	26.0	4,022.0	555.0	58.0	2.4	7.8	6.6	4.0	5.0	381.0	3.0	8	48	44



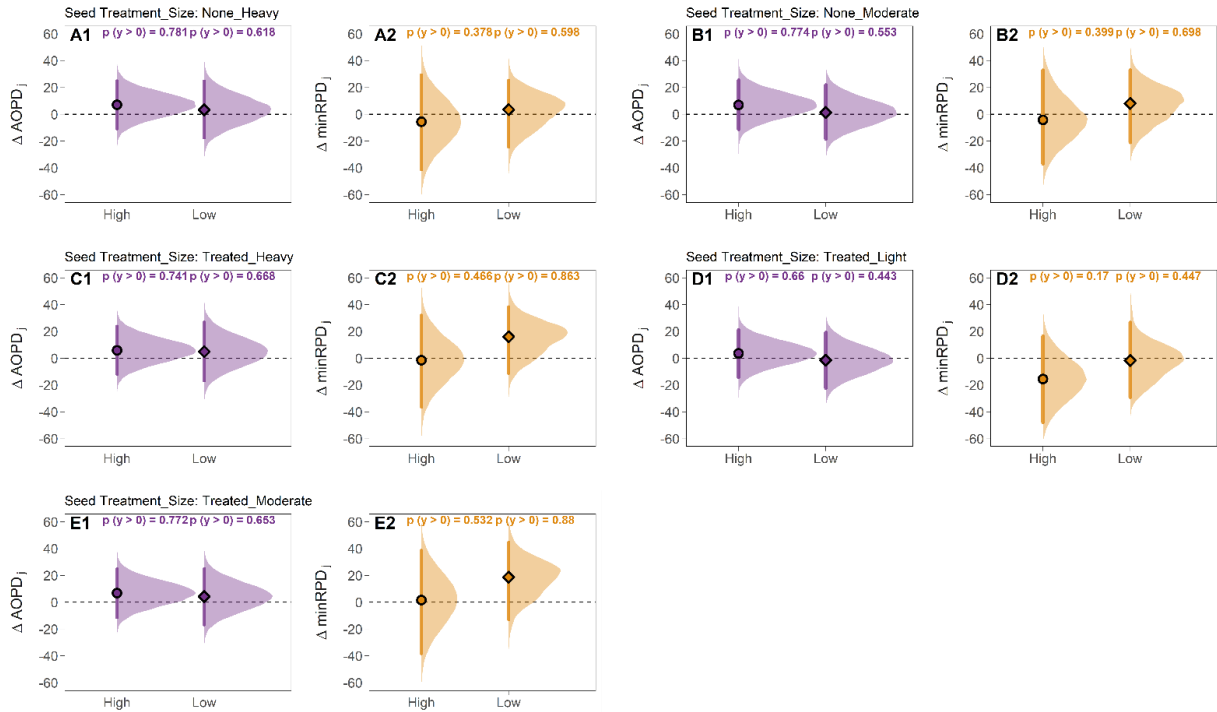
Appendix Figure C.2. Panels .1 shows the expected grain yield (μ_{ij}) in response to plant density (s_{ij} , purple); panels .2 shows standard deviation of yield (derived from yield variance, σ_{ij}^2) in response to plant density (yellow); panels .3 shows the posterior predictive distribution of grain yield (y_{ij}) response to plant density (brown) for the j th treatment $\times$ environment combination (sub panels title). Solid black lines represent the median and ribbons the 95% credible interval.



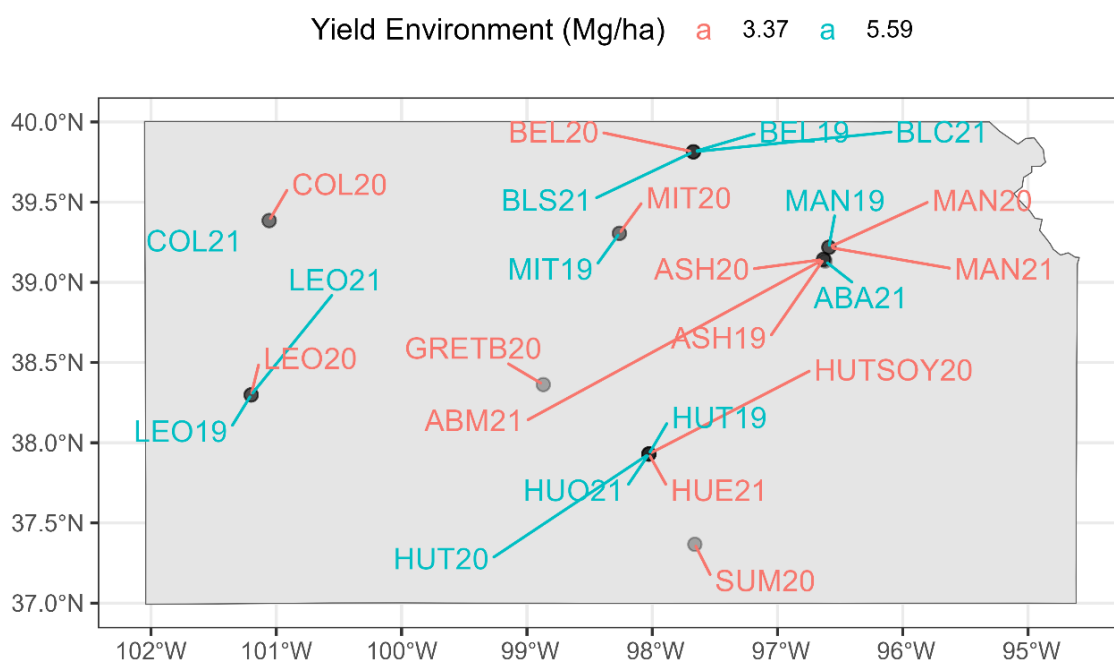
Appendix Figure C.3. Posterior distributions of expected grain yield response to seed management evaluated at the AOPD to seed management (Table 1, Eq. 11); B) standard deviation of yield response to seed management evaluated at the minRPD (Table 1, Eq. 12) in high and low yielding environments. Contrasts represent all treatment (seed treatment x seed size) combinations compared against light seed, untreated control treatment (Eq. 11, 12). Points represent the median and whiskers are the 95% credible interval; p represents the posterior probability of $\Delta\mu_j$, $\Delta\sigma_j$ being greater than zero.



Appendix Figure C.4. Posterior distributions of AOPD (A) and minRPD (B) for all seed management treatments under high (circles) and low (diamond) yielding environments. Points represent the median and whiskers are the 95% credible interval.



Appendix Figure C.5. Posterior distributions of AOPD (1, purple) and minRPD (2, yellow) as affected by seed management treatments under high (circles) and low (diamond) yielding environments. Contrasts represent all seed treatment x seed size combinations against light, untreated (control) seeds. Points represent the median and whiskers are the 95% credible interval. The description of the calculations used for contrasts between treatments are listed in Table 1, Eq. 13 (AOPD, purple) and Eq. 14 (minRPD, yellow).



Appendix Figure C.6. Geographic reference and environmental classification of trials conducted in Kansas US included in the study.

Appendix D - Chapter 4 Supplementary Material

Variety testing network data from a sample of wheat producing regions.

The data presented in Figure 4.1 were retrieved from variety testing network across wheat producing regions. Data was retrieved from either publicly available sources, such as the United Kingdom Recommended Lists trials (retrieved from <https://ahdb.org.uk/knowledge-library/recommended-lists-archive>) or accessed with permission to reproduce the data. Details of datasets are presented in Appendix Table D.1.

Appendix Table D.1. Description of datasets used to describe associations of yield per se and yield plasticity on global wheat producing regions. Each environment represents the combination of year and site.

Country or region	Number of observations	Number of genotypes	Number of environments
Alberta, Canada	27,950	168	391
Argentina	14,154	145	150
Australia	96,475	318	193
Manitoba, Canada	15,175	132	305
United Kingdom	19013	263	435
Uruguay	688	17	42

Appendix Table D.2. List of cultivars tested in at least 25 environments, their year of release and values for the four traits explored in this study. Year of release data were not available in empty cells. Yield plasticity was estimated as the slope of the reaction norm described in Equation 2. Estimation of yield traits is described in Equation 4.

Genotype (commercial name or experimental line identification)	Number of environments tested	Year of release	Yield 95 th percentile	Yield 5 th percentile	Yield mean	Yield plasticity
2137	214	1995	5.06	1.46	3.03	0.98
ABOVE	187	2001	5.17	1.24	3.16	0.92
AKRON	114	1994	5.61	1.1	3.05	0.94
ALLIANCE	83	1993	5.51	1.11	3.1	0.92
AP502_CL	120	2001	4.73	1.09	2.98	0.91
AVALANCHE	102	2001	5.3	1.24	3.11	0.9
CO970547	25					
COSSACK	26	1998	3.97	1.54	2.99	0.89
ENHANCER	70	1998	5.47	1.31	2.95	0.89
HALT	30	1994	4.96	1.31	2.94	0.96

JAGGER	418	1994	5.06	1	3.09	0.97
LAKIN	83	2000	5.15	0.85	2.88	0.97
NUPLAINS	38	1999	5.01	1.51	2.92	0.81
PRAIRIE_RED	144	1998	5.52	1.2	3.11	0.93
PROWERS_99	77	1997	4.23	0.83	2.79	0.81
STANTON	90	2000	5.61	1.05	3	0.97
TAM_107	49	1984	5.09	1.29	2.96	0.94
TAM_110	70	1996	5.44	1.3	3.08	0.94
TREGO	216	1999	5.26	1.14	3.09	0.96
VENANGO	56	2000	5.43	1.53	2.94	0.94
YUMA	85	1991	5.16	1.13	3.12	0.97
YUMAR	54	1997	4.94	1.12	3	0.96
2163	29	1989	4.84	1.1	2.63	0.66
2174	201	1997	4.98	1.1	2.99	0.98
BETTY	35	1998	5.04	0.97	2.83	0.92
CUSTER	114	1994	4.59	1.07	2.9	1
DOMINATOR	53	1995	5.23	1.17	2.99	1.02
HEYNE	38	1998	4.55	1.15	2.71	1.01
IKE	56	1993	5.76	1.2	3.08	0.93
KARL_92	70	1992	5.47	0.95	2.92	1.01
MILLENNIUM	37	2000	5.78	1.23	3.07	0.9
INTRADA	124	2000	5.01	1.19	2.86	0.98
ONAGA	70	1998	5.17	1.18	2.85	0.98
ORO_BLANCO	26	1994	4.05	0.96	2.64	0.89
SCOUT_66	30	1967	4.55	0.81	2.52	0.69
TAM_302	58	1998	4.69	1.37	2.83	1.05
THUNDERBOLT	150	1999	4.85	1.26	2.98	0.92
WESLEY	39	1998	6.47	1.5	3.21	1.03
T81	39	1995	5.29	1.43	3.24	0.97
CHISHOLM	66	1983	4.68	1.27	2.89	1
CORONADO	51	1994	4.33	1.36	2.88	0.93
LOCKETT	49	1998	4.34	1.16	2.71	0.98
OGALLALA	34	1993	4.8	1.49	2.84	1.02
OK101	138	2001	4.96	1.16	2.94	0.98
TOMAHAWK	34	1991	4.61	1.25	2.75	0.98
ANKOR	84	2002	5.27	0.98	3.1	0.92
HATCHER	224	2004	5.91	1.19	3.44	1.04
NUFRONTIER	80	2000	5.55	1.02	3.05	0.94
NUHORIZON	51	2000	5.63	0.94	2.79	0.92
CUTTER	146	2001	5.32	1.13	3.18	0.99
OK102	107	2002	5.07	1.43	2.96	1
BOND_CL	118	2004	5.32	1.04	3.32	0.99
JAGALENE	278	2001	5.33	1.04	3.18	1.02
PROTECTION	78	2004	5.4	0.7	3.09	1.02

