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

Nicolas Giordano [a,*,1], Victor O. Sadras [b,c,2], Romulo P. Lollato [a,*,3]

[a] Department of Agronomy, Kansas State University, 2004 Throckmorton Center, 1712 Claflin Rd., Manhattan, KS 66506, USA
[b] South Australian Research and Development Institute, Australia
[c] School of Agriculture, Food and Wine, The University of Adelaide, Australia

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ABSTRACT

Context: 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.

Objectives: 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.

Methods: 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 The search resulted in 38 articles that, in addition to one unpublished trial from our group, evaluated 542 pairwise comparisons in 127 environments.

Results: 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 consistently 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.

Conclusions: Enhancing GPC through late N applications should consider associations between management, environmental, and physiological factors.

Implications: Future research should focus on forecasting GPC response to late N, based on GPC response drivers identified in the current research.

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

* Corresponding authors.
E-mail addresses: ngiordano@ksu.edu (N. Giordano), lollato@ksu.edu (R.P. Lollato).
[1] ORCID: 0000–0003-0159–4958
[2] ORCID:0000–0002-5874–6775
[3] ORCID:0000–0001-8615–0074

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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 × 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.

2. Method

2.1. Database construction

We searched 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:

$$SOURCE-ID(78796 \quad OR \quad 59988 \quad OR \quad 38753 \quad OR \quad 15639) \quad AND$$

$$\text{TITLE}-\text{ABS}-\text{KEY}((\text{wheat OR nitrogen})\text{AND}(\text{yield OR protein}))\,AND \tag{1}$$

$$PUBYEAR \quad > \quad 1980$$

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 PUBYEAR 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 5734 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 Fig. 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 m^2 and either directly reported or reported in a manner that allowed trait calculation;
(iii) Data were from field studies without manipulation of atmospheric CO_2 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 (Fig. 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 treatment 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.

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 $N-NO_3$ available in the soil profile at sowing:

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

This approach does not consider N mineralised from soil organic

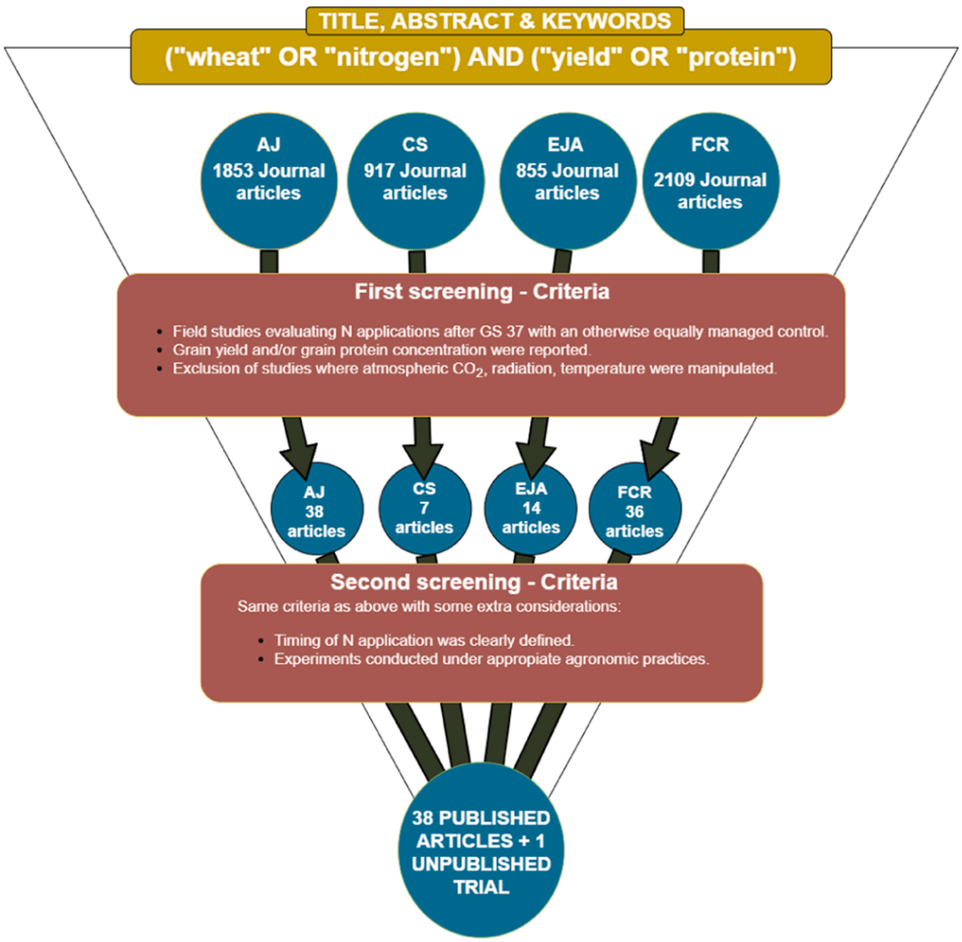


Fig. 1. Approach to screen articles from AJ (Agronomy Journal); CS (Crop Science); EJA (European Journal of Agronomy); and FCR (Field Crops Research).

