Article Title

Wheat grain yield decreased over the past 35 years, but protein content did not change

Short Title

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Highlights

Annual field trials in California from 1985 to 2019 indicated that common wheat, when exposed to gradual CO_2 enrichment, sacrificed grain yield and protein yield for stable grain protein content.

Abstract

The extent to which rising atmospheric CO_2 concentration has already influenced food production and quality is uncertain. Here, we analyzed annual field trials of fall-planted common wheat in California from 1985 to 2019, a period during which global atmospheric CO_2 concentration increased 19%. Even after accounting for other major factors (cultivar, location, degree-days, soil temperature, total water applied, nitrogen fertilization, and pathogen infestation), wheat grain yield and protein yield declined 13% over this period, but grain protein content did not change. These results suggest that exposure to gradual CO_2 enrichment over the past 35 years has adversely affected wheat grain and protein yield, but not grain protein content.

Keywords

Food Security, Grain Yield, Protein Content, Rising Atmospheric CO_2, Trends over Time, Wheat Field Trials

Box 1. Key developments in understanding changes in wheat grain yields and protein over the past few decades.

- **Experiments on plant responses to atmospheric CO_2 enrichment expose plants to unphysiological conditions**

  Broberg et al. (2019) and Tcherkez et al. (2020) documented that experiments on the influence of elevated CO_2 concentrations on field-grown wheat (*Triticum aestivum* L.) exposed plants to CO_2 concentrations that were at least 38% above ambient levels, an increase double that which occurs *in situ*.

- **Long-term wheat field trials expose plants to realistic CO_2 enrichments, but usually cannot differentiate among the factors which influence yield and grain protein content**

  Eichi et al. (2020) found that the experimental design of most wheat field trials was not adequate to separate the complex genetic by environment interactions that influence yield and grain protein content.

- **Thirty-five years of annual field trials on 654 cultivars of fall-planted, common wheat conducted in 7 counties throughout the valleys of central California, USA, avoided many of the usual short-comings**

  Lundy and Dubcovsky (2021) and the California Department of Water Resources (2021) compiled data that can distinguish between the influence of year, cultivar, location, degree-days, soil temperature, total water applied, nitrogen fertilization, pathogen infestation, and vapor pressure deficit on wheat grain yield and protein content.

- **Wheat, when exposed to gradual CO_2 enrichment, sacrifices grain yield and protein yield for stable grain protein content**

  Bloom and Kameritsch (2017) and Bloom et al. (2020) highlighted two compensatory mechanisms—altered manganese to magnesium ratio in chloroplasts and altered balance between shoot and root nitrate assimilation—through which wheat sacrifices grain yield for more stable grain protein content.

Introduction

Nearly all studies of plant responses to rising atmospheric CO_2 compare plants grown at an ambient CO_2 concentration (currently, slightly over 410 ppm CO_2) with those exposed to an elevated concentration that is at least 38% above ambient (Broberg *et al.*, 2019; Tcherkez *et al.*, 2020). In most plants, such CO_2 enrichment stimulates carbon fixation and inhibits photorespiration (Cousins and Bloom, 2004), accelerating organic carbon accumulation but decreasing conversion of nitrate nitrogen into protein in leaves (Bloom, 2015b; Bloom and Lancaster, 2018; Rubio-Asensio and Bloom, 2017). These changes increase the ratio of carbon to nitrogen in the shoots of the elevated CO_2 treatment by about 20% (Sardans *et al.*, 2012; Wang *et al.*, 2019).

The overall increase in atmospheric CO_2 concentration at Mauna Loa, Hawaii between 1985 and 2019 was 19% (Fig. S1 at Dryad Digital Repository, https://doi.org/10.25338/B8G34C; Bloom and Plant, 2021) (Lindsey, 2020), an increase which is half that used in most elevated

CO_2 studies. Thus, evaluation of plant responses to recent increases in atmospheric CO_2 should subject plants to a smaller difference in CO_2 concentration than is usual in most experiments. Of course, a smaller difference in CO_2 concentration elicits a smaller change in plant responses and challenges our ability to discern it. One approach for discerning such a subtle difference is to increase sample size. An untapped source for extensive information on plant responses to rising CO_2 is crop field trials, some of which have generated datasets that contain several thousand entries and span several decades.

Datasets based on crop field trials present several challenges (Eichi *et al.*, 2020). Primarily field trials serve to compare in a given year the performance of many cultivars for one crop at a few locations. Discerning trends over time is difficult because field trials (*a*) generally introduce new genotypes and new agricultural practices as they become available, (*b*) may change locations from year to year depending on rotations with other crops, and (*c*) periodically suffer breakdowns in resistance to local pathogens (Bogard *et al.*, 2010; Fan *et al.*, 2008; Hellemans *et al.*, 2018; Laidig *et al.*, 2017; Mackay *et al.*, 2011; Ormoli *et al.*, 2015; Rao *et al.*, 1993; Verrell and O'Brien, 1996). Thus, the experimental design of most field trials are not well suited for exploring the complex interactions between genotype and environment that strongly influence grain yield/quality relationships over time (Eichi *et al.*, 2020).

Here, we examined 35 years of annual field trials on 654 cultivars of fall-planted, common wheat (*Triticum aestivum* L.) conducted in 7 counties throughout the valleys of central California, USA, ranging south more than 1000 km from the flood plains near the Sacramento River west of Chico, CA, to the deserts near the border with Mexico (Table S1 at Dryad (Lundy and Dubcovsky, 2021). These trials avoided many of the usual short-comings in that they (*a*) followed best agricultural practices such as ample irrigation and fertilization, (*b*) included quantitative evaluation for pathogen infestations when they became evident, (*c*) used the same cultivars as checks nearly every year, and (*d*) were conducted nearly every year at similar locations close to weather stations. Our focus was on trends in wheat *grain yield*, *grain protein content*, and *grain protein yield* over time. *Year* served as a proxy for atmospheric CO_2 concentration because it was very highly correlated ($r = 0.996$) with the average CO_2 concentrations at Mauna Loa, Hawaii. We used CO_2 data from Mauna Loa from January through March, the primary growing season for fall-planted wheat in California, because the longest record for daily atmospheric CO_2 concentrations in California (Vaira Ranch in the foothills of central California) extends only from 2000 to 2019 (Fig. S1 at Dryad).

Analyses

Field trials: The dataset of fall-planted, common wheat cultivars from field trials conducted at multiple locations throughout central California has 6,508 records with values for (*a*) year; (*b*) cultivar entry number; (*c*) cultivar name; (*d*) location; (*e*) grain protein (%); (*f*) grain yield (kg); (*g*) quantitative scores for stripe rust, leaf rust, Septoria leaf blotch, and Yellow dwarf virus (area of flag-1 leaf affected at soft dough stage: 1 = 0 – 3%, 2 = 4 – 14%, 3 = 15 – 29%, 4 = 30 – 49%, 5 = 50 – 69%, 6 = 70 – 84%, 7 = 85 – 95%, 8 = 96 – 100%); (*h*) planting date; (*i*) rainfall; (*j*) irrigation; and (*k*) N fertilizer application (Lundy and Dubcovsky, 2021). Soil temperatures, air degree-days, and Vapor Pressure Deficit (VPD) were derived from hourly data collected at the closest California Irrigation Management Information System (CIMIS) station (California Department of Water Resources, 2021); degree-days were calculated based on temperatures measured during January, February, and March via the single sine method with a horizontal upper cutoff with a maximum temperature for common wheat of 30°C and a minimum temperature of 7°C (Statewide Integrated Pest Management Program, 2021); and VPD was calculated from average air temperatures (Huang, 2018) and vapor pressures during January, February, and March at the closest California Irrigation Management Information System (CIMIS) station. Protein yield is the product of grain protein percentage and yield, and total water addition is the sum of rainfall and irrigation. Data for the cultivars Blanca Grande, Patwin, and Summit were merged with data for derivatives in which stripe rust resistance genes Yr5 and Yr15 were introduced by four backcross generations into the susceptible parent cultivar (Jackson, 2011).