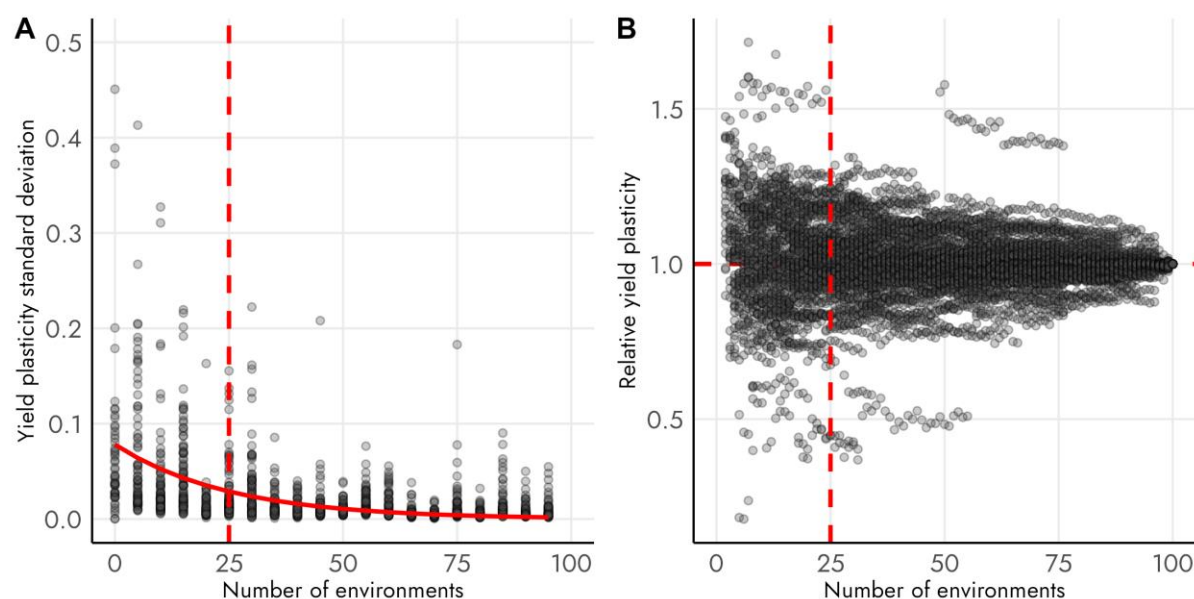
TAM_111	239	2002	5.49	0.91	3.25	1.03
2145	114	2001	5.21	1.04	3.06	1.07
WAHOO	31	2000	6	0.72	3.06	0.96
RIPPER	137	2006	5.71	1.19	3.33	0.91
GOODSTREAK	63	2002	4.98	1	2.98	0.8
HARRY	34	2002	5.63	0.89	3.12	0.87
OVERLEY	196	2003	5.18	0.97	3.19	1.02
SANTA_FE	136	2005	5.1	0.95	3.31	1.02
ENDURANCE	308	2004	4.89	1.11	3.33	0.97
DELIVER	151	2004	4.72	0.95	3.1	0.97
NUHILLS	42	2003	5.16	0.88	3.12	0.94
DANBY	155	2005	5.74	1.07	3.27	1.05
FANNIN	88	2004	4.6	0.69	2.95	0.99
OK_BULLET	166	2005	4.96	1.04	3.18	0.98
OK_RISING	77	2008	5.16	1.04	3.07	1.02
BILL_BROWN	119	2007	5.26	1.08	3.4	0.96
INFINITY_CL	76	2004	5.59	1.19	3.34	1.02
KEOTA	91	2005	5.18	1.17	3.22	0.97
NUGRAIN	36	2006	4.59	0.79	3.11	0.9
STURDY_2K	31	2004	4.44	0.98	3.03	0.98
POSTROCK	82	2005	5.65	1.11	3.23	1.1
GUYMON	34	2005	5.17	0.77	3.08	0.94
OKFIELD	60	2005	4.88	0.84	2.95	0.93
DUSTER	351	2006	5.32	1.06	3.36	0.96
CO02W237	29					
NUDAKOTA	48	2005	5.93	1.1	3.48	1.11
RONL	42	2006	4.94	0.71	2.94	0.91
THUNDER_CL	82	2008	5.05	1.1	3.24	0.93
SMOKY_HILL	57	2006	6.24	1.44	3.22	1.1
FULLER	231	2006	5.23	1.22	3.3	1.02
TAM_112	219	2005	5.98	1.27	3.32	0.95
CENTERFIELD	108	2006	4.46	0.86	3.05	0.89
HAWKEN	52	2006	5.69	1.91	3.24	0.98
OVERLAND	38	2007	6.08	1.81	3.34	1.03
ART	41	2006	5.87	1.27	3.25	1.1
ASPEN	25	2006	5.77	1.36	3.43	1.05
SHOCKER	89	2005	5	0.89	3.1	1.01
WINTERHAWK	261	2007	6.05	1.3	3.55	1.06
DOANS	127	2006	4.61	0.98	3.15	0.91
BILLINGS	166	2009	5.08	0.91	3.36	1.1
PETE	70	2009	4.6	0.69	3.01	1.06
CAMELOT	34	2008	5.6	1.4	3.27	1.06
SETTLER_CL	86	2008	6.35	1.44	3.44	1.04
ARMOUR	196	2008	5.35	0.98	3.29	1.07

HITCH	30	2008	5.72	2.35	3.41	0.89
TAM_304	62	2006	5.53	1.11	3.45	1.11
TAM_203	65	2007	4.7	1.04	3.31	0.96
JACKPOT	174	2008	5.07	1.05	3.37	1.08
MACE	31	2007	4.89	0.6	2.99	0.9
SNOWMASS	112	2009	6.26	1.32	3.39	1.07
SY_GOLD	45	2010	6.03	1.88	3.28	1.04
WB-STOUT	55	2009	4.96	0.79	3.16	1.02
WB-CEDAR	196	2011	5.67	1.43	3.48	1.06
RUBY_LEE	238	2011	5.43	1.13	3.41	0.97
BRAWL_CL_PLUS	198	2011	6.25	1.24	3.45	1.05
BYRD	190	2011	6.58	1.23	3.55	1.07
CO050233-2	25					
CO05W111	33					
COWBOY	49	2011	7.08	2.11	3.54	1.05
DENALI	147	2011	6.62	1.57	3.53	1.05
EVEREST	247	2009	5.56	1.23	3.38	1.02
LCS_MINT	247	2014	6.48	1.2	3.47	1.03
T158	228	2009	6.66	1.06	3.52	1.07
CJ	54	2010	5.12	1.06	3.2	1.05
GREER	117	2009	4.94	0.96	3.38	1.06
TAM_401	43	2008	4.22	0.75	3.26	1.06
GARRISON	130	2011	4.73	0.91	3.16	1
ANTERO	101	2012	7.34	1.46	3.99	1.15
MCGILL	28	2010	4.4	0.7	3.17	0.96
ROBIDOUX	48	2010	5.94	0.89	3.35	1.06
SY_WOLF	143	2010	6.88	1.54	3.47	1.1
T163	28	2010	4.44	0.62	3.29	0.98
GALLAGHER	304	2012	5.86	1.12	3.53	1.08
IBA	266	2012	5.81	1.14	3.53	1.02
1863	121	2012	5.68	1.44	3.36	1
CLARA_CL	49	2011	5.61	0.93	3.43	1.02
T154	86	2008	5.16	1.06	3.4	1.06
T153	69	2008	5.25	0.94	3.41	1.07
SY_SOUTHWIND	63	2012	5.55	1.85	3.39	1.11
DOUBLESTOP_CL+	243	2013	5.76	1.51	3.55	0.95
BENTLEY	185	2015	6.16	1.29	3.7	1.05
BEARPAW	26	2011	6.18	0.43	2.86	0.98
LCS_WIZARD	129	2013	5.8	1.19	3.24	0.99
OAKLEY_CL	114	2013	7.25	1.52	3.75	1.06
WB-GRAINFIELD	256	2012	6.86	1.22	3.68	1.12
WB4458	173	2012	6.09	1.06	3.56	1.12
WB-REDHAWK	87	2012	5.32	1.56	3.27	1.07
AVERY	109	2015	7.2	1.8	3.61	1.01

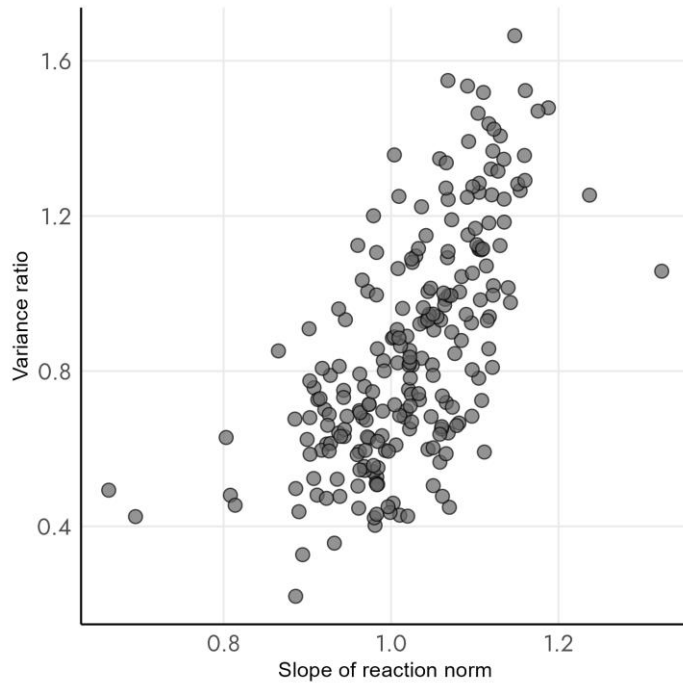
KANMARK	120	2014	6.35	1.58	3.44	1.08
LANGIN	155	2016	7.37	1.89	3.79	1.11
LCS_PISTOL	152	2015	5.82	1.33	3.39	0.99
SUNSHINE	73	2014	7.24	1.55	3.71	1.14
SY_MONUMENT	221	2014	6.83	1.73	3.71	1.06
HOT_ROD	49	2015	6.41	1.6	3.65	1.14
SPIRIT_RIDER	54	2017	6.09	1.62	3.51	1.03
STARDUST	36	2017	5.53	0.9	3.29	1
JOE	121	2015	7.75	1.68	4.01	1.09
RUTH	32	2015	7.18	2.14	3.52	1.12
SPUR	37	2017	6.54	1.47	3.23	0.97
TAM_114	139	2014	7.24	1.82	3.62	1.11
TAM_204	143	2014	6.83	0.95	3.44	1.1
LARRY	119	2016	6.34	1.25	3.6	1.14
SY_LCS_FLINT	88	2015	6	1.2	3.52	1.01
LCS_CHROME	230	2016	6.42	1.53	3.64	1.03
SY_SUNRISE	35	2015	7.39	2.52	3.67	0.94
SMITH'S_GOLD	146	2017	5.86	1.32	3.55	1.05
BRECK	86	2017	8.17	2.11	3.74	1.12
INCLINE_AX	45	2017	6.45	1.85	3.31	0.98
WB4721	68	2018	6.62	1.27	3.6	1.07
ZENDA	128	2016	6.71	1.85	3.63	1.04
AG_GALLANT	52	2014	6.6	1.99	3.55	0.9
AG_ROBUST	37	1992	6.7	1.75	3.48	1.12
LONG_BRANCH	159	2016	6.97	1.67	3.53	1.02
SY_GRIT	111	2017	6.67	1.28	3.35	1.07
TATANKA	79	2016	7.64	1.9	3.72	1.11
WB4303	103	2015	7.18	1.32	3.61	1.13
SHOWDOWN	25	2018	7.17	1.33	3.81	1.12
WB4515	55	2017	6	1.33	3.59	0.96
LONERIDER	107	2017	7.58	1.17	3.56	1.15
BYRD_CL_PLUS	74	2018	6.54	2.01	3.66	1.05
CANVAS	147	2018	7.77	1.89	3.87	1.09
FORTIFY_SF	54	2019	6.87	1.98	3.74	1.12
VALLEY	34					
MONARCH	75	2018	8.06	2.24	3.84	1.09
SNOWMASS_2.0	58	2018	7.53	1.87	3.85	1.13
SY_RUGGED	146	2017	6.48	1.36	3.58	1.07
WB4462	54	2015	7.1	2.38	3.52	1.11
WHISTLER	108	2018	7.18	2	3.84	1.08
AG_ICON	136	2019	6.71	1.63	3.65	1.05
BOB_DOLE	112	2017	6.36	1.38	3.77	1.09
AM_EASTWOOD	135	2017	7.32	1.57	3.32	1.14
PARADISE	59	2017	7.37	1.69	3.53	1.12