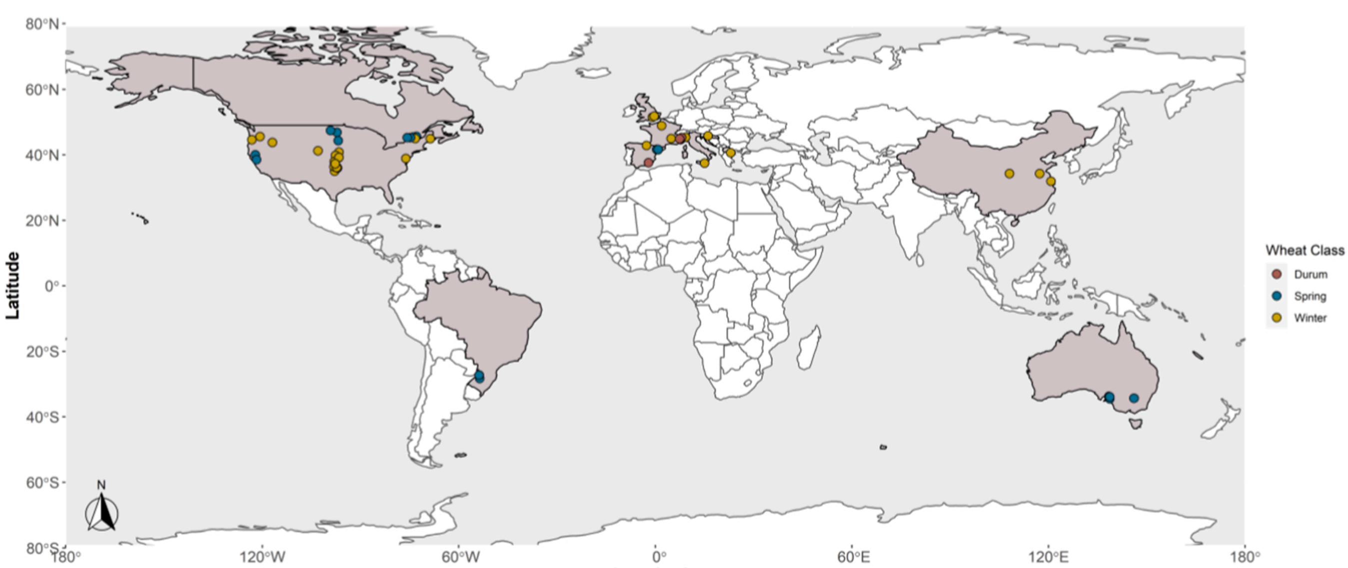


Fig. 2. Distribution of field trials evaluating wheat response to late-season N application in the current meta-analysis.

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 et al., 1974) 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).

2.3. Environment

Weather data were collected from studies that reported the geo-coordinates 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 $+100$ °Cd (°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 $+100$ °Cd to $+600$ °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 (Supplementary Figure 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., 2021). A single weather data source across worldwide experimental sites 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.

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 ($\%N_{UP}, Eq3$), stover N concentration ($\%N_S, Eq4$), and stover biomass ($S_B, Eq5$) as:

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

$$\%N_S = \frac{N_{UP}}{WP_B - YLD} \tag{4}$$

$$S_B = WP_B - YLD \tag{5}$$

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).

2.5. Dough rheological properties

A subset of studies ($n = 5$, 59 pairwise comparisons) allowed 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).

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 1000 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; Cook, 1979). 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.

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).

$$\mathrm{lnRR_i} = \ln\left\{\frac{\overline{X}_{\mathrm{Late}N}}{\overline{X}_{\mathrm{Basal}N}}\right\} \tag{6}$$

$$\text{Late N } Effect(\%) = \left\{\frac{\overline{X}_{\mathrm{Late}N}}{\overline{X}_{\mathrm{Basal}N}} - 1\right\} * 100 \tag{7}$$

Where $\overline{X}$ 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:

$$w_i = v_i^{-1} \tag{8}$$

$$v_i = \frac{SD_{LN}^2}{n_{LN}\overline{X_{LN}}} + \frac{SD_{BN}^2}{n_{BN}\overline{X_{BN}}} \tag{9}$$

where $\overline{X}$ 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 × environment × management interactions and variation between studies. Thus, the variance component was divided in three sources: (i) between studies, (ii) between environments, and (iii) genotype × management combination. The model was then expressed as:

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

where $\widehat{\theta_{ijk}}$ is the estimated effect on the kth genotype × management combination nested within the jth environment, in the ith study. β_0 is the intercept representing the overall population effect. The parameters $\zeta(1)\mathrm{i}$, $\zeta(2)\mathrm{ij}$, $\zeta(3)\mathrm{ijk}$ represent the between studies, environments, and genotype × 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).

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 multilevel 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).