Dataset: California fall-planted wheat field trials (Lundy and Dubcovsky, 2021) provided at least 16 years of data for each of five *locations*: Sacramento Delta ("Delta"), Imperial County ("Imperial"), Kern County ("Kern"), Kings County ("Kings"), and Yolo County at the University of California Davis ("UCD"). We merged the data for Butte County and Colusa County, two adjacent counties that had very little temporal overlap, to form a sixth *location* ("North") with more than 16 years of data. The six locations extend between latitudes 32.8°N and 39.8°N, from deserts near the Mexican border (Imperial and Kern) where plants received nearly all of their water from irrigation to the Sacramento River flood plain (Delta and North) where plants received much of their water from precipitation and ground water. The trials also provided at least 18 years of data for each of six check *cultivars* (Anza, Blanca Grande, Express, Klasic, Serra, and Yecora Rojo). The dataset of wheat parameters and environmental parameters that we used is available at Dryad Digital Repository https://doi.org/10.25338/B8G34C (Bloom and Plant 2021).

Statistics: We fit the models using generalized least squares linear regression implemented in R version 3.5.3 (R Core Team, 2013) using the *gls* function of the *nlme* package (Pinheiro *et al.*, 2017). All models were initially tested for temporal autocorrelation by testing at the $p = 0.05$ level with the null hypothesis of no temporal autocorrelation against the alternative hypothesis of autocorrelation as modeled by an AR1 relationship. The null hypothesis was rejected for some, but not all, of the models, so for consistency all tests were carried out using the AR1 autocorrelation model (Plant, 2019). By including the five environmental factors we were able to account for their effect, giving us the best ability to focus on the factors of interest: *year*, *location*, and *cultivar*. Models were developed using the standard mixed model analytical approach (Pinheiro and Bates, 2000) in which predictors were added to models in which *grain yield*, grain *protein content*, and grain *protein yield* were the response variables, and the significance of each additional predictor was tested. Probabilities ≤ 0.05 were considered significant.

In the initial analysis we pooled across locations and cultivars. To account for factors that might influence grain yield, protein yield, and protein content we formulated for each of these quantities the following linear model

$$Y_{ij} = b_0 + b_1 year_i + b_2 DD_{ij} + b_3 ST_{ij} + b_4 TW_{ij} + b_5 N_{ij} + b_6 P_{ij} + e_{ij},$$

where Y_{ij} is the value of the response variable (grain yield, protein yield, or protein content) in year i, $DD_{ij},$ is the degree-days, ST_{ij} is the mean soil temperature, TW_{ij} is the total applied water, N_{ij} is the total applied N fertilizer, and P_{ij} is an indicator of the pathogen level, at *location* or *cultivar j*.

The models were tested for the influence of *year* along with the five other factors: *degree-days*, *soil temperature*, *total water applied* = precipitation + irrigation, *N* (nitrogen) *fertilization*, and *pathogen infestation level* (Table 1, Fig. 1A–E). Data were sufficiently homoscedastic that no transformations were necessary. Regression analysis is quite robust to non-normality of residuals, and it is common practice not to test these for normality (Plant, 2019). *Vapor Pressure Deficit* (VPD) was not included because it did not change significantly over time in five of the six locations (Fig. 1f); moreover, VPD itself depends on degree-days and total water applied, and including this factor in the model would result in multiple pathways of influence in the model that would disrupt the analysis. In both cases, grain yield and grain protein yield declined significantly over time, but grain protein content did not (Table 1). The five other factors usually, but not always, had a significant influence on grain yield, grain protein content, and grain protein yield (Table 1). Grain protein content generally decreased with grain yield (Fig. 2).

We then used the same procedure to fit generalized least square models that included the influence of the same five factors to the data for (*a*) six *locations* and six check *cultivars*, (*b*) six *locations* and all 654 *cultivars* grown in these locations, (*c*) a particular *location* and six check *cultivars*, or (*d*) six *locations* and a particular check *cultivar* (Table 2 – 3).

$$Y_{ij} = b_0 + b_1 Year_i + b_2 X_j + b_{12} Year_i \times X_j + b_3 DD_{ij} + b_4 ST_{ij} + b_5 TW_{ij} + b_6 N_{ij} + b_7 P_{ij} + e_{ij},$$

where X_j represents the value of location or cultivar.

Findings: Grain yield and grain protein yield for data pooled over the six locations and six check cultivars decreased significantly in general least squares models both excluding and including the influence of the factors *degree-days*, *soil temperature*, *total water applied* (precipitation plus irrigation), *N* (nitrogen) *fertilization*, and *pathogen infestation level*, whereas grain protein content did not change significantly (Table 1). Data for all 654 *cultivars* aggregated over the six *locations* also decreased significantly over time (Table 2). When data were disaggregated by location, grain yield decreased over time in four of the six *locations*, significantly in two, and grain protein yield decreased significantly over time in three of the six *locations*, and changes in grain yield and grain protein yield over time in the other *locations* were not significant (Table 3). When data were disaggregated by cultivar, grain yield and grain protein yield in the six *locations* decreased significantly over time for five of the six check *cultivars*, but protein yield did not change significantly for the *cultivar* Blanca Grande (Table 3). Grain protein content (%) changed significantly over time in two of the six *locations* (increasing at North and decreasing at UCD) but did not change significantly for any of the six check *cultivars* (Table 3). We did not feel that a Bonferroni correction on the Locations or Cultivars models would provide any useful additional information.

We investigated the breakdown of pathogen resistance over time for the 654 *cultivars* tested in 7 California counties with a focus on the influence of pathogen infestation level on grain yield, grain protein content, and grain protein yield (Fig. 5). As described above, each sample in these trials received an infestation score for stripe rust, leaf rust, Septoria leaf blotch, and Yellow dwarf virus (a score of “1” indicated that 0 to 3% of the area of the flag-1 leaf at the soft dough stage showed symptoms; “2” indicated that 4 to 14% of the area showed symptoms; “3” indicated that 15 to 29% showed systems; “4” indicated 30 to 49%; “5” indicated 50 to 69%; “6” indicated 70 to 84%; “7” indicated 85 to 95%; and “8” indicated 96 to 100%). Pathogen infestation level for a *cultivar* in a particular *location* and *year* was the highest infestation score among the four diseases. Years after introduction was the difference between the particular *year* and the first year in which the cultivar was placed in a California field trial. Plotted (Figs. 5A & 5B) are the pathogen infestation level, grain protein yield, grain yield, and grain protein content (mean ± SE) averaged over all cultivars and all locations having the same years after introduction. We also plotted protein yield, grain protein yield, and grain protein content versus pathogen infestation level (Fig. 5C).