SY_BENEFIT	75	2017	6.03	1.12	3.43	1.04
WB4269	120	2017	6.68	1.93	3.84	1
SHOWDOWN	29	2018	7.17	1.33	3.81	1.12
SHOWDOWN	102	2018	7.17	1.33	3.81	1.12
SY_ACHIEVE_CL2	72	2017	5.86	0.94	3.39	1.05
STEAMBOAT	46	2020	7.45	1.73	3.81	1.13
GUARDIAN	98	2019	7.31	1.81	3.78	0.98
CRESCENT_AX	122	2018	7.21	1.91	3.68	1.11
SY_LEGEND_CL2	44	2018	6.85	1.78	3.38	1.04
WB4418	67	2018	7.42	2	3.5	1.11
KS_SILVERADO	90	2019	7.42	1.74	3.54	1.15
SY_WOLVERINE	86	2019	8.44	2.25	3.67	1.19
LCS_VALIANT	70	2019	7.05	2.06	3.65	1.07
ROCK_STAR	53	2019	7.72	2.3	3.85	1.09
WB4792	101	2019	7.85	1.93	3.82	1.13
CP7869	37	2017	8.24	2.01	3.77	1.07
CP7909	66					
WB4699	77	2018	7.4	1.66	3.88	1.12
GREEN_HAMMER	48	2018	6.15	1.52	3.64	1.02
AM_CARTWRIGHT	62	2020	7.24	1.24	3.57	1.16
KS_DALLAS	69	2019	7.37	1.86	3.73	1.1
KS_WESTERN_STAR	81	2019	7.31	1.68	3.65	1.04
WB4401	61	2020	6.99	1.19	3.73	1.24
WB4595	78	2018	8.14	2.22	3.85	1.12
AP_EVERROCK	37					
BAKER'S_ANN	53	2018	6.23	1.44	3.51	1.03
BREAKTHROUGH	43	2020	7.51	1.82	3.48	1.04
AP_BIGFOOT	32	2022	7.04	1.34	3.47	1.1
AP_ROADRUNNER	47	2020	7.58	1.39	3.86	1.07
KS_HAMILTON	41	2020	7.5	1.6	3.83	1
LCS_ATOMIC_AX	54	2019	7.64	1.45	3.86	1.1
LCS_HELIX_AX	58	2019	7.85	1.73	3.79	1.18
LCS_JULEP	47	2019	7.84	1.38	3.48	1.11
LCS_PHOTON_AX	49					
LCS_REVERE	28	2018	7.2	1.92	3.31	1.32
MS_MAVERICK	29	2021	6.88	1.88	3.7	1.01
HIGH_COUNTRY	30					
AG_RADICAL	29					
KS_AHEARN	26	2021	6.54	1.35	3.68	1.08
OK_CORRAL	55	2020	6.69	1.21	3.62	1.1
SKYDANCE	30	2018	5.48	1.3	3.51	1.08
CP7017AX	49	2020	7.29	1.5	3.94	1.13
KIVARI_AX	33	2020	6.51	1.74	3.79	1.01
BIG_COUNTRY	39	2020	6.19	1.38	3.59	0.98

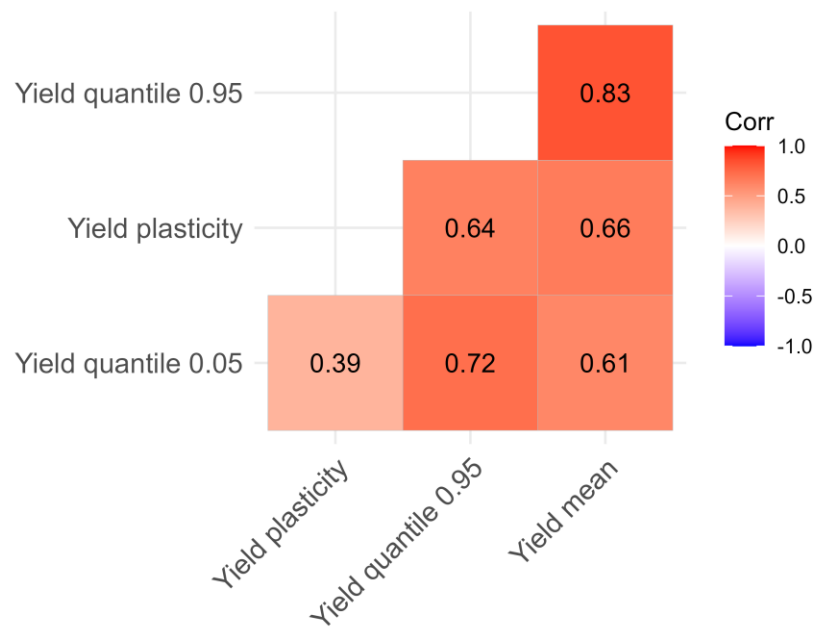
UNCHARTED	34	2020	5.86	1.55	3.66	0.92
STRAD_CL+	25					
CP7050AX	26	2020	6.92	1.77	3.52	1.06
AMPLIFY_SF	25	2021	6.96	1.65	3.56	0.98
CO16SF067	25					
CO16SF032	25					



Appendix Figure D.1. Sensitivity analysis to determine the minimum number of environments (n) required to get a reliable estimate of yield phenotypic plasticity. Only cultivars replicated in at least 100 environments are included in the sensitivity analysis. In A, each point represents the standard deviation of plasticity estimates for a given genotype in a sliding window of 5 environments. In B, relative yield plasticity represents the plasticity estimate for a given cultivar relative to its estimate when n = 100. Dashed vertical lines represent the selected threshold for genotypes to be included in the analyses. When n = 25 the predicted standard deviation of plasticity based on the exponential decay model was equal to 0.03.



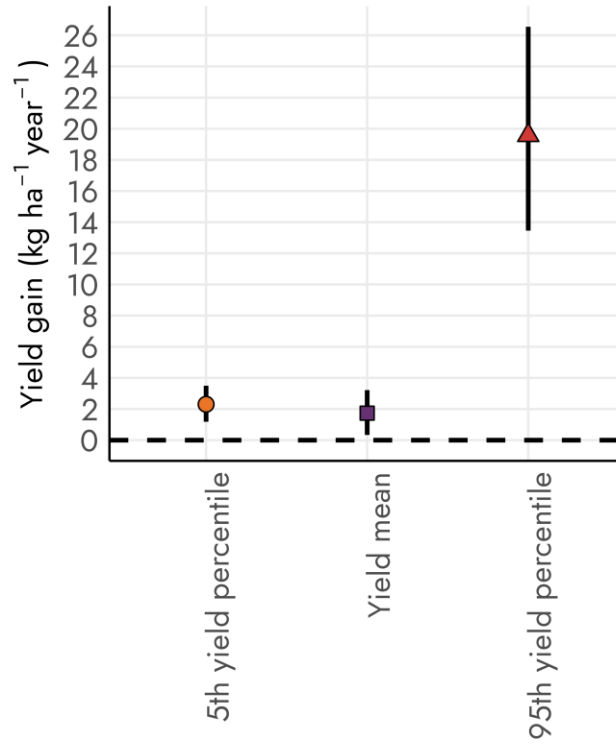
Appendix Figure D.2. Comparison of genotype-dependent phenotypic plasticity of yield calculated with two methods: the slope of the reaction norm (Equation 2) and the variance ratio, i.e., the ratio between the observed genotypic variance over the total variance of the population (Dingemanse et al., 2010).



Appendix Figure D.3. Linear correlations between yield phenotypes evaluated in this study. All correlations are significant at $p < 0.05$.

Appendix Table D.3. Summary, average and range, of environmental descriptors tested to its association with environmental mean yield. Summary statistics are calculated over 779 environments resulting from the combination of site and year. Abbreviations: critical period (CP), grain filling period (GF), number of gays with temperatures lower than 0 °C (ETE_CP), number of gays with temperatures lower than 30 °C (ETE_GF), cumulative precipitation (PP), photothermal quotient (PQ), daily mean temperature (Tmean) and vapor pressure deficit (VPD).

Environmental variable	Units	Average	Minimum	Maximum
Duration_CP	days	40.6	25.0	63.0
Duration_GF		31.0	24.0	40.0
ETE_CP_CP	count	7.3	0.0	61.0
ETE_GF_CP		2.3	0.0	11.0
ETE_GF_GF		11.1	0.0	23.0
PP_CP	mm	85.7	0.0	322.6
PP_GF		109.5	0.0	542.0
PQ_CP	Mj °Cd	1.9	1.1	2.8
PQ_GF		1.1	0.8	1.4
Tmean_CP	°C	12.4	-1.9	19.9
Tmean_GF		20.7	17.0	25.1
VPD_CP	Pa	746.3	200.8	1529.4
VPD_GF		1353.7	476.4	2048.6



Appendix Figure D.4. Yield gains associated with yield phenotypic plasticity for three levels of yield. Yield gains were simulated as the product between the posterior distribution of slopes on Figure 4.3B and Figure 4.4A. Yield gains were simulated as the product between the posterior distribution of β_1 term in Equation 4 and α_1 term in Equation 6.

Appendix Table D.4. SNPs associated with wheat yield phenotypes. SNPs are sorted from top to bottom according to their absolute effect on each yield phenotype. Abbreviations: chromosome (Chr.), single nucleotide polymorphism (SNP), P-value (P), minor allele frequency (MAF).

Yield phenotype	Chr.	SNP	Effect	–log₁₀(P)	MAF
Yield mean	6B	S6B_726368246	0.16	3.45	0.06
	2D	S2D_206645004	0.12	3.21	0.16
	6B	S6B_651770832	0.10	3.57	0.30
	6B	S6B_649190074	0.10	3.10	0.22
	1A	S1A_14289872	0.10	3.05	0.18
	6B	S6B_651828250	0.09	3.26	0.30
	2B	S2B_13713678	0.09	3.07	0.27
	3A	S3A_691148254	0.08	3.22	0.40
Low yielding environments	3A	S3A_638758053	0.16	3.55	0.19
	2B	S2B_97794355	0.14	4.02	0.24
	2B	S2B_98371953	0.14	3.48	0.21
	2B	S2B_98371995	0.14	3.48	0.21
	1A	S1A_27594593	0.13	3.95	0.26
	1A	S1A_27594591	0.13	3.95	0.26
	6B	S6B_523472016	0.13	3.03	0.20
	4B	S4B_593675566	0.13	3.08	0.20
	7D	S7D_13070644	0.12	3.77	0.46
	7D	S7D_13070614	0.11	3.42	0.47
	6B	S6B_172236638	0.11	3.60	0.41
	7D	S7D_13415400	0.11	3.12	0.46
	3A	S3A_701725274	0.10	3.00	0.25
High yielding environments	1A	S1A_14289872	0.35	9.37	0.18
	3A	S3A_613683508	0.30	5.06	0.10
	1B	S1B_493165543	0.28	3.05	0.09
	7B	S7B_724961593	0.22	6.24	0.40
	3B	S3B_754137029	0.22	4.76	0.27
	5D	S5D_547030857	0.19	4.80	0.43
	1D	S1D_410695550	0.18	3.39	0.27
	6B	S6B_412147528	0.17	3.42	0.20
	3A	S3A_19633305	0.16	3.46	0.44
	7B	S7B_692663450	0.15	3.58	0.43
	5D	S5D_134802435	0.14	3.07	0.46
Yield phenotypic plasticity	7A	S7A_29330974	0.03	6.04	0.09
	5B	S5B_704099016	0.02	4.65	0.12
	6A	S6A_13708715	0.02	3.53	0.10
	5A	S5A_34753008	0.02	3.48	0.09
	2B	S2B_781222236	0.02	3.69	0.22
	3A	S3A_726890110	0.02	4.15	0.31

	2B	S2B_805527600	0.02	3.82	0.38
	3B	S3B_587824478	0.02	3.59	0.39

Appendix E - Chapter 5 Supplementary Material

Appendix Table E.1. Dates of crop husbandry operations and details of treatments for each location-season evaluated in this study. Abbreviations: days after sowing (DAS), grams of active ingredient (g.a.i), Zadoks growth stage (GS), environment (env), picoxystrobin (Pxys), fluxapyroxad (Fxy), propiconazole (Pzole), azoxystrobin (Azbin), pyraclostrobin (Pybin), propiconazole (Pzole), cyproconazole (Czole), metconazole (Mzole) . Hyphen ‘ - ‘ indicates data was not available.