Table 1

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

3. Results

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). 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 (Fig. 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 (Fig. 3A). Across all sources of variation, GPC decreased with increasing yield at the same rate for basal N and late N crops (Fig. 3B); analysis of residuals showed late N fertilisation increased GPC by 7 g kg^{-1} at a given yield (inset Fig. 3B).

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 (Fig. 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 % (Fig. 4). Grain protein concentration response to late N tended to be higher at greater yield levels ($p = 0.15, r = 0.19$) (Fig. 4, Supplementary Table 2), and was negatively correlated with GPC environment (defined by the GPC of the basal N crop; $p = 0.06$, $r = -0.43$) (Supplementary Table 1). However, there was substantial heterogeneity in the response ($I^2 = 84$ %), indicating a high inconsistency across studies, environments and genotype × management combinations ($p < 0.01$), warranting further exploration of the factors driving GPC response to late N fertiliser.

3.3. Fertiliser management affected GPC response

Grain protein concentration increased linearly with the proportion of late N (Fig. 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 (Fig. 5B). Likewise, analysis of residuals indicated that GPC response to late N was independent of fertiliser placement (Fig. 5C). Grain protein concentration response to late N did not vary with the source of fertiliser (Fig. 5D).

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) (Fig. 6A, B). 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 (Fig. 6C). Significance of the means comparisons are provided in Supplementary Table 1. There were no clear trends for the environment during grain filling period modulating GPC response to late-season N (Fig. 6C). Cumulative precipitation did not show clear patterns in any period.

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 (Fig. 7).

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 (Fig. 8).

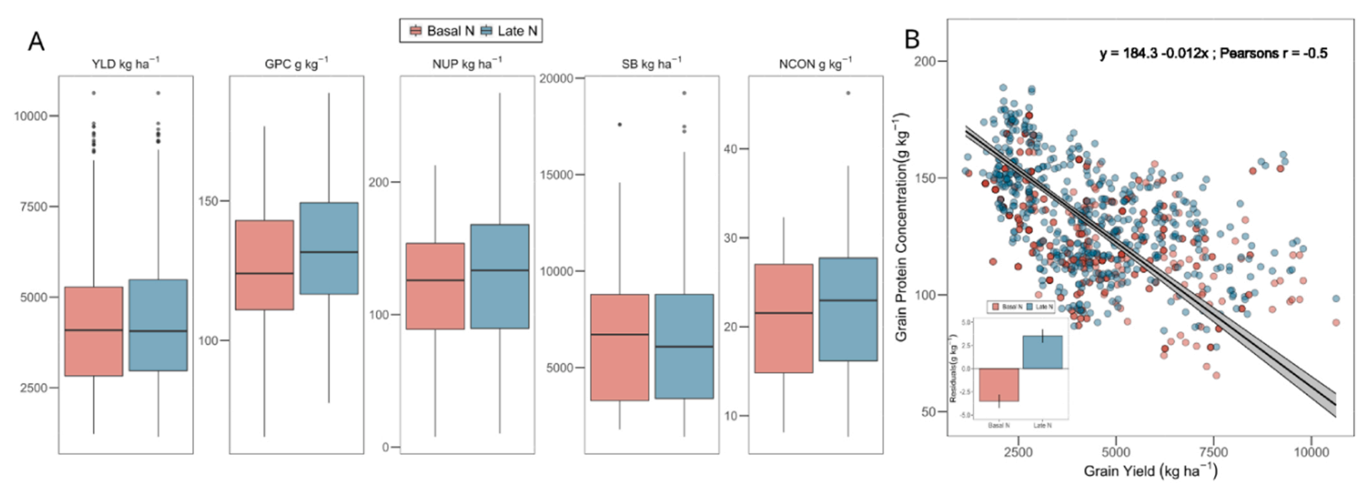


Fig. 3. (A) Comparisons of wheat grain yield (YLD), grain protein concentration (GPC), stover nitrogen uptake (NUP), stover biomass (SB) and stover nitrogen concentration (NCON) between basal N (red) and late N crops (blue). Basal N crops received N fertiliser before and late N after GS 37. Boxplots 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.).