Many *cultivars* exhibited noticeable pathogen infestation in the year that they were introduced (pathogen infestation level = 1.46 ± 0.02, mean ± SE, n = 3777) (Fig. 5A). In subsequent years, up to 20 years after introduction, average pathogen infestation level remained between 1.0 ± 0.1 (n = 28) and 2.3 ± 1.8 (n = 34) perhaps because cultivars that displayed high pathogen infestations for several years were more likely to be eliminated from further testing. Average pathogen infestation level jumped to 5.3 ± 2.4 (n = 37) at 21 years after introduction as most cultivars became highly susceptible to pathogens in most locations (Fig. 5A). Grain yield and grain protein yield were highly negatively correlated with pathogen infestation level, whereas grain protein content was not (Fig. 5C).

Conclusions

Wheat grain directly supplies not only about 20% of the carbohydrate in the human diet, but also about 20% of the protein (FAOSTAT, 2021). Of critical concern to food security, therefore, is whether wheat grain yields (Hochman *et al.*, 2017; Ray *et al.*, 2012) and wheat protein yields (Amthor, 2001; Broberg *et al.*, 2017; Carlisle *et al.*, 2012; Fan *et al.*, 2008; Fufa *et al.*, 2005; Hellemans *et al.*, 2018; Lollato *et al.*, 2019; Myers *et al.*, 2014; Ormoli *et al.*, 2015; Taub *et al.*, 2008; Wang *et al.*, 2013) will keep pace with human population growth under future environmental conditions. Wheat grain yields worldwide increased 1% per year over the past 35 years (Fig. 6). Nonetheless, after accounting for changes in precipitation and temperature—but not for cultivars or agricultural practices—global wheat yields declined 0.9% from 1974 to 2008 (Ray *et al.*, 2019). Indeed, wheat yields have remained stagnate for about two decades in regions that have practiced high-input agriculture (Brisson *et al.*, 2010; Hochman *et al.*, 2017; Schauberger *et al.*, 2018) (Fig. 6). Wheat yields in California, for example, have not changed during the past 35 years (Fig. 6).

Wheat grain nutritional quality may decline over time because newly introduced cultivars may have lower grain protein contents (%) than those introduced decades ago (Fufa *et al.*, 2005; Laidig *et al.*, 2017; Mariem *et al.*, 2020; Shewry *et al.*, 2016; Voss-Fels *et al.*, 2019) (Fig. S2 at Dryad). This might be an artifact of breeders releasing more feed wheat varieties (for animal consumption), which do not have to fulfill the same quality criteria (especially protein content) as wheat cultivars for human consumption, but we have no information about this possibility. In some studies, wheat grain protein contents of new cultivars have not changed significantly (Guzmán *et al.*, 2017; Hucl *et al.*, 2015). Here in California, for instance, grain protein contents of wheat cultivars during the year that they were introduced remained relatively constant (Fig. 7).

Rising atmospheric CO_2 concentration—a 19% increase over the past 35 years (Fig. S1 at Dryad)—probably has influenced wheat grain yields and protein yields. Elevated CO_2 inhibits photorespiration and thereby malate production in shoots (Abadie *et al.*, 2020; Gámez *et al.*, 2020). Oxidation of this malate generates the reductant required for converting nitrate and sulfate into respectively organic nitrogen and sulfur in amino acids (Abadie and Tcherkez, 2019; Bloom, 2015a; Bloom *et al.*, 2002; Cousins and Bloom, 2004; Rubio-Asensio and Bloom, 2017). CO_2 enrichment, thus, results in slower shoot amino acid production and lower wheat grain protein content (Broberg *et al.*, 2017; Carlisle *et al.*, 2012; Pleijel *et al.*, 2019).

In most California locations, wheat grain yield and grain protein yield of most *cultivars* declined significantly over the past 35 years even after accounting for changes in degree-days, soil temperature, total water applied, N fertilization, and pathogen infestation level (Table 2, Figs. 3 and 4 left and right panels). On average for the six *locations* having the most data, grain yield and grain protein yield declined 0.4% per year. Notice that grain protein yield declined most rapidly in the Imperial location (Table 2), a desert area where plants are highly dependent on irrigation and where they experienced no detectable pathogen infestation (Fig. 1e), and in the Delta location, an island in the Sacramento River delta where plants have highly dependent on precipitation and ground water (Fig. 1C). The 13% decline in grain yield and grain protein yield over the 35 years of this study is a matter of concern, given that the world population rose 58% during this period. In contrast, grain protein content remained relatively constant over this period (Table 1, Figs. 3 and 4 center panels) and did not vary with pathogen infestation level (Fig. 5C).

Developmental stage of a plant may alter the influence of environmental factors (e.g., degree-days, soil temperature, total water applied, N fertilization, and pathogen infestation level) on grain yield and grain protein yield, but our dataset (Lundy and Dubcovsky, 2021) generally provides only information about planting date. This dataset, however, has additional information on days to heading and days to maturity for a few years, a few sites, and a few cultivars. Such information may prove useful in future investigations about the interactions between plant developmental stage and environmental factors.

We sought information about wheat field trials in locations outside of California, but datasets for these locations were much more limited. For example, the AHDB (Agriculture and Horticulture Development Board) Cereals & Oilseeds Recommended Lists for Great Britain has only 433 entries extending back only to 2002, and only one cultivar has values for fifteen years (AHDB Cereals & Oilseeds, 2020). A dataset for North Dakota extends back to 2001, but only one cultivar has values for fifteen years (NDSU Publications, 2020); one for South Dakota extends back to 2002, but only one cultivar has values for eleven years (SDSU Extension, 2020); another for Australia only has data for the past 11 years (Eichi *et al.*, 2020).Trends in grain protein over these shorter periods were not evident (data not shown). These datasets will warrant further analysis when information for additional years becomes available.

Some may question whether wheat trends in California over the past 35 years are related to the 19% increase in atmospheric CO_2 concentration that occurred during this period. Although exposure of wheat to elevated CO_2 atmospheres generally increases grain yield (Broberg *et al.*, 2019; Pleijel *et al.*, 2019) and decreases grain protein content (Broberg *et al.*, 2017; Pleijel *et al.*, 2019), most studies subject plants to an elevated CO_2 treatment in which the CO_2 concentration is more than 38% above an ambient control treatment (Broberg *et al.*, 2019; Tcherkez *et al.*, 2020). Such an elevated CO_2 treatment upsets the balance between carbon fixation and photorespiration (Cousins and Bloom, 2004) and increases shoot carbon to nitrogen ratio by about 20% (Sardans *et al.*, 2012; Wang *et al.*, 2019) because carbohydrates accumulate and conversion of nitrate into shoot protein decelerates when deprived of the reductant generated during photorespiration (Abadie *et al.*, 2020; Bloom and Lancaster, 2018). Grain protein content, in that it derives mostly from shoot protein, declines under more severe elevated CO_2 treatments.

In the field trials examined here, the overall difference in atmospheric CO_2 between 1985 and 2019 was less than half of that used in most elevated CO_2 studies. Under less extreme CO_2 enrichment, wheat increases the manganese to magnesium ratio in chloroplasts. Substituting manganese for magnesium in the metal binding sites of Rubisco significantly inhibits the carboxylation reaction while it accelerates the oxygenation reaction (Bloom, 2019), slowing carbon fixation while enhancing photorespiration and nitrate assimilation, thus bringing plant organic carbon and nitrogen back into balance (Bloom and Kameritsch, 2017; Bloom and Lancaster, 2018). Also exposure to elevated atmospheric CO_2 increases carbohydrate export from shoot to roots, which enhances root nitrate assimilation and thus offsets diminished shoot nitrate assimilation (Bloom *et al.*, 2020).