Env.	Sowing date	GS 25	GS 31	GS 25			GS 55						Harvest date
		Nitrogen application	Fungicide application	Mode of action 1	Mode of action 2	Fungicide rate	Fungicide application	Mode of action 1	Mode of action 2	Mode of action 3	Fungicide rate		
		DAS				g a.i./ha-1	DAS				g a.i./ha		
AS19	11/1/2018	141	167	182	Pxys	-	36	211	Pxys	Czole	-	70	242
CO16	10/13/2015	115	139	149	Fxy	Pxys	53	191	Fxy	Pybin	Pzole	117	238
CO17	10/11/2016	-	148	168	Fxy	Pxys	53	189	Fxy	Pybin	Pzole	117	254
CO18	10/18/2017	134	-	-	Fxy	Pxys	53	-	Fxy	Pybin	Pzole	117	244
ELL16	10/9/2015	-59	126	152	Fxy	Pxys	53	196	Fxy	Pybin	Pzole	117	284
ELL17	10/7/2016	133	152	172	Fxy	Pxys	53	193	Fxy	Pybin	Pzole	117	263
ELL18	10/17/2017	31	-	-	Fxy	Pxys	53	-	Fxy	Pybin	Pzole	117	245
GB18	10/12/2017	151	185	185	Pxys	-	36	211	Pxys	Czole	-	70	263
GB19	10/2/2018	176	199	195	Pxys	-	36	226	Pxys	Czole	-	70	273
MP16	10/7/2015	101	138	155	Fxy	Pxys	53	198	Fxy	Pybin	Pzole	117	265
MP17	10/11/2016	-	148	168	Fxy	Pxys	53	189	Fxy	Pybin	Pzole	117	252
MP18	10/19/2017	133	-	-	Fxy	Pxys	53	-	Fxy	Pybin	Pzole	117	245
OK14	10/22/2013	100	155	155	Pzole	-	63	168	Azbin	Pzole	-	101	234
OK15	10/21/2014	85	143	143	Pzole	-	63	171	Pybin	Mzole	-	69	227
OK16	10/20/2015	-	136	136	Pzole	-	63	171	Pxys	Czole	-	70	234
OK17	10/21/2016	-	133	133	Pzole	-	63	167	Fxy	Pybin	Pzole	168	227
OK18	10/30/2017	-	133	133	Pzole	-	63	169	Pxys	Czole	-	70	219
OK19	11/6/2018	101	154	112	Pzole	-	63	171	Fxy	Pybin	Pzole	168	219
OK21	10/23/2020	126	152	152	Pzole	-	64	171	Fxy	Pybin	Pzole	170	238

CS17	11/3/2016	-	99	99	Pzole	-	63	148	Azbin	Pzole	-	101	180
TH18	11/7/2017	-	101	115	Pzole	-	63	146	Azbin	Pzole	-	101	191

Appendix Table E.2. Cultivars tested in at least 16 location-seasons, their maturity score, deviation from mean anthesis date, their yield phenotypic plasticity and stripe rust resistance phenotypes. Abbreviations: resistant (Res), intermediate (Int), susceptible (Sus).

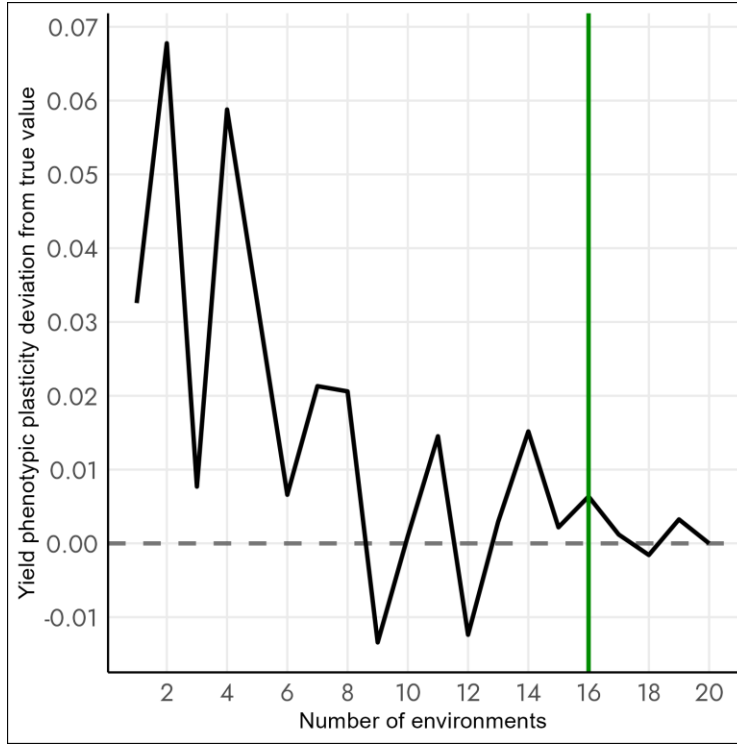
Cultivar	Maturity Score	Deviation from mean anthesis date (days)	Yield phenotypic plasticity	Stripe rust resistance
T158	3	-3	1.02	Res
WB4303	3	-3	1.46	Sus/Int
Bentley	4	-1	0.99	Sus/Int
SY Flint	4	-1	1.13	Int
WB4458	4	-1	1.15	-
Zenda	4	-1	1.08	Res/Int
Gallagher	5	1	1.26	Res
Larry	5	1	0.87	Res/Int
LCS Pistol	5	1	0.72	Sus
SY Grit	5	1	1.15	Sus/Int
WB Grainfield	5	1	0.86	Int
Doublestop CL Plus	7	5	0.42	Res/Int
LCS Mint	7	5	1.01	Int
LCS Chrome	8	7	0.78	Res/Int

Appendix Table E.3. Priors, their distribution and hyperparameters used in models implemented. Abbreviations: φ (truncated normal distribution, first moment is the mean , second the standard deviation and third the upper bound which is equivalent to 12,900 kg ha⁻¹); Γ (Gamma distribution, first moment is the shape and second moment is the scale parameter; U(uniform distribution, first moment is the lower bound and second moment is the upper bound, both moment have percentage, %, units); N(normal distribution, first moment is the mean and second moment is the standard deviation).

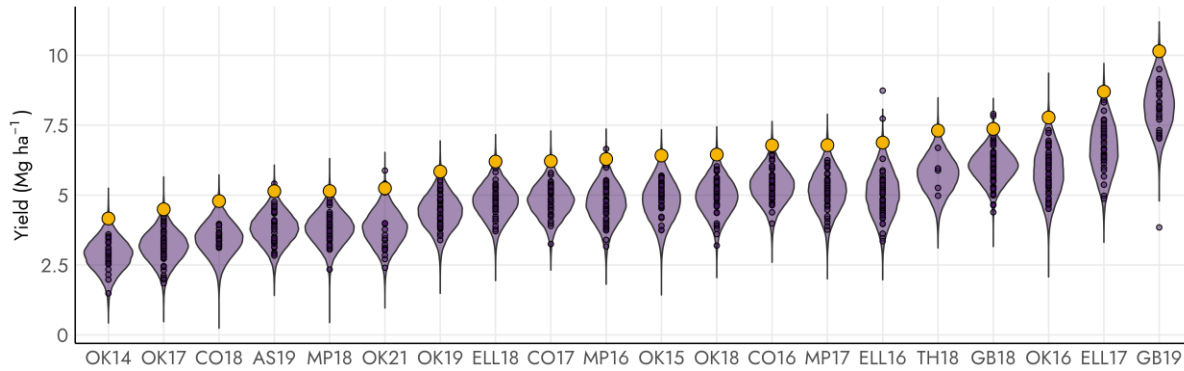
Equation in manuscript	Model parameter	Distribution and hyperparameters
Eq. 1, Eq. 2	β_{0jk}	$\varphi(0, 1000, 12900)$
	β_{1jk}	
	ϕ	
Eq. 3	α_0	$U(-100, 100)$
	α_1	$N(0, 25)$
	α_2	$U(0, 12900)$
Eq. 8	μ_{jkl}	$\varphi(0, 1000, ub = 12900)$
Eq. 10	ϕ_1	$N(0, 25)$
	θ_{0k}	
	θ_{1k}	
	θ_{2k}	
	θ_{3k}	

Appendix Table E.4. Summary of weather conditions during experiments carried out in 21 location-years in Central Great Plains between 2014 and 2021. Plant available water at sowing (PAWS), was estimated using a crop simulation model calibrated for the region (Lollato et al., 2017).