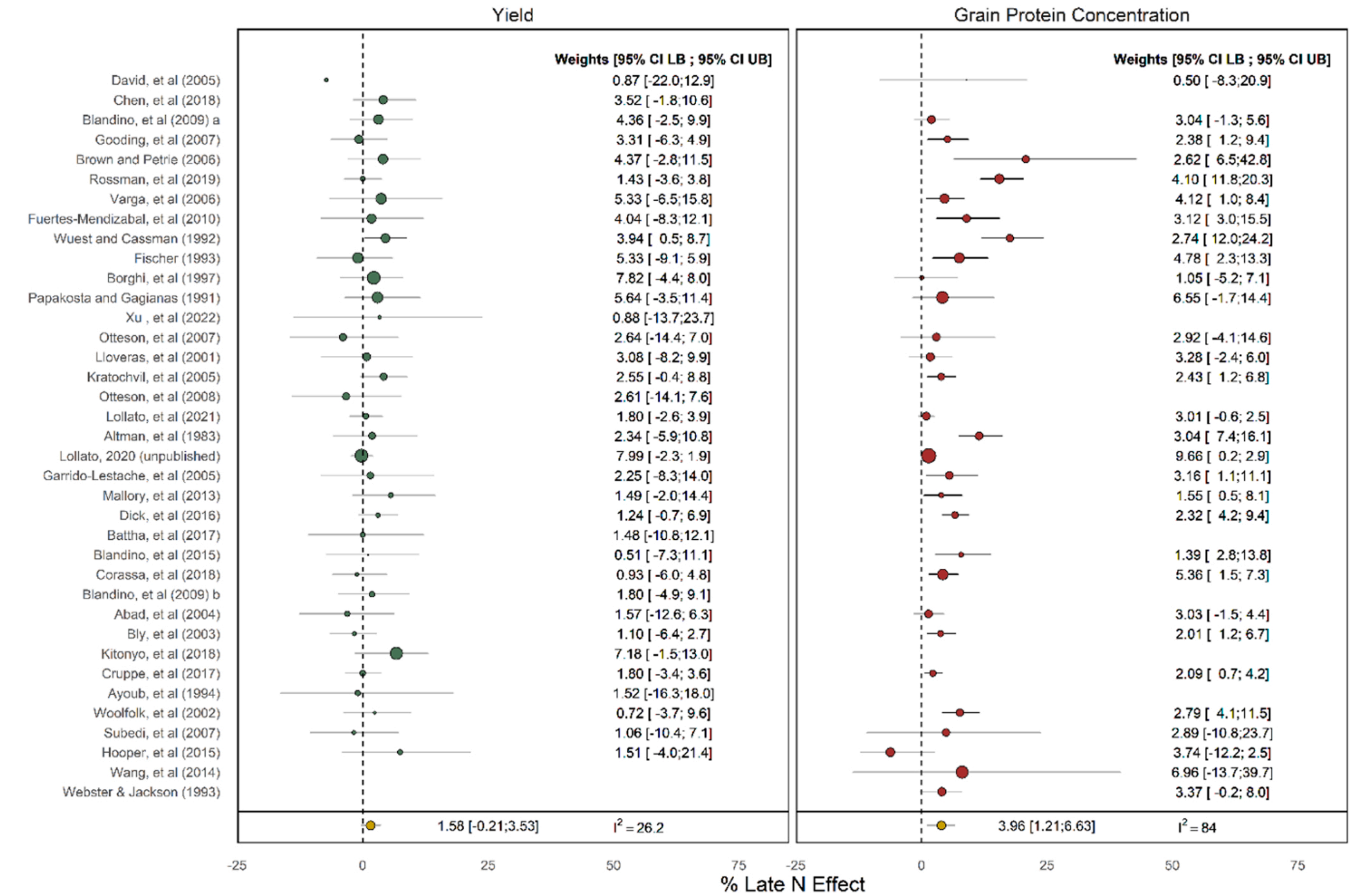


Fig. 4. Pooled effects for grain yield (green symbols) and grain protein concentration (red symbols). Symbols and their whiskers represent the mean effect and 95 % bootstrapped CI for each of the studies in this analysis. The yellow symbols are the mean estimate and its 95 % bootstrapped confidence interval. 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 (%).

4. Discussion

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 N 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., 2015). 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, 2009), 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, 2022; Cruppe et al., 2021), factorial experiments are needed to separate the effect of late N, fungicide, and their interaction.

We showed that GPC is usually responsive to late N fertilisation, but benefits are subject to complex environment × management interactions. In common with many studies, we found a negative relationship between GPC and yield (Fig. 3) (Calderini et al., 1995; Triboi et al., 2006; Jaenisch et al., 2019; Lollato et al., 2019). 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 (Supplementary Table 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).