These two compensatory mechanisms—altered manganese to magnesium ratio in chloroplasts and altered balance between shoot and root nitrate assimilation—sacrifice grain yield for more stable grain protein content. Both natural selection and wheat breeding should favor stable grain protein content because this trait is critical for sustaining both the vigor of seedlings after germination and the value of the crop for human nutrition (Wakasa and Takaiwa, 2013). Consequently, from an evolutionary perspective, the observed declining yields but stable protein contents in the wheat field trials seem reasonable. Consistent with this trend are recent meta-analyses of FACE (Free-air CO_2 enrichment) experiments on wheat in which elevated CO_2 downregulated carbon fixation, altered grain metabolism, and had minimal effects on grain yield and grain protein content (Broberg *et al.*, 2019; Tcherkez *et al.*, 2020).

Data Availability

The supplementary figures S1 and S2 as PDF files and the full dataset as an Excel spreadsheet are available at https://doi.org/10.25338/B8G34C.

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Author contributions

A.J.B. conceptualized the study, collected the data, administered the project, wrote the original manuscript, reviewed the comments and suggestions, and revised the manuscript. R. P. conducted the statistical analyses and reviewed and edited the manuscript.

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Figure Legends

Fig. 1A – F. *Degree-days*, *soil temperature*, *total water applied*, *N fertilization*, *pathogen infestation level*, and *vapor pressure deficit* during the growing season for fall-planted common wheat versus *year* at six Californian locations where field trials were conducted. Symbols represent the values for each year during which trials were conducted, and the lines are the least square linear regressions over the entire period to aid the eye in discerning patterns in the data; Table S1 provides the slopes, intercepts, and r^2 values for these lines.

Fig. 2. G*rain protein content* versus *grain yield* at six Californian locations where field trials were conducted. Symbols represent the values for each year during which trials were conducted, and the lines are the least square linear regressions over the entire period to aid the eye in discerning patterns in the data. The linear trends are

Delta: $y = -0.3582x + 14.326$, $r^2 = 0.1152$;
Imperial: $y = -0.1092x + 13.951$, $r^2 = 0.0255$;
Kern: $y = -0.2495x + 14.867$, $r^2 = 0.1109$;
Kings: $y = -0.3008x + 14.964$, $r^2 = 0.1109$;
North: $y = -0.1092x + 13.951$, $r^2 = 0.0233$;
UCD: $y = -0.0907x + 13.175$, $r^2 = 0.0229$.

Fig. 3. Regressions of grain yield (Mg ha^{-1}) (left column); protein content (%) (middle column); and protein yield (Mg ha^{-1}) (right column) versus year at six locations in California common wheat field trials. These are based on generalized linear models that included the influence of year, degree-days, soil temperatures, total water applied, N fertilization, and pathogen infestation. A data point at a given year is the mean for one of six check cultivars. The slopes and intercepts of the lines are generated from the generalized least squares model for the subset of data for a location. The coefficients of the lines are given in Table S2.

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Fig. 5A & B. Changes in pathogen infestation level, grain protein yield, grain yield, and grain protein content with the years after a cultivar was introduced. Shown are means ± SE. **C.** Changes in pathogen level, grain protein yield, grain yield, and grain protein content with pathogen infestation level. Shown are linear regressions labelled with slopes, intercepts, and correlations squared.

Fig. 6. Wheat grain yields over time at different locations. Symbols represent the values for each year, and the lines are the quadratic polynomial regressions for the entire period. "Austral./NZ" denotes Australia and New Zealand; "Least devel." denotes those nations that the United Nations considers to be least developed in terms of economic activities. Data derived from public databases (FAOSTAT, 2021; National Agricultural Statistics Service, 2021). The quadratic trends are

UK: $y = -15.747x^2 + 63537x - 6\times10^7$, $r^2 = 0.5384$;
Germany: $y = -28.154x^2 + 113254x - 1\times10^8$, $r^2 = 0.6466$;

France:	$y = -22.544x^2 + 90582x - 9\times10^7$, $r^2 = 0.3741$;
California:	$y = -5.1093x^2 + 20487x - 2\times10^7$, $r^2 = 0.0134$;
China:	$y = 7.1205x^2 - 27688x + 3\times10^7$, $r^2 = 0.9753$;
USA:	$y = 4.0775x^2 - 16050x + 2\times10^7$, $r^2 = 0.7370$;
World:	$y = 4.6593x^2 - 18293x + 2\times10^7$, $r^2 = 0.9614$;
Austral./NZ:	$y = 0.8438x^2 - 3254x + 3\times10^6$, $r^2 = 0.1220$;
Least devel.:	$y = 15.398x^2 - 61276x + 6\times10^7$, $r^2 = 0.9497$.

Fig. 7. Wheat grain protein content (%) of spring-planted common wheat cultivars during the year they were introduced into Californian field trials. Shown are mean ± SE and the linear trend line ($y = -0.0017\,x + 16.106$, $r^2 = 0.0007$).

Tables:

Table 1. Coefficients (Coef.) and probabilities (*p*) for generalized least squares models of *grain yield* (kg ha^{-1}), *grain protein content*, and *grain protein yield* (kg ha^{-1}) for data pooled at six *locations* in California and for six check *cultivars* from 1985 to 2019 (n = 754). The models included the influence of *year* alone or *year* with *degree-days*, *soil temperature*, *total water applied* (precipitation plus irrigation), *N* (nitrogen) *fertilization*, and *pathogen infestation level*.

	Grain Yield		**Protein %×10^{-4}**		**Protein Yield**	
Factor	**Coef.**	***p***	**Coef.**	***p***	**Coef.**	***p***
Year alone	–47.63	<0.001	0.55	0.57	–5.62	<0.001
Year with other factors	–25.19	0.019	0.99	0.91	–2.98	0.040
Degree-days	1.86	0.001	–0.004	0.393	0.22	0.005
Soil temperature	–187.6	0.008	16.5	0.012	–12.50	0.195
Total water applied	–0.49	0.162	0.007	0.026	–0.005	0.910
N fertilization	2.54	0.027	0.20	0.041	0.45	0.004
Pathogen infestation level	–-340.5	<0.001	0.02	0.568	–42.70	<0.001

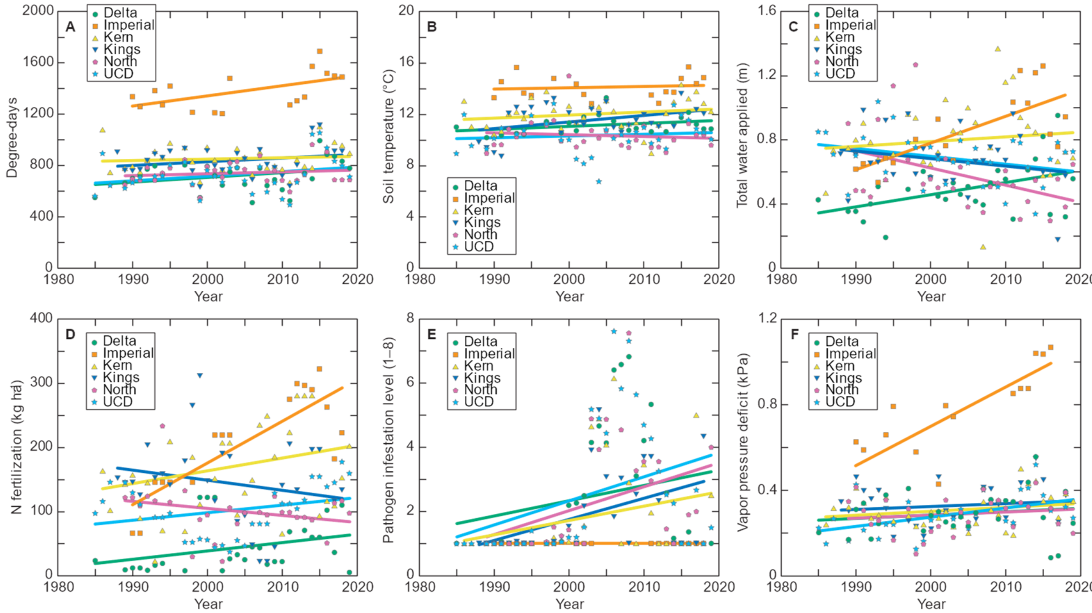
Table 2. Coefficients (Coef.) and probabilities (*p*) for the influence of *year* in generalized least squares models of *grain yield* (kg ha^{-1}), *grain protein content* (%) and *grain protein yield* (kg ha^{-1}) at six *locations* in California and for six check *cultivars* or all 654 *cultivars*. The models included the influence of *year*, *degree-days*, *soil temperature*, *total water applied*, *N fertilization*, and *pathogen infestation level*.