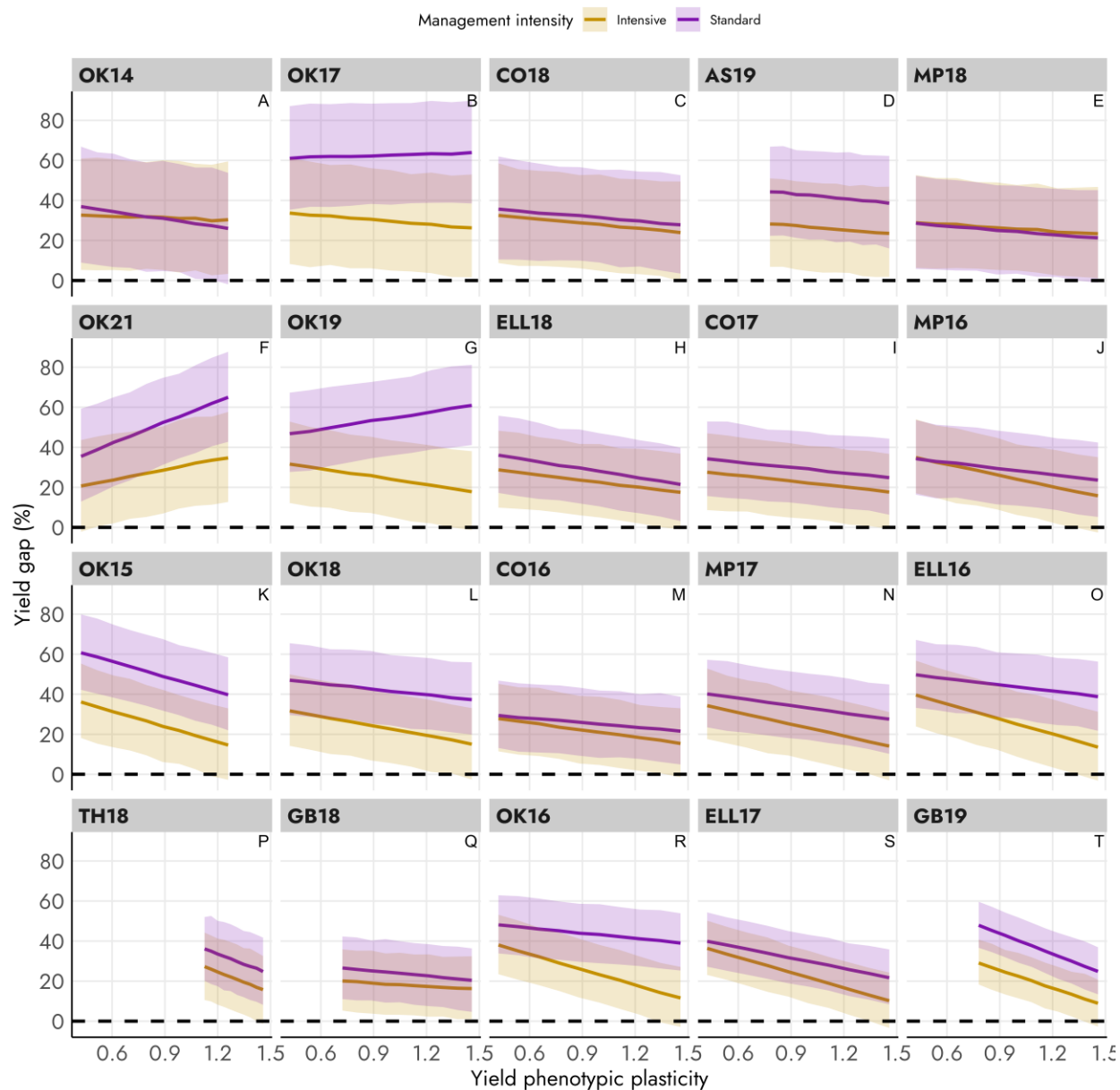
Period	Environmental Variable	Minimum	Average	Maximum
Critical period for yield determination (-300°Cd before until 100°Cd after anthesis)	Precipitation (mm)	51	126	278
	Mean temperature (°C)	10.4	14.6	19.8
	Duration (d)	25	37	47
	Photothermal quotient (MJ °Cd ⁻¹)	1.1	1.7	2.1
	Vapor pressure deficit (Pa)	378.7	910.1	1535.2
Grain filling period (100°Cd after until 600°Cd after anthesis)	Precipitation (mm)	50	161	515
	Mean temperature (°C)	16.3	19.8	24
	Duration (day)	25	33	40
	Photothermal quotient (MJ °Cd ⁻¹)	0.8	1	1.3
	Vapor pressure deficit (Pa)	984.5	1502.9	1931.4
Between GS 25 and GS 31	Days with rainfall	1	6	18
	Precipitation (mm)	4	41	88
	Days with temperature between 7°C and 12°C	6	12	21
Sowing	Plant available water (mm)	73	162	219
Seasonal	Cumulative solar radiation (unit)	2284	3245	4023.4
	Mean temperature (°C)	7.1	10.6	16.8
	Water supply + PAWS (mm)	302	639	940



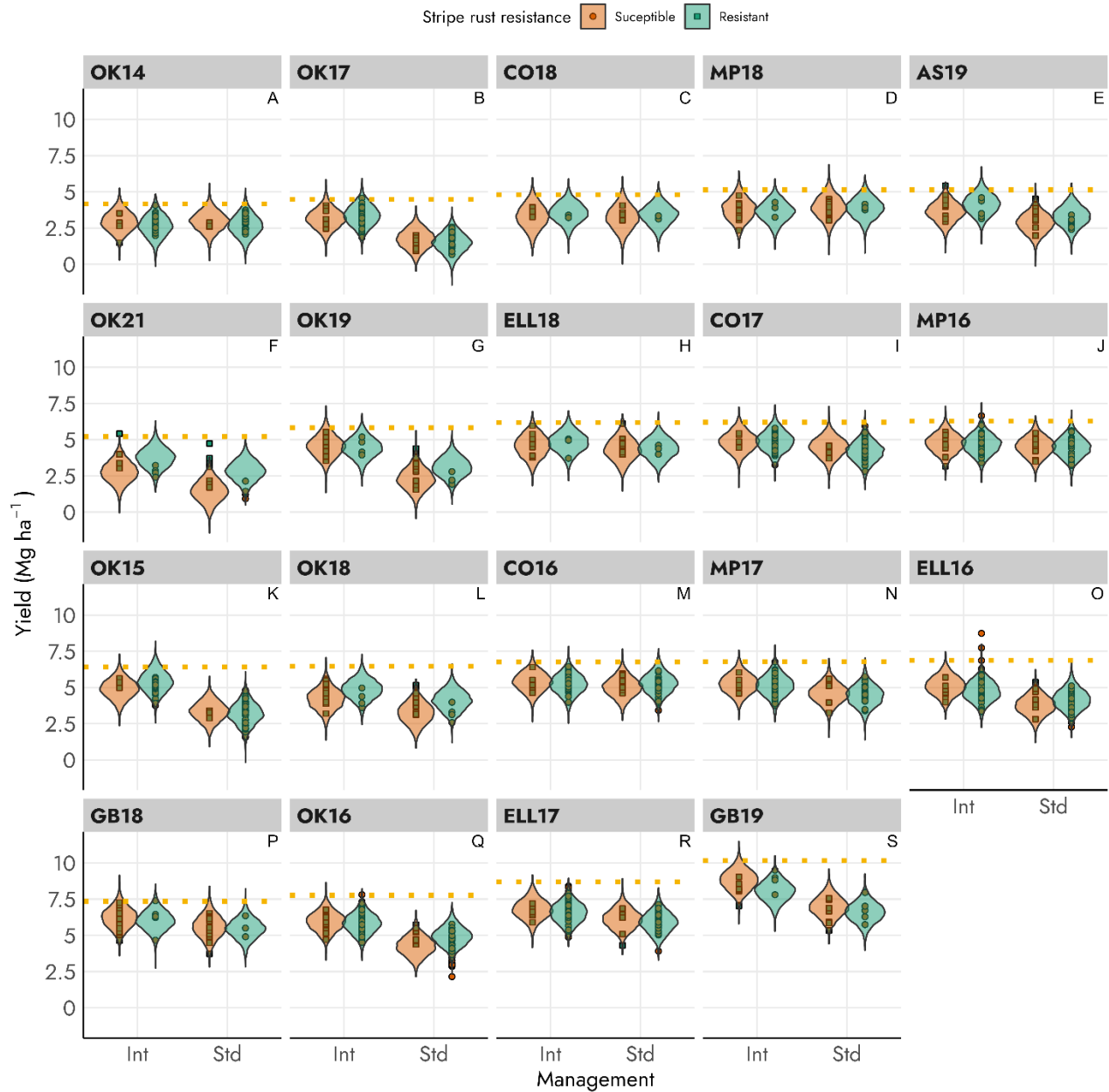
Appendix Figure E.1. Permutation test to determine the minimum number of environments (n) needed to obtain reliable estimate of yield phenotypic plasticity. For a set of cultivars replicated in at least 16 environments, we calculate the deviation from the value of plasticity obtained when $n=20$ against the value of yield phenotypic plasticity at each ‘ n ’ interval. The green vertical line represents the minimum number of environments for each cultivar to be included in the analysis.



Appendix Figure E.2. Purple violins show the posterior predictive distribution of grain yield ($\mu_{ij1}|\mathbf{y}$) in each of the 20 environments included in the analysis under the intensive management treatment. Yellow points represent the estimated water-limited yield potential, $\mathbf{Yw}_j$, which is equal to $\mathbf{Q}_{0.99}(\mu_{ij1}|\mathbf{y})$ (Eq. 4). Black points represent the observed grain yield in each environment under intensive management.



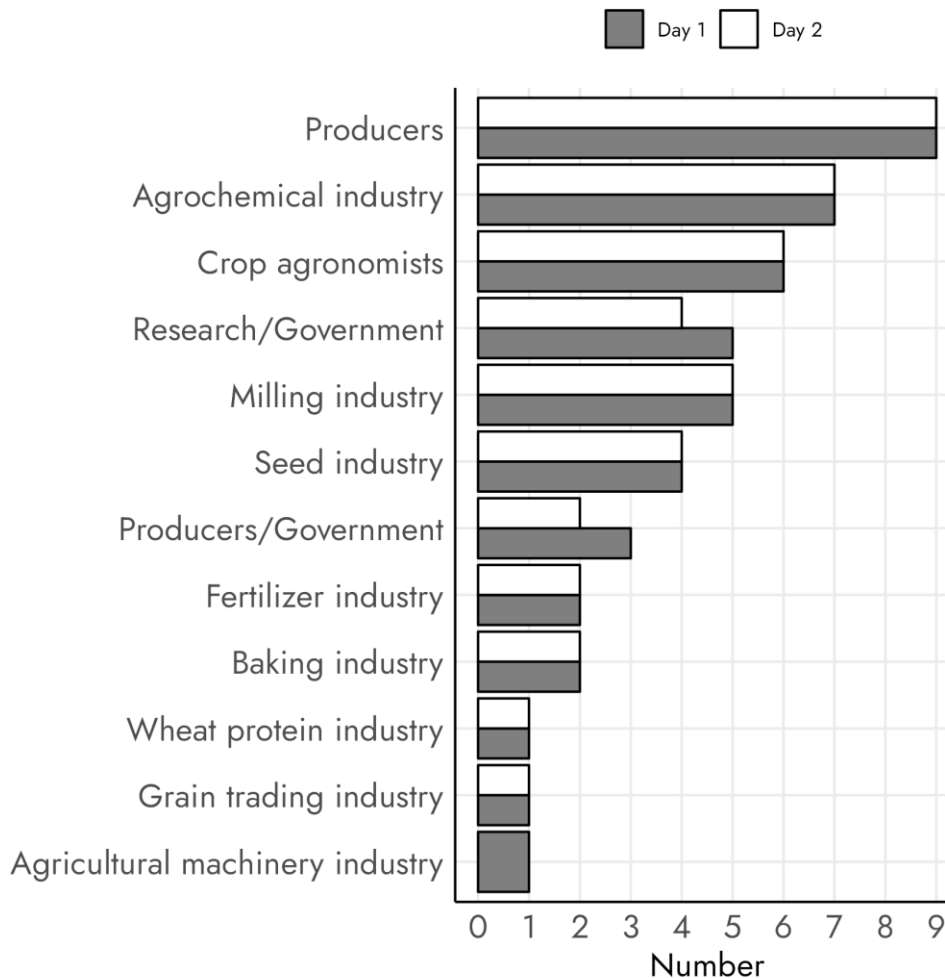
Appendix Figure E.3. Relationship between **Yg** and yield phenotypic plasticity for winter wheat grown in 20 location-seasons in the Great Plains under intensive (yellow) and standard (purple) management intensity. Solid lines represent the mean and ribbons the 95% credible interval of the posterior predictive distribution of **Yg**. **Yg** is calculated as the quotient between $Y_a - Y_w$ and Y_w times 100 and its expressed in percentage (%) units. Panels are ordered from top left to bottom right according to **Yw** of the environment.



Appendix Figure E.4. Grain yield as affected by management intensity (Int: intensive, Std: standard) for cultivars differing on their resistance to stripe rust (orange: susceptible, green: resistant) at 19 environments. Dashed lines represent the estimated water-limited yield potential (Y_w , Eq. 4). Points represent observed grain yield y_{ijk} while density distributions around them are the posterior predictive distribution of grain yield. Details of this analysis are presented in section 5.2.3. Panels are ordered from top left to bottom right according to Y_w .

Appendix F - Chapter 6 Supplementary Material

Supplementary Figures



Appendix Figure F.1. Distribution of participants of the expert elicitation according to their associated sector in the wheat industry network. Grey bars represent the number of participants during day 1, where participants were divided by sectors, while white bars are the number of participants during day 2 when participants from different sectors were in the same group.

Appendix Table F.1. Participating companies in the workshop represented the wheat industry. The `group assigned in workshop` column represents how participants were sorted during day 1, based on their expertise and focus of the company they were representing.