4.2. Influence of late season N management on GPC response

The proportion of late N applied after GS 37 over the total N avail-

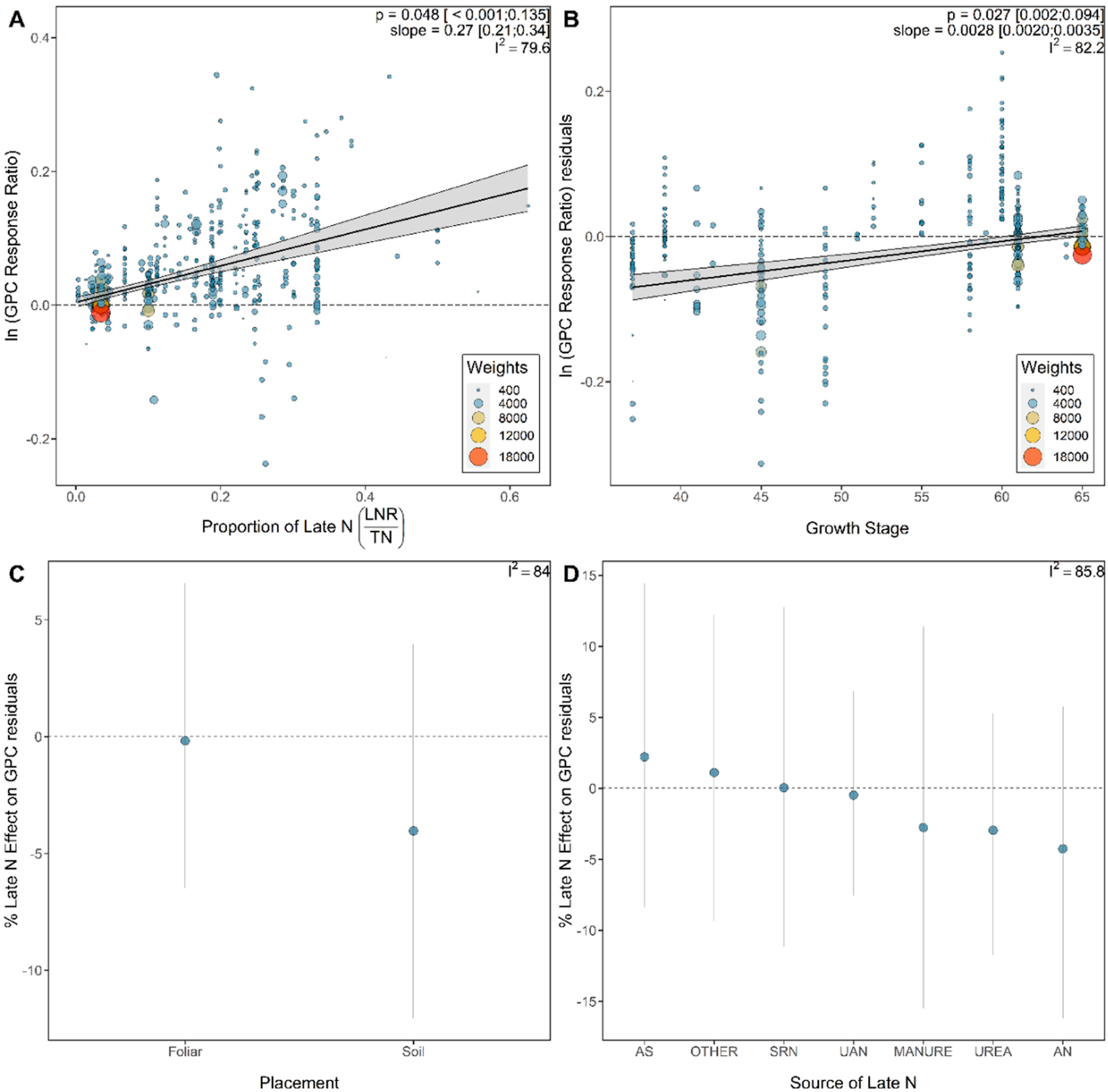


Fig. 5. Impact of late nitrogen management practices on grain protein concentration response: (A) Grain protein concentration increased with the proportion of the late applied N (LNR) relative to the total N available (TN). Effect of different late N fertiliser timings of application (B), placement (C) 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).

able for the crop in the season reflects variation in both early season N supply (i.e., the soil N-NO_3 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 NO_3^- 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 (Fig. 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