				Grain Yield		**Protein %**		**Protein Yield**	
Location	**Cultivar**	**Years**	***n***	**Coef.**	***p***	**Coef.×10^{-4}**	***p***	**Coef.**	***p***
6 locations	6 cultivars	85–19	754	–25.19	0.019	0.01	0.917	–2.98	0.040
6 locations	654 cultivars	85–19	6508	–16.15	0.001	0.59	0.170	–1.62	0.016

Table 3. Coefficients (Coef.) and probabilities (*p*) for the influence of *year* in generalized least squares models of *grain yield* (kg ha^{-1}), *grain protein content* (%) and *grain protein yield* (kg ha^{-1}) at six *locations* in California and for six check *cultivars*. The models included the influence of *year*, *location* or *cultivar*, *location* × *Year* or *cultivar* × *Year*, *degree-days*, *soil temperature*, *total water applied*, *N fertilization*, and *pathogen infestation level*, and, as indicated, *location* or *cultivar*.

				Grain Yield		Protein %		Protein Yield	
Location	**Cultivar**	**Years**	***n***	**Coef.**	***p***	**Coef.×10^{-4}**	***p***	**Coef.**	***p***
Delta	6 cultivars	85–19	122	–66.7	0.004	5.74	0.002	–9.66	0.015
Imperial	6 cultivars	90–18	69	–85.3	0.005	–3.20	0.20	–12.77	0.036
Kern	6 cultivars	86–19	141	23.8	0.27	–1.72	0.32	1.57	0.562
Kings	6 cultivars	88–18	132	18.0	0.46	–0.67	0.74	3.74	0.171
North	6 cultivars	89–19	152	–23.8	0.33	7.80	<0.0001	–0.50	0.885
UCD	6 cultivars	85–19	138	–7.0	0.74	–2.19	0.20	–8.84	0.001
6 locations	Anza	85–17	171	–29.1	0.03	–1.20	0.31	–7.56	<0.001
6 locations	Blanca Grande	01–19	101	–62.8	0.01	–1.09	0.57	2.28	0.593
6 locations	Express	88–13	126	–35.5	0.04	–2.42	0.09	–11.99	<0.001
6 locations	Klasic	85–03	86	–63.3	0.02	0.14	0.95	–19.27	<0.001
6 locations	Serra	85–04	91	–65.2	0.009	2.04	0.31	–17.68	<0.001
6 locations	Yecora Rojo	85–19	179	–41.9	0.002	–0.93	0.43	–8.54	0.001

Figures and figure legends:



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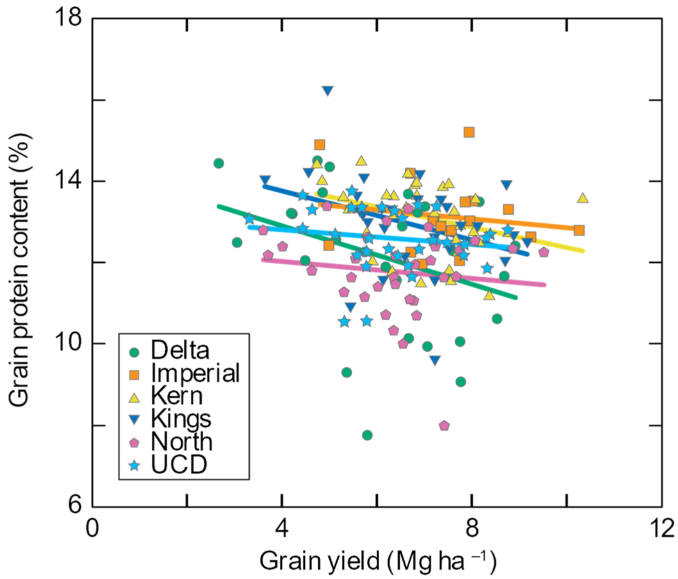

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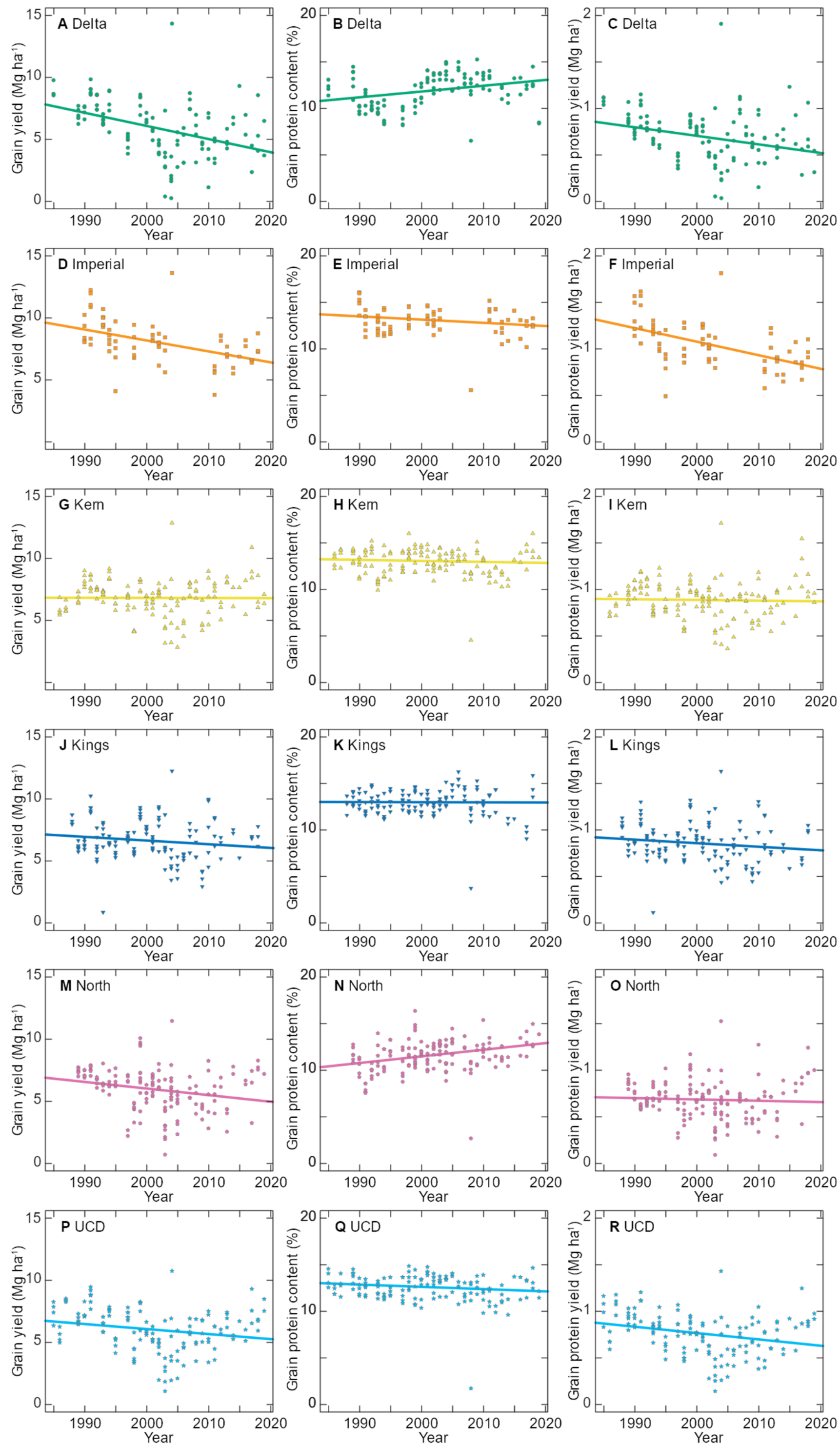