Company/Institution	Number of participants	Footprint	Focus of the company	Group assigned in workshop
ADM Milling	2	Global	Wheat milling	Milling and baking
BASF	2	Global	Agrochemical/Seed industry	Input supply
Bay State Milling Company	1	Regional - US and Canada	Wheat milling	Milling and baking
Bayer Crop Science	2	Global	Agrochemical/Seed industry	Agronomy
Farm Strategy	2	Regional - Great Plains	Agronomic advisory services	Growers, milling and baking
FMC	1	Global	Fertilizer industry	Input supply
Grain Craft	1	Regional - US	Wheat Milling	Milling and baking
Grupo Bimbo	2	Global	Baking industry	Milling and baking
Heartland Plant Innovations	1	Regional - Great Plains	R & D	Breeding
Helena Agri Enterprises	1	Regional - US	Fertilizer industry	Input supply
John Deere	1	Global	Agricultural machinery	Agronomy
Kansas Farm Bureau	2	Regional - Great Plains	Policy	Consumer, producers
Kansas State University Agronomy	1	Regional - Great Plains	Crop modeling	Breeding
Kansas State University Wheat Breeding	1	Regional - Great Plains	R&D, seed industry	Breeding
Kansas Wheat Alliance	1	Regional - Great Plains	Seed industry	Breeding
Kansas Wheat Commission	1	Regional - Great Plains	Policy, R&D	Producers
Kansas Wheat Commission/Farm Owner	1	Regional - Great Plains	Policy	Producers
Knopf Farms Inc.	1	Local - Central Kansas	Wheat production, policy	Producers
Koch Agronomic Services	1	Regional - US and Canada	Fertilizer industry	Input supply
Louis Dreyfus Company	1	Global	Grain trading	Consumer
Oklahoma Genetics Inc.	1	Regional - Great Plains	Seed industry	Breeding
Oklahoma State University	1	Regional - Great Plains	R & D	Agronomy
Peterson Sustainability	1	Global	Sustainability assessments	Agronomy
Pivot Bio	2	Regional - US	Agrochemical/Seed industry	Agronomy, input supply
PureField Ingredients	1	Regional - Great Plains	Wheat protein manufacturing	Milling and baking

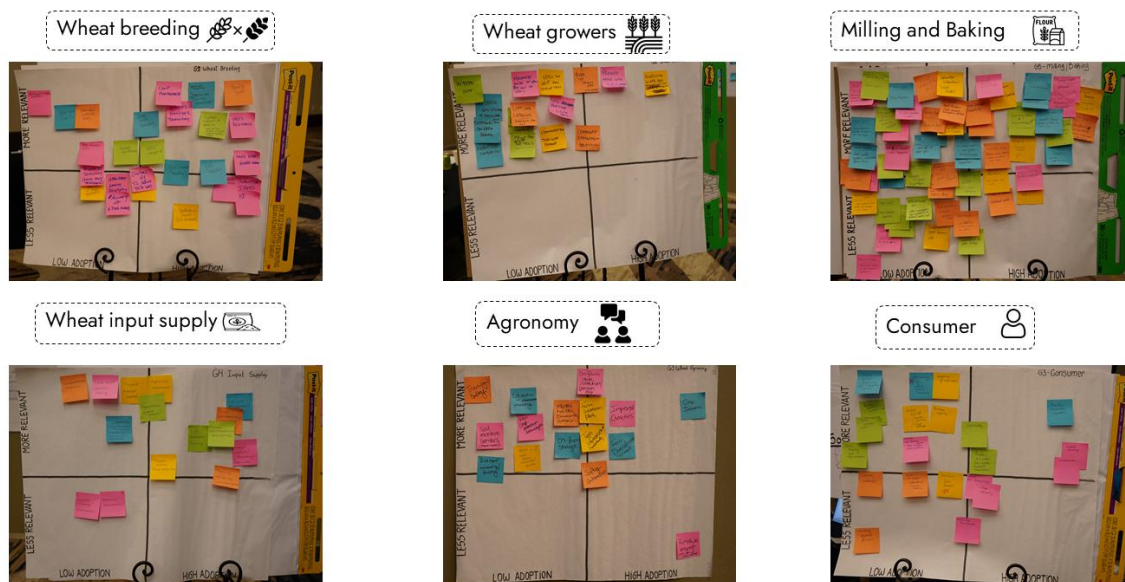
ServiTech, Inc.	1	Regional - Great Plains	Agronomic advisory services	Consumer
Sidwell Enterprises	1	Regional - Great Plains	Agronomic advisory services	Consumer
State Line Growers	1	Regional - Great Plains	Agronomic advisory services	Producers
Suppes Farm	1	Local - Western Kansas	Wheat production	Producers
Syngenta AgriPro	2	Regional - Great Plains	Seed industry	Breeding, agronomy
Tanner Farm	1	Local - ? Kansas	Wheat production	Producers
The Mosaic Company	1	Global	Fertilizer industry	Input supply
Turek Farms	1	Local - ? Kansas	Wheat production	Producers
University of Nebraska-Lincoln	1	Regional - Great Plains	R & D	Breeding
USDA-ARS	2	Regional - US	R & D	Breeding, milling and baking
VariMax	1	Regional - US	Precision agriculture	Consumer
Winfield United	1	Regional - US	Agrochemical industry	Input supply



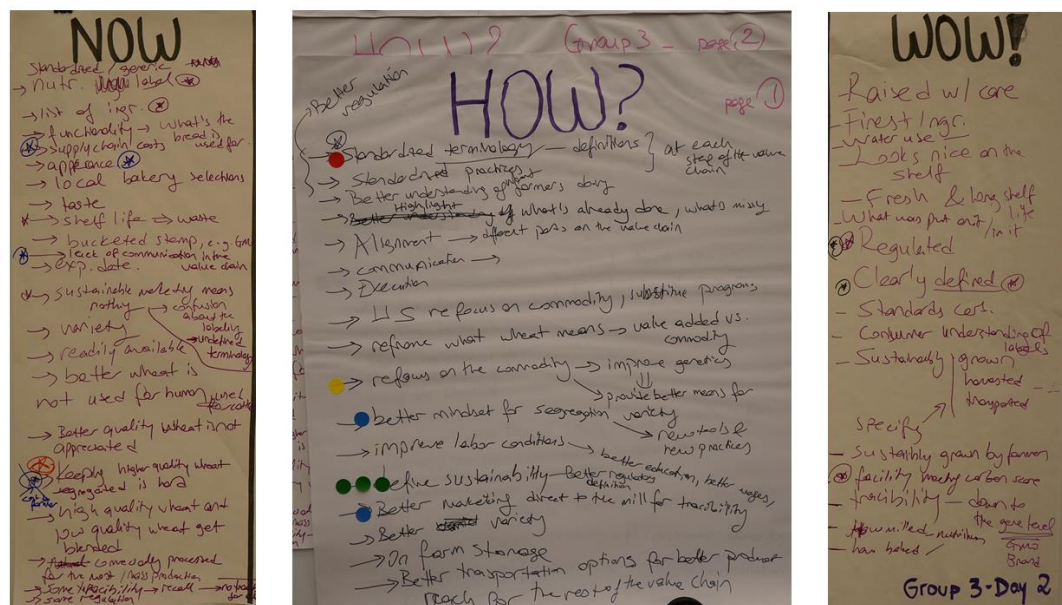
Appendix Figure F.2. Photos of group discussions during first day of expert elicitation workshop. Participants were sorted in six different sectors representing the wheat industry. In each table, one facilitator guided the group discussion and helped participants to complete the activities, two scribes created a written record of group discussions.

Economic Sustainability Indicators Comparisons										
A <u>risk management</u>	Total A	A	A	A	A	A	A	A	A	A
		B	C	D	E	F	G	H	I	J
B <u>farm unit economy</u>	Total B	B	B	B	B	B	B	B	B	B
		C	D	E	F	G	H	I	J	K
C <u>reliable markets</u>	Total C	C	C	C	C	C	C	C	C	C
		D	E	F	G	H	I	J	K	
D <u>investment in research</u>	Total D	D	D	D	D	D	D	D	D	
		E	F	G	H	I	J	K		
E <u>infrastructure</u>	Total E	E	E	E	E	E	E	E		
		F	G	H	I	J	K			
F <u>input cost</u>	Total F	F	F	F	F	F				
		G	H	I	J	K				
G <u>farm income</u>	Total G	G	G	G	G					
		H	I	J	K					
H <u>available finance</u>	Total H	H	H	H						
		I	J	K						
I <u>labor availability</u>	Total I	I	I							
		J	K							
J <u>succession planning</u>	Total J	J								
		K								
K <u>digital technology access</u>	Total K									

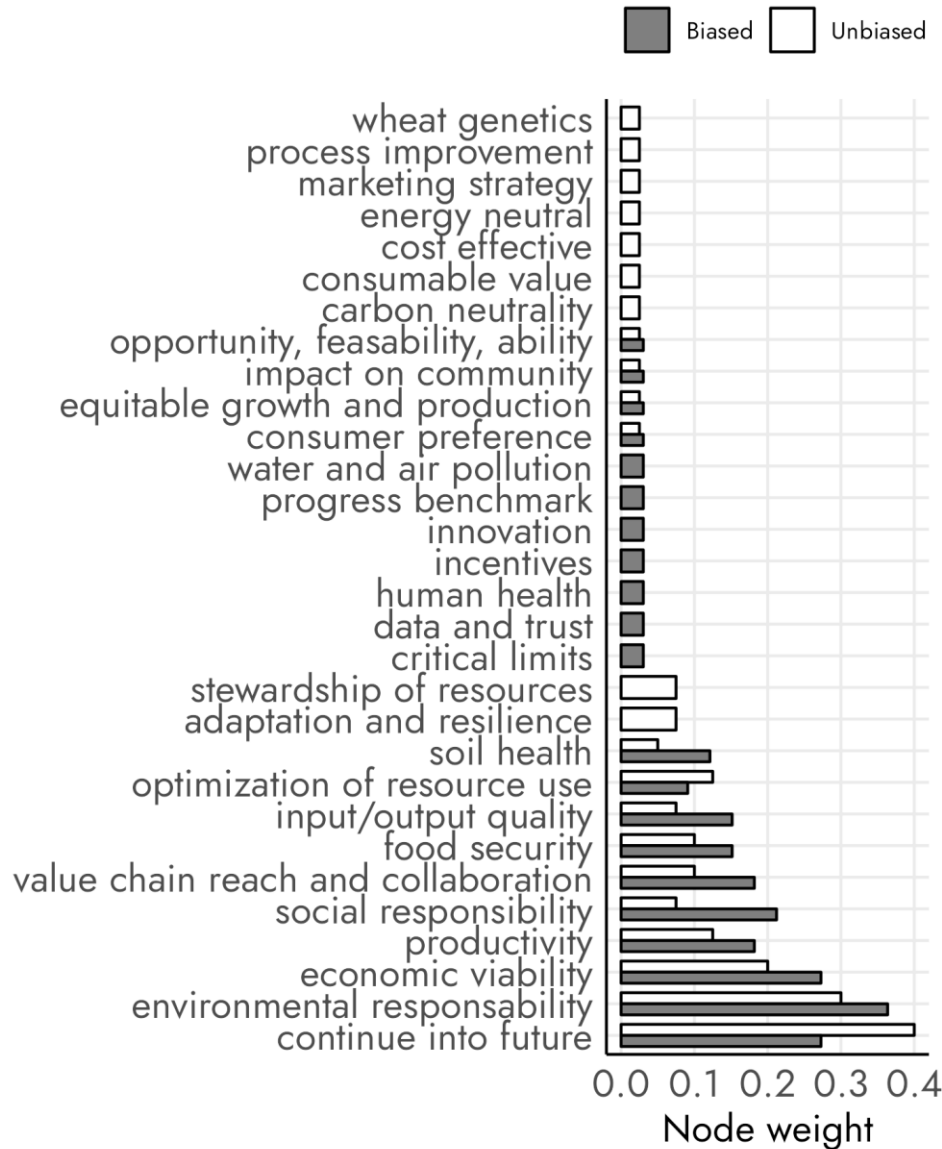
Appendix Figure F.3. An example of paired comparisons matrix used to rank sustainability indicators in each domain. This example corresponds to sustainability indicators proposed within the “Economic” dimension by the “Wheat breeding” group. If a participant ranked higher “risk management” compared to “farm unit economy” then option “A” would be circled in the A/B cell in the top left of the matrix.