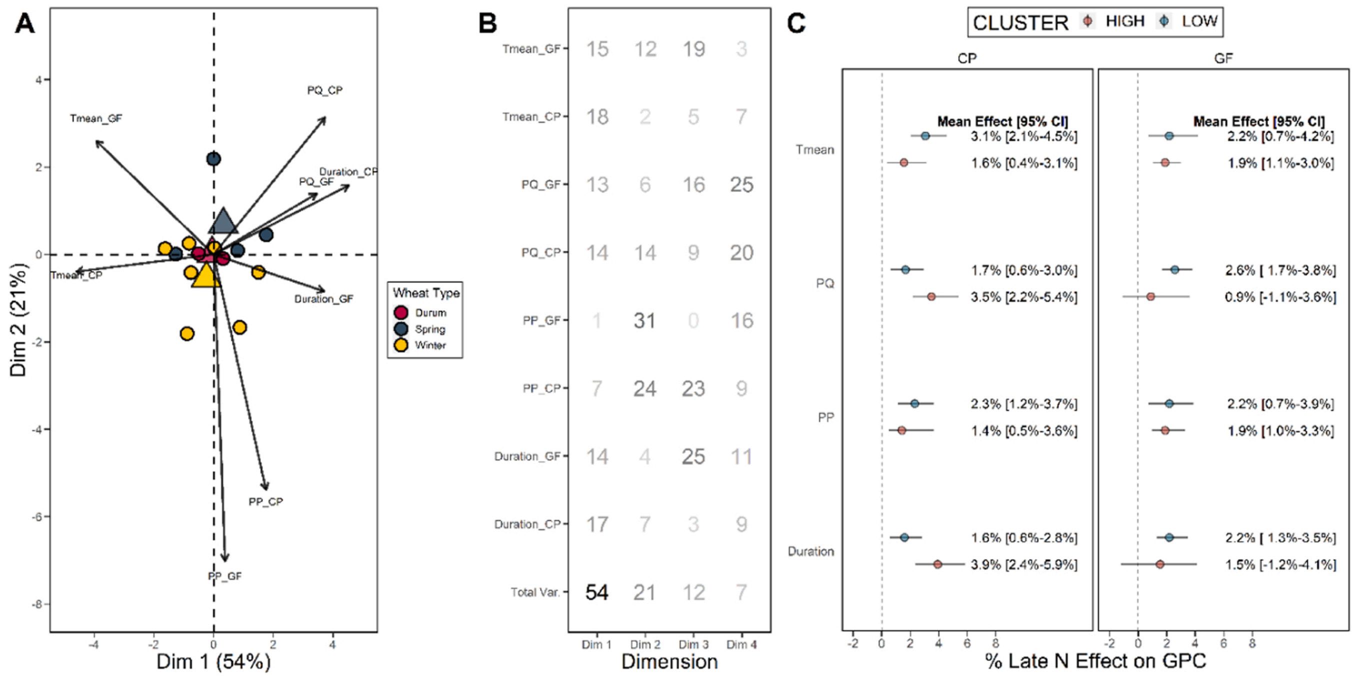


Fig. 6. Environmental descriptors of the GPC response to late-season N fertilisation. (A) Bi-plot with first two dimensions of the principal component analysis, points represent studies and triangles the corresponding centroids for wheat type clusters; (B) individual contribution of the weather attributes 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 Supplementary Table 1. Variables evaluated were: mean temperature (Tmean), photothermal quotient (PQ), duration of the period (Duration), accumulated precipitation (PP).

typical in many wheat growing regions (Sadras et al., 2006, Sadras et al., 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 37–71 window (Fig. 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 Box 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 (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 (Supplementary Table 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., 2001a, 2001b; 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 (Fig. 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