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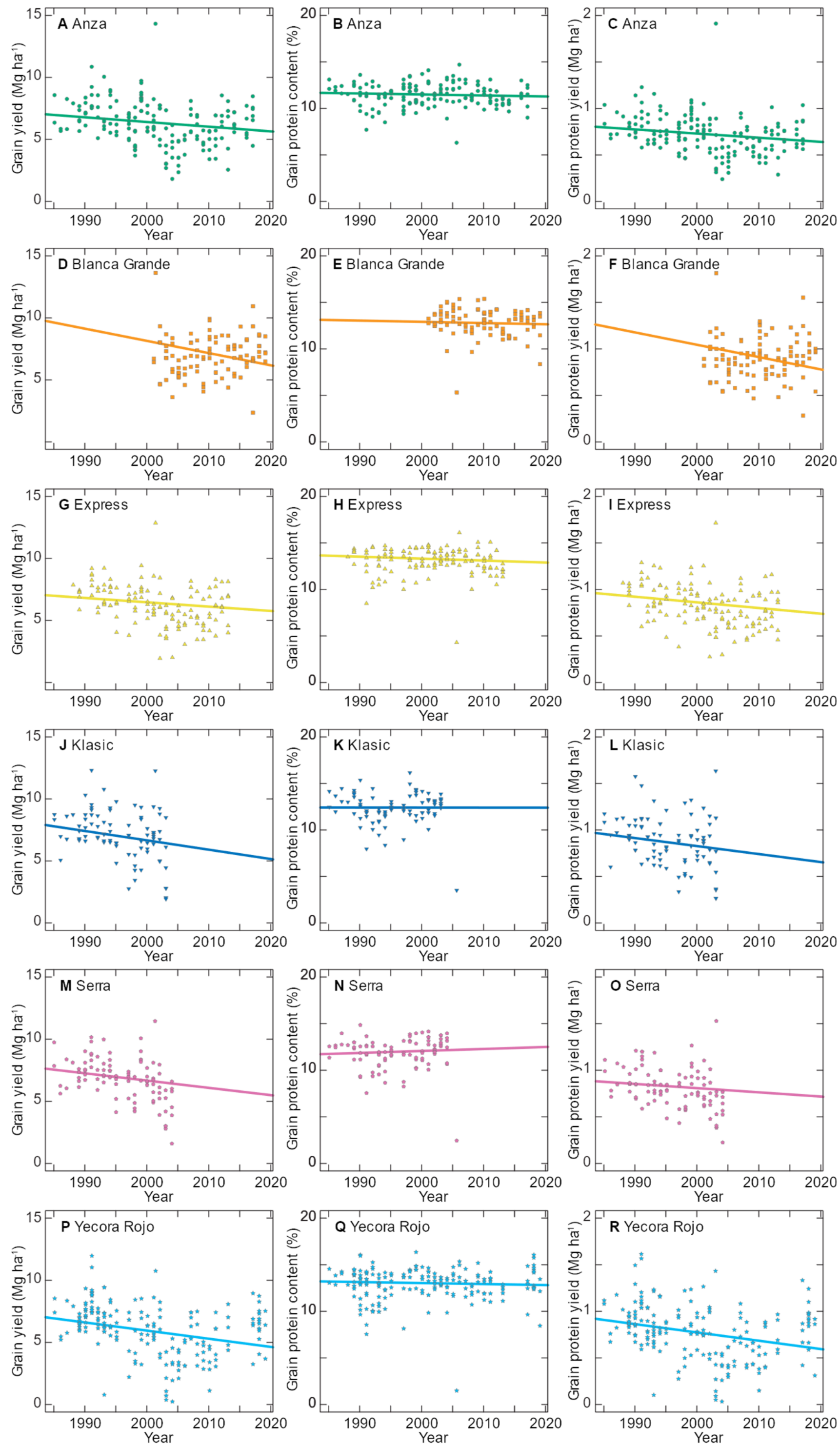

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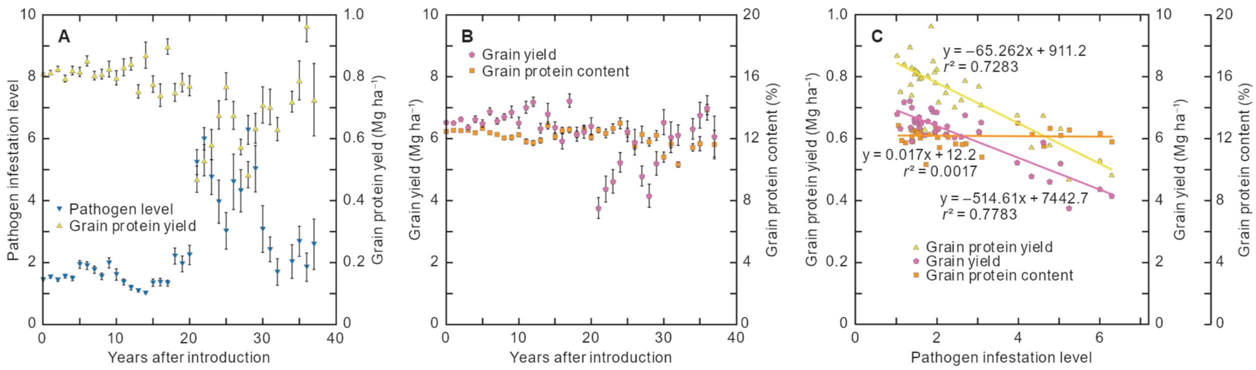