Appendix Figure F.4. Photos of quadrants used to classify technologies and practices according to their relevance to sustainability and their current level of adoption in the wheat industry. Each quadrant corresponds to one group discussion, where participants were sorted in six different sectors representing the wheat industry. In each table, one facilitator guided the group discussion and helped participants to complete the activities, two scribes created a written record of group discussions.



Appendix Figure F.5. Raw output created by participants to summarize collaboration strategies towards a unified sustainability stamp on a loaf of bread. The “now-how-wow” method was deployed during discussion in the second day of the expert elicitation, when participants were sorted so that each group-table had representatives from the entire wheat value chain.



Appendix Figure F.6. Node weight for each of the concepts extracted from the open-ended answers to the question: “*what does sustainability mean to you?*”. Unbiased answers were written before the start of discussion sessions, while biased answers were written after two days of discussions among wheat industry stakeholders.

Appendix Table F.2. Written sustainability by participants upon arrival to expert elicitation, before starting discussions. Two independent coders extracted concepts from definitions, and only matching concepts between coders were retained.

Group-table	Participant code	Definition	Concept 1	Concept 2	Concept 3	Concept 4	Concept 5
Breeding	B1	Ability to make continental improvement in wheat genetics while not outstripping our environmental limitations (<i>e.g.</i> , soil fertility water etc.).	wheat genetics	environmental responsibility			
	B3	equivalent to durability. Optimization of resource use to sustain production and the environment (soil/water/air/people) that supports it.	optimization of resource use	environmental responsibility	productivity		
	B4	the ability to produce a safe, affordable food supply to feed the world with economic benefit throughout the supply chain.	food security	economic viability			
	B5	growing up on a farm. Sustainability to me means passing the farm to the next generation in as good or better shape than what it was to begin with. Economically, environmentally, impact on the community, etc. This can be applied to any sector. Leaving it better than what it was to begin with.	economic viability	environmental responsibility		continue into future	impact on community

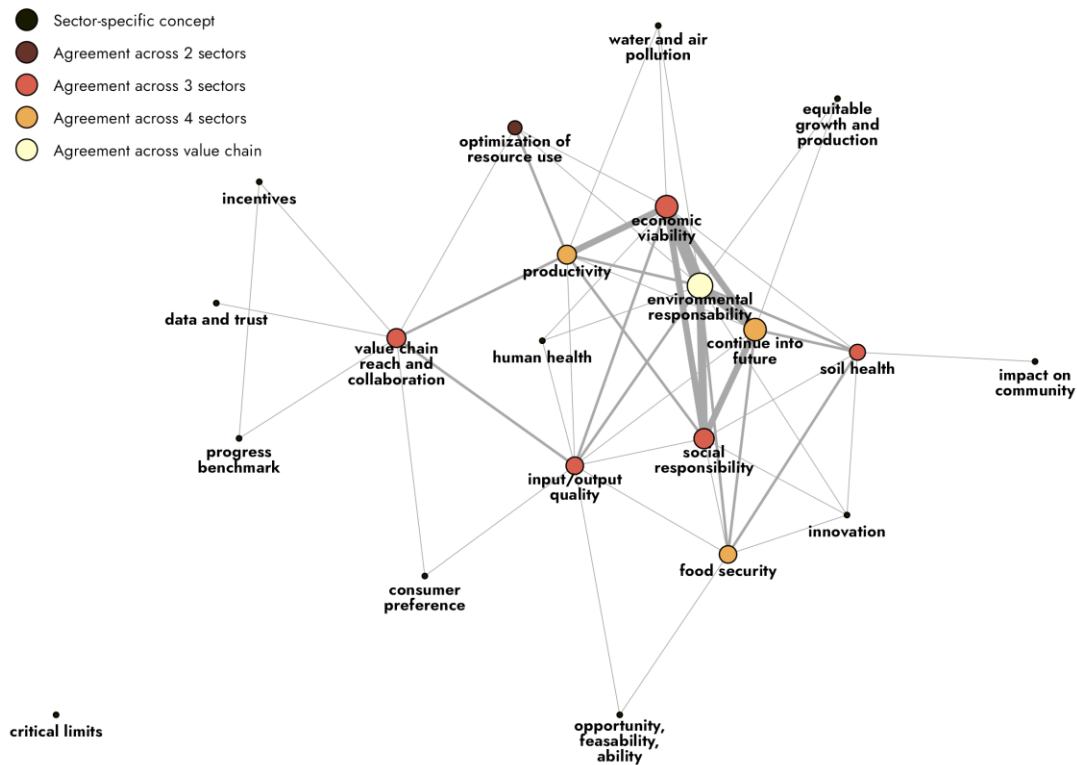
	B7	Has some desirable and measurable property that is more constant in time than the environment in which the object is built, used or "exported". All models are wrong, but some are useful. I go through life making things that are wrong out of the gate. "Sustainable" means to me something that, for whatever reason, is useful longer.	continue into future				
Consumer	C1	Carbon neutrality throughout the wheat supply chain.	carbon neutrality	environmental responsibility			
	C2	Maximizing output through minimizing inputs towards the end goal of creating a product that can continue to be produced with those same sustained inputs into perpetuity.	optimization of resource use	continue into future			
	C3	The ability to produce and function today without denying myself or others the ability to do the same .		social responsibility			
	C4	Asset I can use to sell grains to costumers. Ability to supply other costumers.	opportunity, feasibility, ability				
	C6	Ability to bring together a set of valued data points to achieve a desired out-come that brings a consumable value.	consumable value				

	C7	Marketing strategy that accounts for all segments of the production marketing chain.	marketing strategy	value chain reach and collaboration			
	C8	Sustainability means equitable growth and production in a way that we can provide for future generations years to come.	equitable growth and production	continue into future			
Input supply	I1	Sustainability would be the efficient use of resources in the production of products, and the distribution of products.	optimization of resource use				
	I2	It means to me that you don't want to deplete the resources you have but use them wisely and effectively.	optimization of resource use				
	I3	Being efficient with our inputs to deliver highest quality.	optimization of resource use	input/output quality			
	I4	The ability to persist in a cost effective and socioeconomically responsible way.	economic viability	social responsibility		cost effective	continue into future
	I6	The ability to produce crops in a manner that promotes economic, environmental and social excellence throughout the chain from the product production to the end product for costumers.	economic viability	social responsibility		environmental responsibility	value chain reach and collaboration
Milling and baking	M1	A resilient approach and perspective that aligns vision across the value chain participants for the outcome					adaptation and resilience

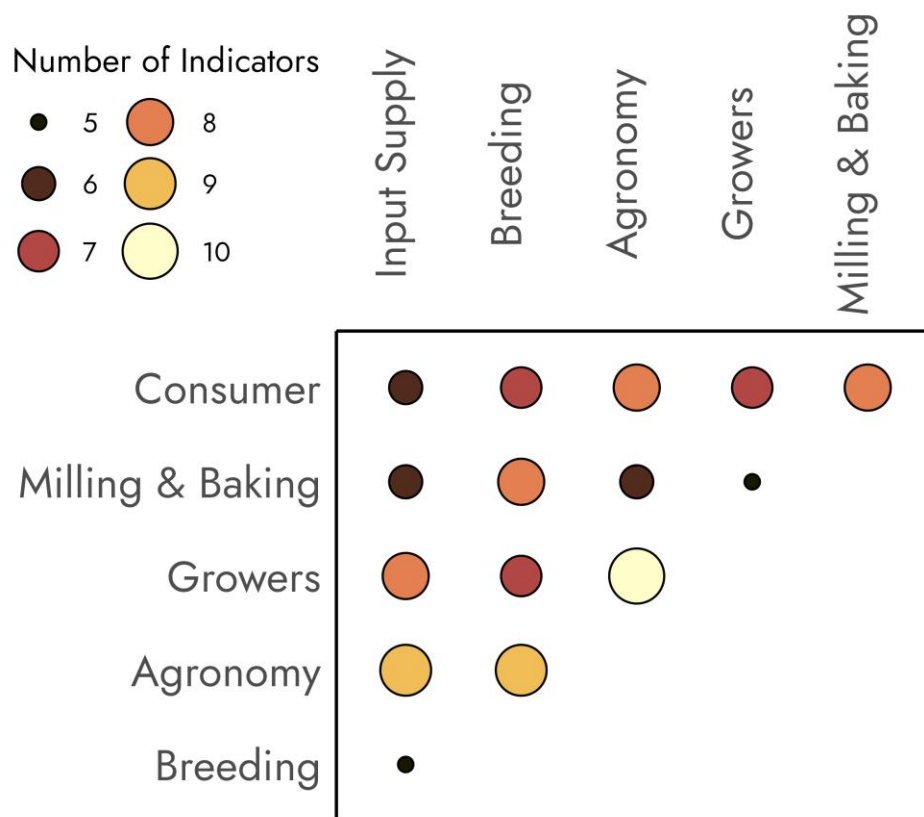
		of human goodness and thriving.					
	M2	Sustainability is about guaranteeing food security for all people globally. Protect the planet and supply chain.				food security	
	M3	Continuing to source wheat that has the right quality parameters (protein, rheological properties) and yield, with disease resistant properties for years to come that will adapt to its changing climate and environment to feed the growing population.	continue into future	input/output quality	food security	productivity	adaptation and resilience
	M4	Sustainability is the improvement of the entire process from growing to processing products. Each part of the industry is at different starting points so decelerating the progress as the biggest challenge.	process improvement	value chain reach and collaboration			
	M6	To continue to be able to provide the consumer with a safe and cost-effective food system. All members of the chain works together to provide.	continue into future	food security		value chain reach and collaboration	
	M8	Being a good steward of the resources and considering the generational impacts of one's activities.	stewardship of resources	continue into future			

Growers	P1	Staying in business while not only maintaining the land but also improving it, leaving it better than it was when we received it	continue into future				
	P2	The opposite of unsustainable. It means a system that will adapt and survive through struggle.	adaptation and resilience				
	P3	Producing a product in a way that is continuously repeatable while being energy and environmentally neutral.	energy neutral	environmental responsibility		continue into future	
	P4	Responsible production of a product or outcome that respects the environment and society facilitating sustained production while limiting negative effects		environmental responsibility		continue into future	
	P5	The ability to maintain a successful operation over an extended period of time.	continue into future				
	P6	Continued access to healthy resources (natural, economic, human) necessary for success across time.	continue into future			stewardship of resources	
	P7	The ability to raise a crop that is profitable without depleting the soils.	economic viability	soil health		productivity	
	P8	1: Profitability-operation must be profitable to continue on. 2: maintain/enhance natural resources for the future.	economic viability	stewardship of resources		continue into future	