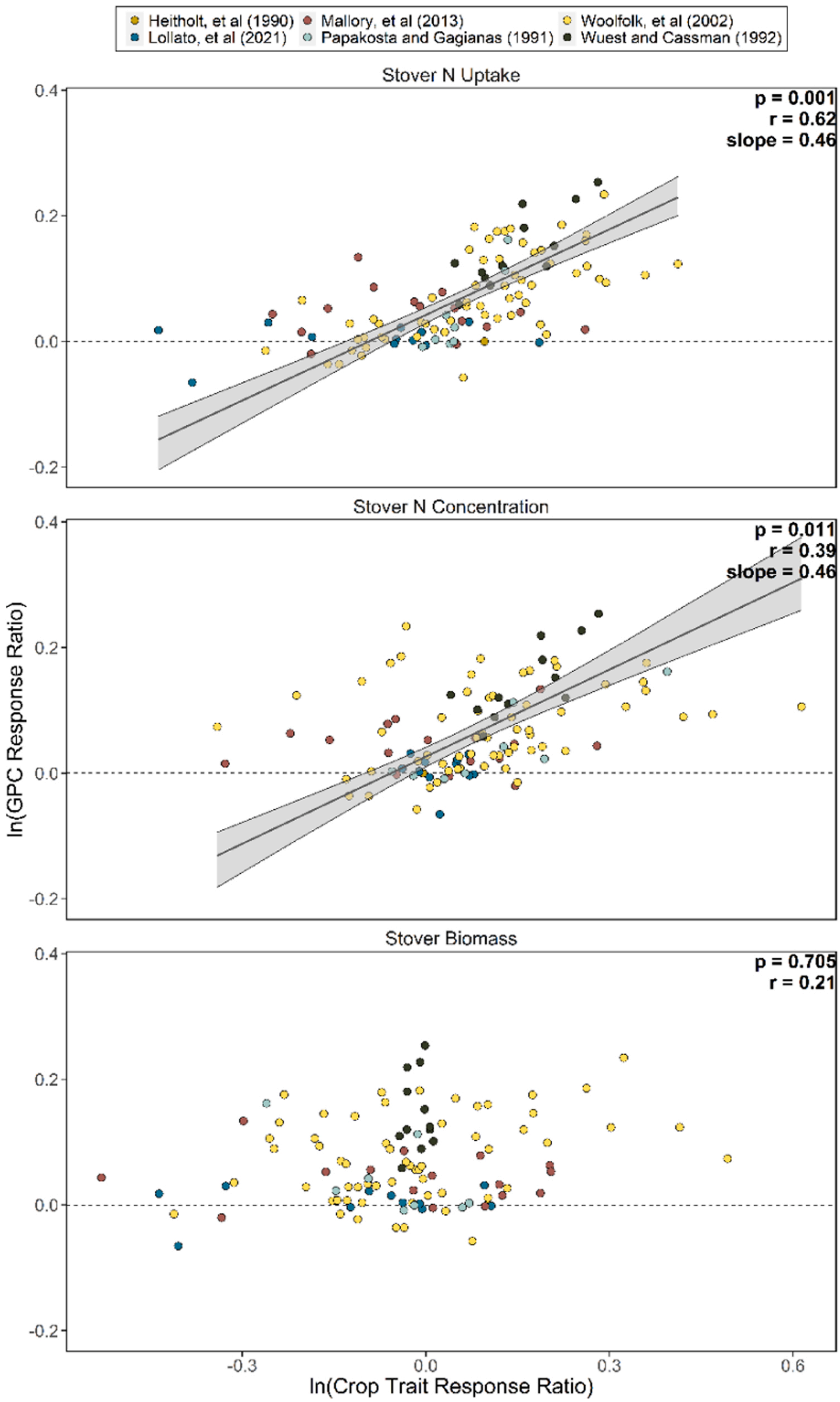


Fig. 7. Relationship between relative GPC response ratio and stover N uptake response ratio, stover nitrogen concentration response ratio and stover biomass response ratio. Colours represent studies. *P*-values correspond to the 0.975 quantile of a resampling distribution. Grey area indicates 95 % bootstrapped CI for the slope of the SMA regression. Mean slope and Pearsons r from a resampled distribution are represented.

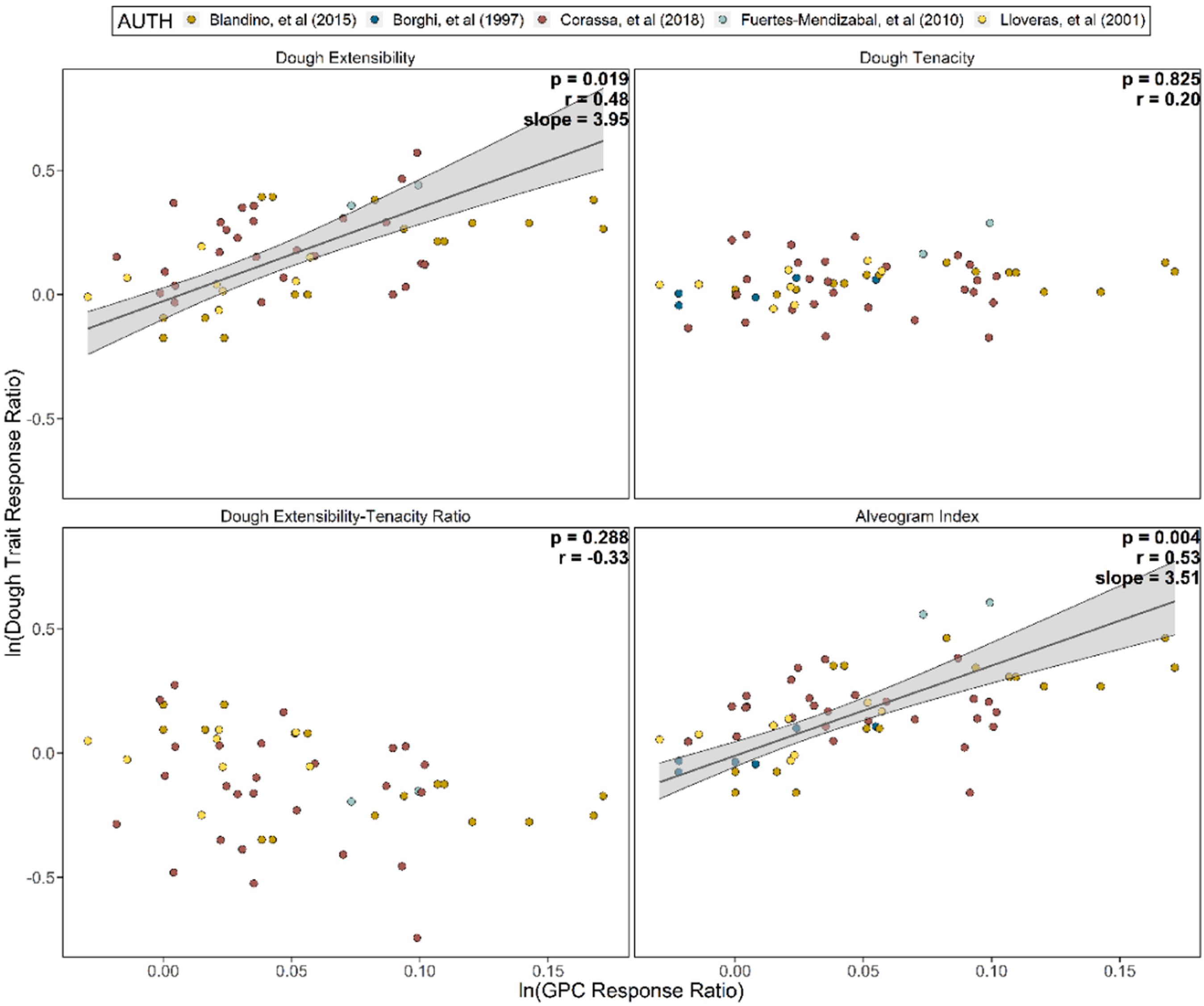


Fig. 8. Grain protein concentration response ratio and its relation with the response in different dough traits: dough extensibility, dough tenacity, dough extensibility-tenacity ratio and alveogram index. *P*-values correspond to the 0.975 quantile of a resampling distribution. Grey area indicates 95 % bootstrapped CI for the slope of the SMA regression. Mean slope and Pearsons r from a resampling distribution are represented.