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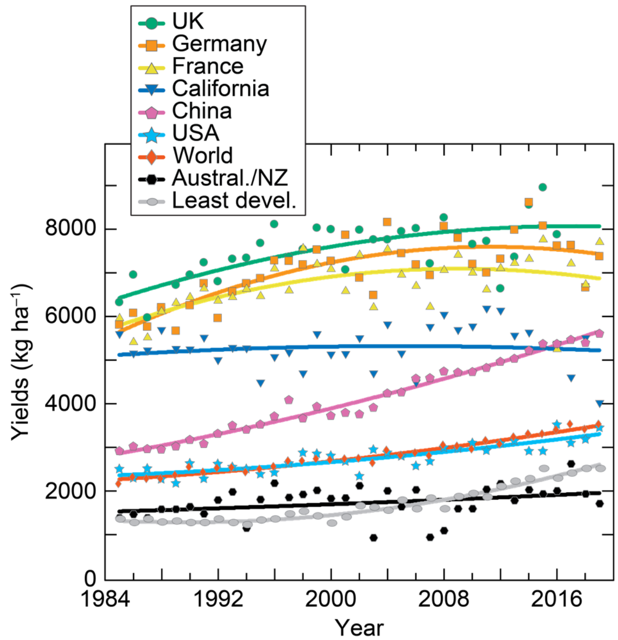

Fig. 6. Wheat grain yields over time at different locations. Symbols represent the values for each year, and the lines are the quadratic polynomial regressions for the entire period. “Austral./NZ” denotes Australia and New Zealand; “Least devel.” denotes those nations that the United Nations considers to be least developed in terms of economic activities. Data derived from public databases (FAOSTAT, 2021; National Agricultural Statistics Service, 2021). The quadratic trends are

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California:	$y = -5.1093x^2 + 20487x - 2\times10^7$, $r^2 = 0.0134$;
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World:	$y = 4.6593x^2 - 18293x + 2\times10^7$, $r^2 = 0.9614$;
Austral./NZ:	$y = 0.8438x^2 - 3254x + 3\times10^6$, $r^2 = 0.1220$;
Least devel.:	$y = 15.398x^2 - 61276x + 6\times10^7$, $r^2 = 0.9497$.

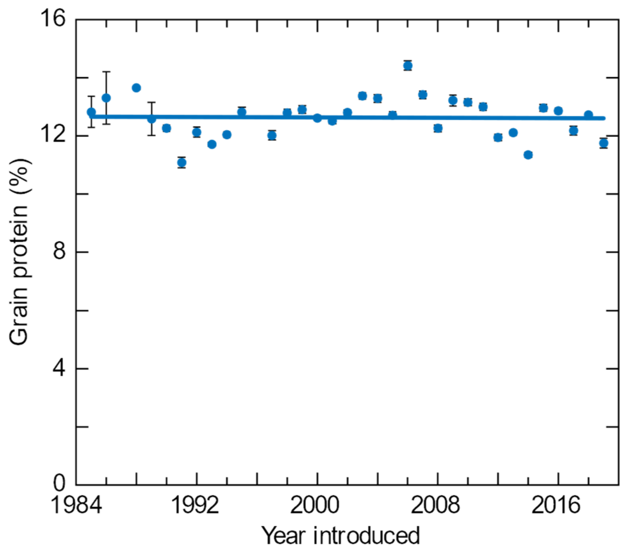

Fig. 7. Wheat grain protein content (%) of spring-planted common wheat cultivars during the year they were introduced into Californian field trials. Shown are mean ± SE and the linear trend line ($y = –0.0017\ x + 16.106$, $r^2 = 0.0007$).

Table S1. Linear least square regressions for the data in Figure 1.

Parameter	Location	Slope	Intercept	r^2
Degree-days	Delta	3.2691	-5822	0.0727
	Imperial	8.4973	-15652	0.3597
	Kern	2.0383	-3232	0.0351
	Kings	4.0883	-7348	0.0906
	North	1.8094	-2883	0.0260
	UCD	4.8974	-9081	0.1071
Soil temp.	Delta	0.0244	-37.65	0.1041
	Imperial	0.0094	-4.665	0.0132
	Kern	0.0333	-54.648	0.0641
	Kings	0.0424	-73.375	0.093
	North	-0.0162	42.91	0.0166
	UCD	0.0144	18.509	0.0101
Total water applied	Delta	0.0087859	-17.117	0.2323
	Imperial	0.016597	-32.407	0.5411
	Kern	0.0007312	-0.6623	0.0009
	Kings	-0.0068206	14.331	0.108
	North	-0.0093402	19.287	0.1188
	UCD	-0.0054087	11.519	0.1025
N fertilization	Delta	1.3473	-2655	0.0995
	Imperial	6.609	13044	0.6970
	Kern	1.7780	-3388	0.0246
	Kings	1.5644	3282	0.0410
	North	0.9277	1956	0.0389
	UCD	2.1899	-4290	0.2408
Pathogen infestation	Delta	0.0182	-34.664	0.0395
	Imperial	0.0	1.0	1.000
	Kern	0.0127	-24.023	0.0249
	Kings	0.0389	-76.248	0.1806
	North	0.0346	-67.579	0.1019
	UCD	0.0251	-48.390	0.074
VPD	Delta	1.4137	-2542.8	0.0234
	Imperial	18.357	-36013	0.7207
	Kern	1.8538	-3405.5	0.060
	Kings	1.3753	-2446.1	0.0167
	North	1.4137	-2542.8	0.0223
	UCD	4.3149	-8354.7	0.239

Table S2. Coefficients (Coef.), intercepts (Int.), and probabilities (*p*) for the influence of *year* in generalized least squares models of *grain yield* (kg ha^{-1}), *grain protein content*, and *grain protein yield* (kg ha^{-1}) for subsets of the data that contained one of six *locations* in California and all six check *cultivars* or that contained one of six check cultivars and all six locations. These values are used to construct the lines shown in Figs. 3 and 4. The columns labeled Int. show the value of the regression in 1985.

				Grain Yield			**Protein %**			**Protein Yield**		
Location	**Cultivar**	**Years**	***n***	**Coef.**	**Int.**	***p***	**Coef. ×10^{-4}**	**Int.**	***p***	**Coef.**	**Int.**	***p***
Delta	6 cultivars	85–19	122	–108.4	7728	0.0002	3.74	0.113	0.27	–9.79	855	0.01
Imperial	6 cultivars	90–18	69	–92.4	9564	<0.0001	–2.68	0.134	0.13	–14.26	1283	<0.0001
Kern	6 cultivars	86–19	141	–0.18	6832	0.99	–1.30	0.132	0.44	–1.01	904	0.72
Kings	6 cultivars	88–18	132	–28.9	7061	0.29	–0.41	0.131	0.83	–4.07	918	0.23
North	6 cultivars	89–19	152	–55.6	6869	0.022	7.38	0.104	<0.001	–1.29	705	0.69
UCD	6 cultivars	85–19	138	–38.0	6665	0.18	–2.41	0.130	0.04	–7.10	874	0.03
6 locations	Anza	85–17	171	–51.8	7155	0.0004	–2.21	0.118	0.10	–6.92	832	<0.0001
6 locations	Blanca Grande	01–19	101	48.0	5712	0.10	–3.98	0.139	0.14	3.97	796	0.37
6 locations	Express	88–13	126	–79.0	7554	<0.0001	–1.99	0.135	0.31	–11.15	1008	<0.0001
6 locations	Klasic	85–03	86	–177.9	8843	<0.0001	–0.02	0.124	0.99	–24.37	1115	<0.0001
6 locations	Serra	85–04	91	–160.2	8541	<0.0001	1.32	0.119	0.67	–17.64	1001	<0.0001
6 locations	Yecora Rojo	85–19	179	–55.1	6864	0.0007	–0.16	0.130	0.92	–7.44	894	0.01