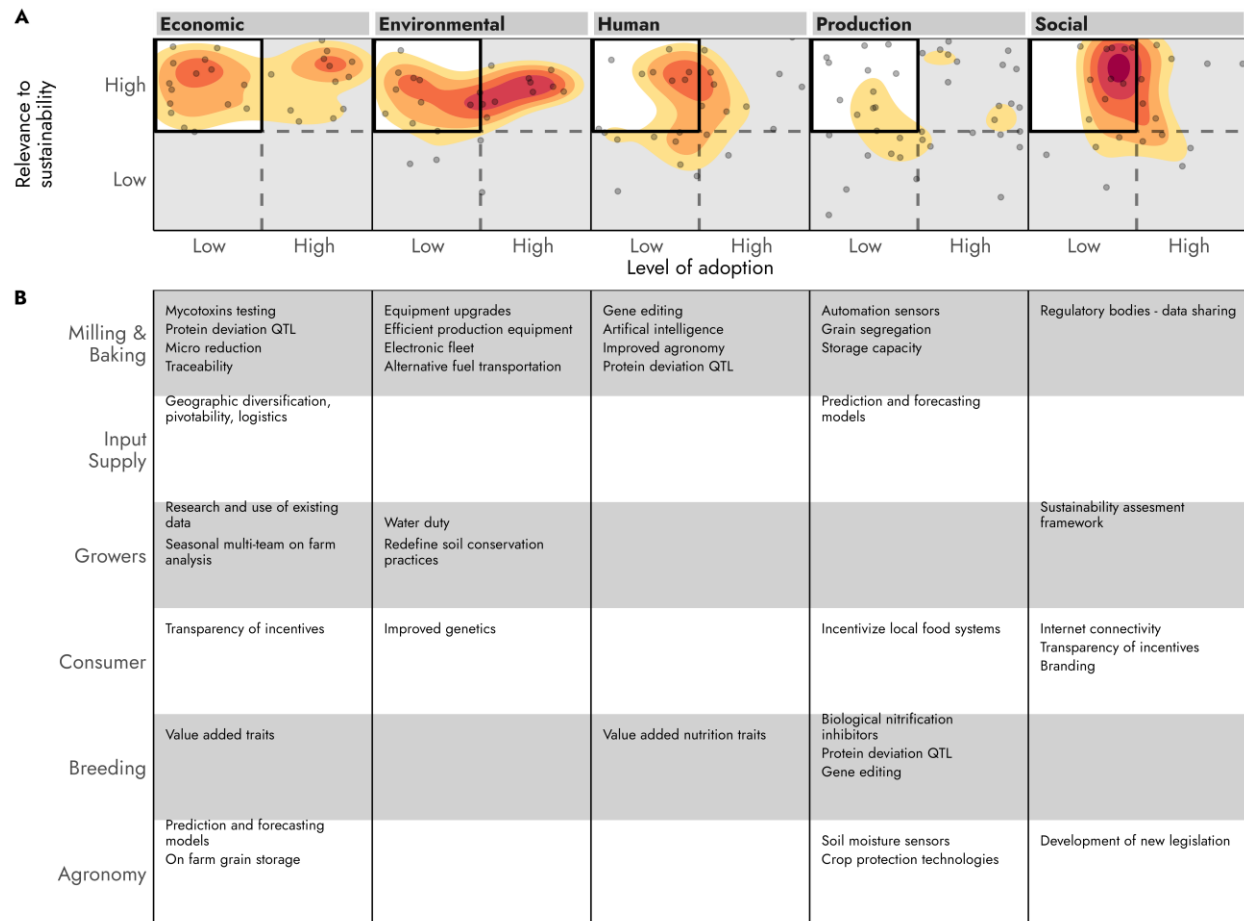
		Conservation is not preservation.					
Agronomy	A4	Ability to maintain production while responsibly using resources, both improving and protecting the environment	productivity	continue into future		environmental responsibility	
	A5	The ability to continue practicing an activity. This could be environmental or economical in basis.	continue into future	economic viability		environmental responsibility	
	A7	Ability to produce food fuel and fiber in environmentally sound and economically positive manner	economic viability	environmental responsibility		productivity	
	A8	Consumer confidence that food is produced with lowest environmental impact	environmental responsibility	consumer preference			



Appendix Figure F.7. Network reflecting common and unique elements in the definitions of sustainability across stakeholders in the wheat network industry. Definitions were given at the end of the 2-day expert elicitation workshop. Node sizes are relative to the number of times a concept appeared while tie weights are relative to the number of times two concepts appeared together in a definition. Colors indicate the number of sector where the same concept appeared, a sector was counted if at least one participant included the concept within the definition. Agreement across sectors (yellow) was assumed when the concept was included in at least five or six industry sectors. Sectors are: i) wheat breeding, ii) wheat agronomy, iii) input supply, iv) wheat growers, v) milling and baking industries and vi) retail and consumers.



Appendix Figure F.8. Number of common sustainability indicators for each sector combination across the wheat industry network. In B, colors are relative to the number of indicators.



Appendix Figure F.9. A) Classification of technologies and practices in quadrants according to their level of adoption and their relevance to sustainability in the five sustainability dimensions. B) Description of technologies and practices present in the top right quadrant: high relevance – low adoption, for each sector x dimension combination.

Guide for structured discussions during the two-day expert elicitation workshop

Day 1

What does sustainability mean to you?

Facilitator's will bring this up to the group.

To be done within initial presentation, before introductive talk to sustainability frameworks.

Participant completes card.

Overview of the sessions and shared expectations (9 – 9.15).

Main facilitator will outline the activities.

Shared expectations. Complete individual Best-Worst Scenario cards. Main facilitator guides, and facilitators help writing for the whole group.

- Facilitator 1 and Facilitator 2 volunteered to be writing

Small group introductions (9.15-9.30).

Main facilitator will give instructions to the entire group (1 min).

Facilitators provide the participants with a card each.

Each participant will design a card that represents you

Design cards (5 min). Participants work independently.

Share cards (9 min). Participants introduce themselves to the group (~1 min each).

Identify sustainability indicators for each domain (9:30 – 10:30).

Materials: Color post-it notes, domains placemats, flip charts, sticky dots.

Objective: Get the group thinking about sustainability indicators and metrics.

Actions:

Are there any questions on how domains are defined? (5-10 min max) where participants can ask questions about the different domains; if no questions, move straight to activity.

Activity will be performed by domain in the order:

- productivity (pink),
- economics (blue),
- environmental (green),
- human (brown) and
- social (yellow)

Within each domain:

- 5 min for individual writing of sustainability indicators
 - o They should write on the placement directly as well as on post-it notes.
- 10 min for discussion on sustainability indicators
 - o Facilitator will need five easel pads (one per domain).
 - o Facilitator will be posting the post it notes on the easel pad.
 - o If a given response comes from more than one participant, stick it on top of each other.

Questions:

- Can you say more about this indicator?
- What do others think?
- Is this discussion raising questions to anyone else?
- What about those people who haven't spoken so far?
- Are those two indicators associated? How?
- How frequently you think about that indicator when you make decisions?

- If needed (e.g., stalled discussion), facilitators can use the pre-populated list of indicators to foment discussion.

Make sure you cover at least 2, preferably 3, domains before the break.

Give sticky dots to the participants just before the break. Let them vote in the top three most important indicators prior to the break.

BREAK (10:30 – 11:00)

Continued. Identify sustainability indicators for each domain.

Materials: Color post-it notes, domains placemats, flip charts, sticky dots.

Objective: Get the group thinking about sustainability indicators and metrics.

Actions:

By domain (order: productivity, economics, environmental, human and social):

- 5 min for individual writing of sustainability indicators on post it notes.
- 10 min for discussion on sustainability indicators.

Each participant gets three sticky dots and place them in the indicator top three indicators they consider more relevant in order of importance following colors of dots.

Questions:

- Use the pre-populated list of indicators in case needed.
- Can you say more about that?
- What do others think?
- Is this discussion raising questions to anyone else?
- What about those people who haven't spoken so far?
- Are those two indicators associated? How?
- How frequently you think about that indicator when you make decisions?

Scribers

- Fulfill the excel sheet with the indicators that came up in the discussion
- Make sure that each indicator is listed under its own domain
- Let Facilitator 3 know that the excel sheet is ready to print

LUNCH (12:00 – 1:00) – print pair comparison sheets with indicators per sector.

Rank indicators by importance (1:00 – 2:00)

Materials: paired comparisons sheets.

Objective: rank indicators by importance. Compare indicators against the others using the paired comparisons tool.

Actions:

Help participants complete the paired comparisons.

Participants sum each total for each indicator and report the value to the group.

Remember them to sum up and across.

One scribe takes the summation of votes and the other records totals in the correspondent worksheet.

The ranking activity should take about 30 min.

The remaining 30 minutes should be used for discussion.

Questions:

- Do these rankings make sense?
- What is emerging here?
- Maybe the most and least important will come up clearly; however, it is important to foment discussion on those that were very important to a few participants but not important to others. Scribes would take notes on these discussions.

Identify technologies and practices (2:00 – 2:30)

Materials: colored Post-it notes, timer.

Objective: Identify technologies and practices relevant to the top-3 most relevant sustainability indicators.

Actions:

- 20 min - By domain, select the three most important indicators from the previous ranking activity.
- Each participant will be asked to think through each indicator and write on individual Post-it notes any technologies or practices that can improve that indicator. Ask them to write on the sticky note the indicator and the technology/practice.

1-minute per indicator (use a timer).

- 10 min – Indicator by indicator, go around the group. Each participant shares one tool/practice Post-it notes, placing it with the indicator. Continue going around the group
 - o Ask them to group technologies spreading sticky notes on the table

Questions:

- Use pre-populated technologies list in case needed.

Categorize technologies and practices according to degree of adoption (2:30-3:00)

Materials: colored Post-it notes, flip chart with quadrants.

Objective: categorize the technologies according to degree of adoption and their relevance to overall sustainability. *As an example: most relevant technologies are the ones impacting more than one sustainability domains.*

Actions:

- 20 min - As a group using the technologies/practices pages, place technologies/practices (colored post it notes) on taped quadrants.
 - o Prioritize (less relevant more relevant) (~7min)
 - o Classify the according to degree of adoption. (~7min).
- 15 min – The spokesperson for each table shares the technologies and practices that are highly relevant but low adoption for each sector with the entire workshop.

How does the technology impact the other domains?

If participants come out with many technologies give some time to come to ask for a consensus.

MEETING ADJOURN. Students take picture of all artifacts and label appropriately.

Day 2

Introductions to new groups (8:00-8:15).

Value chain indicator voting (8:15-9:00).

Materials:

- PowerPoint slide with QR code to access the survey.

Objective:

- Determine associations of indicators within domains.
- Determine associations of indicators across domains.

Actions:

- Participants answer the questions individually.
- Play music.
- Help participants access the survey.

Collaborate across the supply chain (9:00-10:00).

Materials: Now-how-wow chart paper and individual placemats.

Objective:

With the indicators, technologies and practices we discussed yesterday. What would a loaf of bread on the shelf bearing a sustainability stamp would look like?

Actions:

- 20 min – each participant does the now-how-wow individually in their own placements.
- 20-min – WOW. Participants report on their wow. Facilitator promotes discussion and completes the WOW in the chart paper.
 - Facilitator comes up with discussion for consensus and write on ease pad.
- 20-min – NOW. Take a moment to think about where we are with each of these domains, indicators, practices and technologies right now. Facilitator guides discussion and completes the NOW in the chart paper.
 - Facilitator comes up with discussion for consensus and write on ease pad.

BREAK (10:00 – 10:15)

Reconvene on collaboration (10:15-11:00).

Materials: Now-how-wow chart paper and individual placemats.

Objective:

With the indicators, technologies and practices we discussed yesterday. What would a loaf of bread on the shelf bearing a sustainability stamp would look like?

Actions:

- 45 min – HOW. How do we get to the WOW?
 - Facilitator comes up with discussion for consensus and write on ease pad.
- Remember to select a spokes-person for next activity.

Questions:

- What needs to happen for this to make sense for everybody?
- What kind of data needs to be collected to come up with a stamp?
- Is data collection and input from specific fields a barrier? If so, how so (time to input it, data ownership *etc.*)?
- How could we streamline data transfer across the value chain maintaining data ownership?
- Do we need multiple software or could we do it in a single?
- Can this data be centralized with a company or institution and offer to sell to companies who then could claim sustainability?

- Or should we continue to have individual programs bombarding growers with different requirements?

Report out to the entire group (11:00-11:30).

Spokesperson reports out to entire group. Approximately 6 minutes per group.

Wrap up and ticket out (11:30-12:00).

Ticket out:

- 1) Fill definition of sustainability
- 2) Fill what you want from a knowledge graph
- 3) Sticky notes to vote on the best now-how-wow idea

LUNCH and ADJOURN