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).

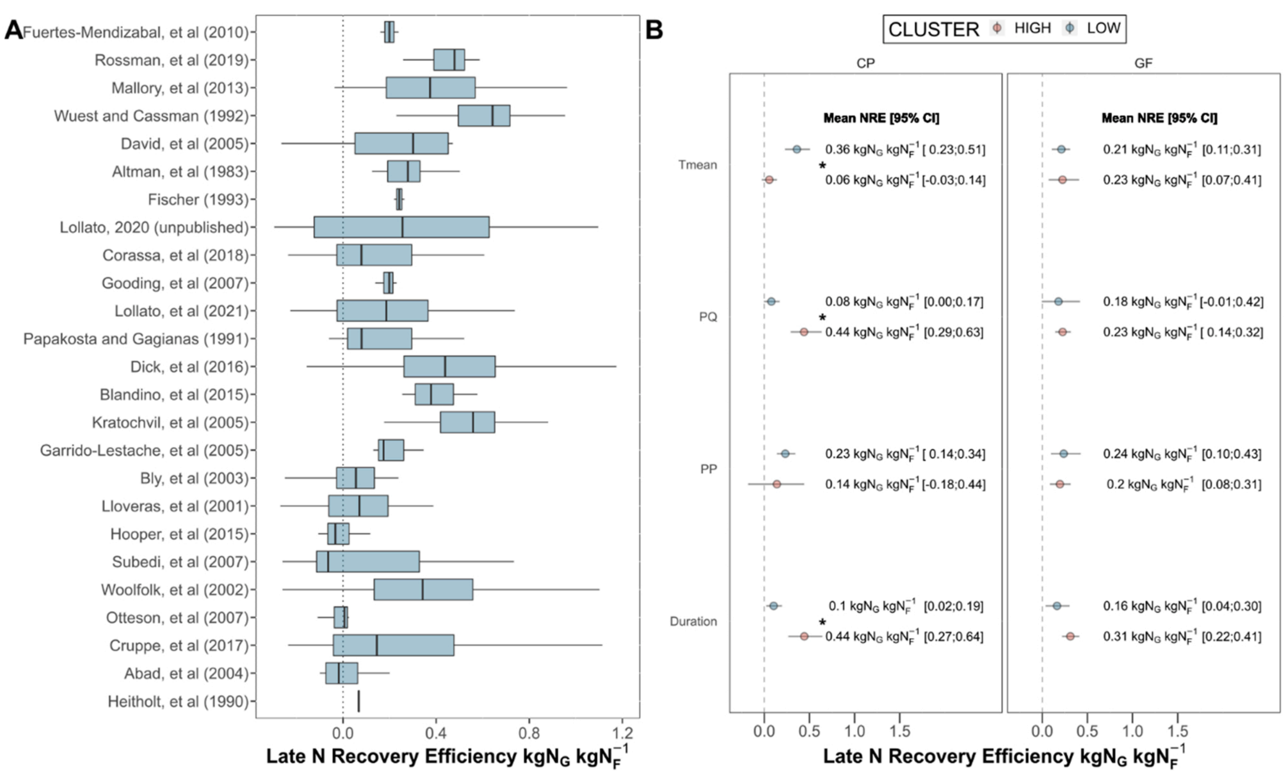
In agreement with our findings, de Oliveira Silva et al. (2020) suggested that plant N concentration was more strongly related to plant N uptake than biomass. Moreover, we found that GPC associated with stover N concentration and not with stover biomass. Concentration of amino acids in the flag leaf 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.

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).

Box 1
Nitrogen recovery efficiency of late-season N applications.

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 − 0.82–1.79 kg grain N kg late N^{-1} (Box 1 Figure A). Conditions favouring crop growth during the critical period (high photothermal quotient, long duration, and low temperatures) were related to high late N recovery efficiency (Box 1 Figure, B). There was no association between recovery efficiency of late N with environmental attributes in the grain filling period (Box 1 Figure, B). Late N placement, source, and timing had no impact on the recovery of late N fertiliser though some trends were observed (Supplementary Figure 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 (Supplementary Figure 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).



Box 1. Figure. (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 starts 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).

5. 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 37–71 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.

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Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Romulo P. Lollato reports financial support was provided by Kansas Wheat Commission. Romulo P. Lollato reports financial support was provided by Kansas Agricultural Experiment Station. Romulo P. Lollato reports financial support was provided by Kansas Cooperative Extension Service.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fcr.2022.108740.

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