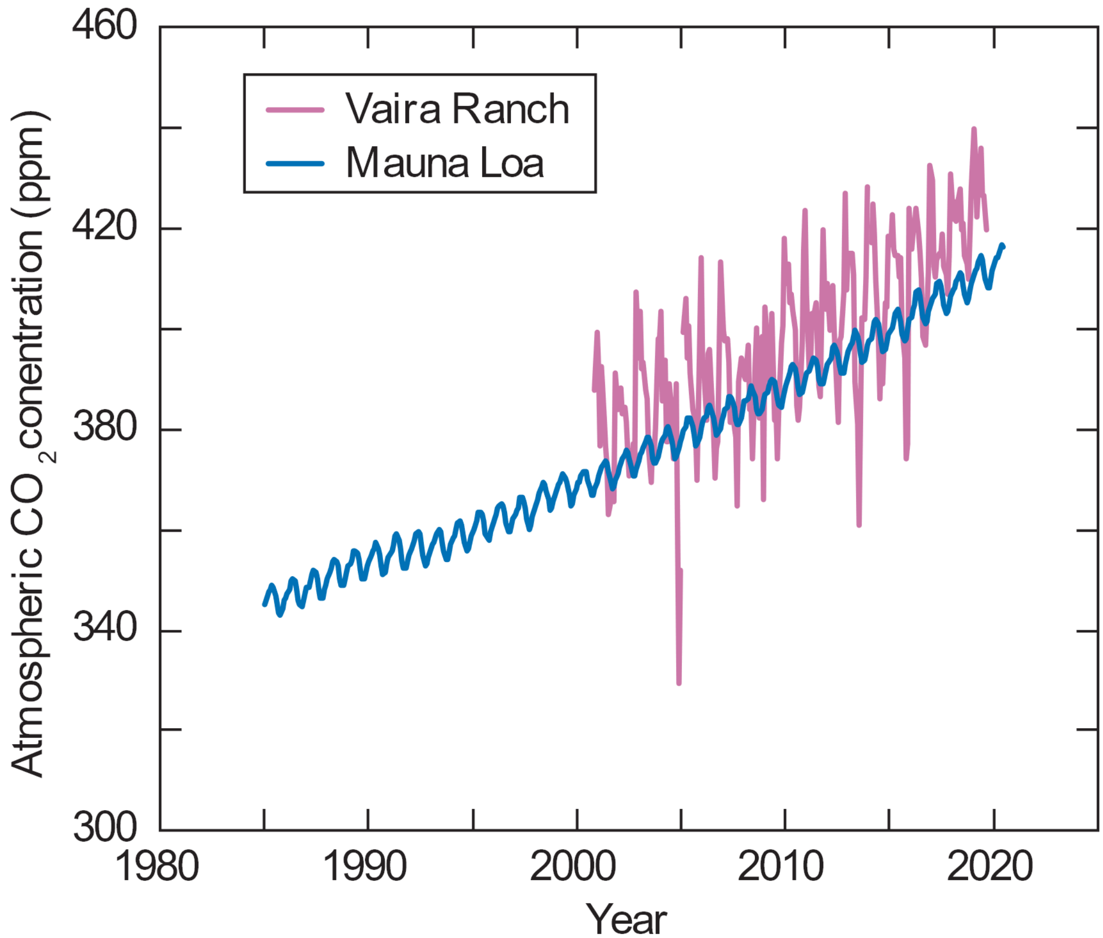

Fig. S1. Monthly average atmospheric CO_2 concentrations (ppm) measured at Vaira Ranch in the foothills of central California (Ma et al., 2007) or at the Mauna Loa Observatory on the big island of Hawaii (Lindsey, 2020). The higher seasonal CO_2 variation in California derives from higher primary productivity.

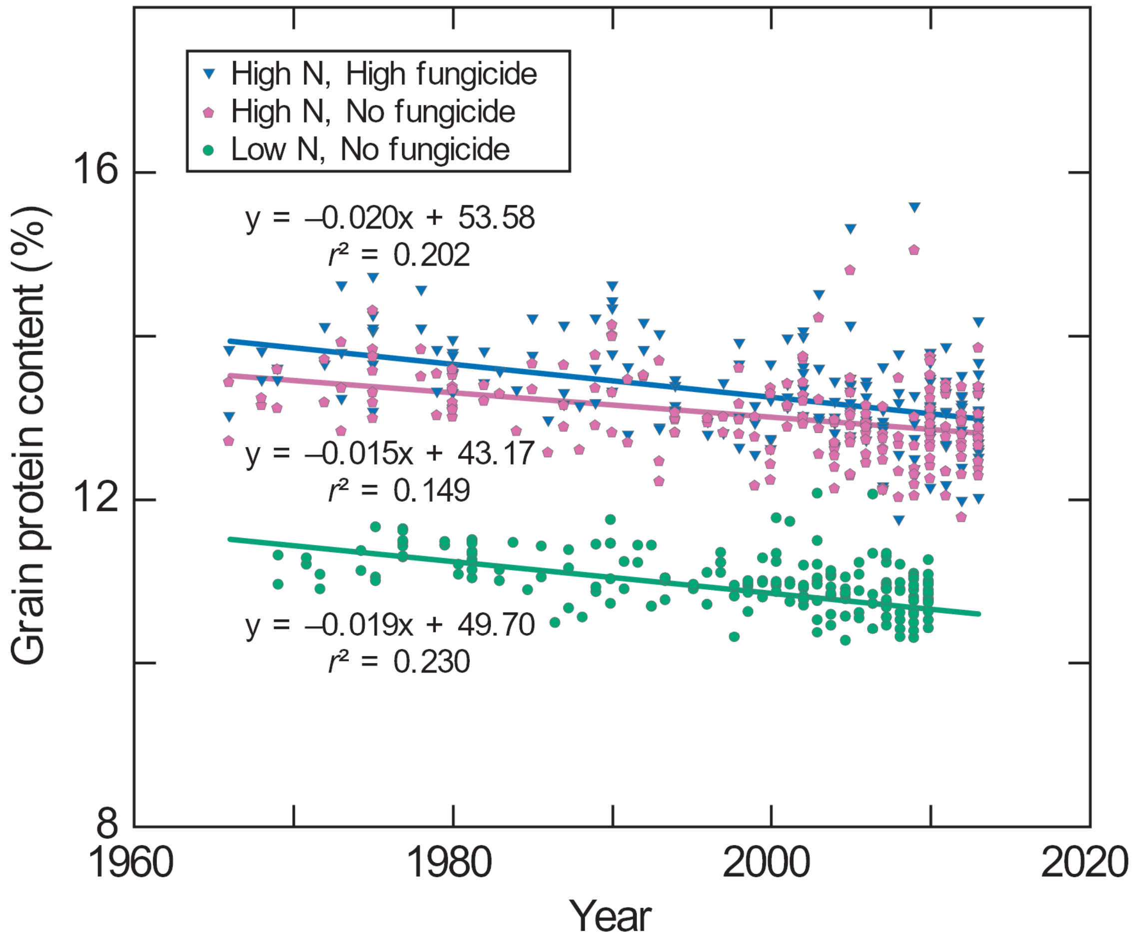

Fig. S2. Changes in wheat grain protein content (%) versus year of registration in field trials of elite winter wheat cultivars released during the past 50 years in western Europe, particularly Germany (Voss-Fels et al., 2019). Plots received 220 kg ha^{-1} N fertilizer and fungicide or no fungicide or 110 kg ha^{-1} N fertilizer and no fungicide. Shown are linear regressions labelled with slopes, intercepts, and correlations squared.