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Research paper

Running title: Climate change and wheat protein

Climate change impact and adaptation for wheat protein

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Abstract

Wheat grain protein concentration is an important determinant of wheat quality for human nutrition that is often overlooked in efforts to improve crop production. We tested and applied a

32-multi-model ensemble to simulate global wheat yield and quality in a changing climate. Potential benefits of elevated atmospheric CO_2 concentration by 2050 on global wheat grain and protein yield are likely to be negated by impacts from rising temperature and changes in rainfall, but with considerable disparities between regions. Grain and protein yields are expected to be lower and more variable in most low-rainfall regions, with nitrogen availability limiting growth stimulus from elevated CO_2. Introducing genotypes adapted to warmer temperatures (and also considering changes in CO_2 and rainfall) could boost global wheat yield by 7% and protein yield by 2%, but grain protein concentration would be reduced by -1.1 percentage points, representing a relative change of -8.6%. Climate change adaptations that benefit grain yield are not always positive for grain quality, putting additional pressure on global wheat production.

Keywords: food security, climate change impact, climate change adaptation, grain protein, wheat

Introduction

If current trends in human population growth and food consumption continue (Bajželj *et al.*, 2014), crop production must be increased by 60% by mid-century to meet food demands and reduce hunger (Godfray *et al.*, 2010), but climate change will make this task more difficult (Olesen *et al.*, 2011, Porter *et al.*, 2014, Waha *et al.*, 2013, Wheeler & Von Braun, 2013). Crop models are used to simulate crop growth and development from local up to global scales to assist in climate change impact assessments (Chenu *et al.*, 2017) and to evaluate agricultural adaptation options (Ruiz-Ramos *et al.*, 2017), for example, to investigate potential effects of altering crop management, like sowing crops earlier or later in the season (Porter *et al.*, 2014) or growing cultivars with different crop traits (Semenov & Stratonovitch, 2015, Tao *et al.*, 2017b). A growing number of studies describe climate change impacts on crop yield, but the impacts on the nutritional value of the crops have received much less attention even though this is a critical aspect of food security (Haddad *et al.*, 2016). Grain protein concentration, the ratio of grain protein amount to grain yield, is an important characteristic affecting the nutritional quality but also the end-use value and baking properties of wheat flour (Shewry & Halford, 2002). Globally, wheat provides 20% of protein for humans (Tilman *et al.*, 2011). Grain protein concentration, like yield, depends on a combination of factors such as the crop genotype, soil, crop management, atmospheric CO_2 concentration and weather conditions (Triboi *et al.*, 2006, Wieser *et al.*, 2008). Elevated CO_2 concentration alone can increase the total amount of protein in grain (Broberg *et al.*, 2017), but reduces its concentration (Broberg *et al.*, 2017, Myers *et al.*, 2014). Grain protein concentration increases with drought stress and higher temperatures as a result of reduced starch accumulation (Triboi *et al.*, 2006).

We aimed to systematically study the combined effects of CO_2, water, nitrogen (N) and temperature on wheat grain protein concentration in a changing climate for the world's main wheat producing regions as part of the Agricultural Model Intercomparison and Improvement Project (AgMIP) (Rosenzweig *et al.*, 2013). This is the most comprehensive study ever done of the effect of climate change on yield and the nutritional quality of one of the three major sources of human food security and nutrition (the others being rice and maize). We previously demonstrated that large ensembles of wheat models accurately simulate wheat yield under different environmental conditions, and especially under high temperatures (Asseng *et al.*, 2015). Here, we used a crop model ensemble to estimate the impact of climate change and a potential adaptation to such changes on global grain protein. To see if crop models can simulate the impact of climate change adequately, we first tested whether an ensemble of 32 different wheat models could reproduce the effects of increased temperature, heat shocks, elevated atmospheric CO_2 concentration, water deficit and the combination of these factors on yield and particularly on grain protein. As there have been many climate change impact studies without adaptation and studies testing the sensitivity of hypothetical traits, here, we included a trait adaptation option based on realistic traits from a wide range of field observations that justify the existence of unique heat stress tolerance traits in wheat.

Materials and Methods

Crop Models

Thirty-two wheat crop models (Supplementary Table S1) were compared within the Agricultural Model Intercomparison and Improvement Project (AgMIP; www.agmip.org), using two data sets from quality-assessed field experiments (sentinel site data) and then applied at representative locations across the world. 18 of these models simulated grain protein. All model simulations were executed by the individual modeling groups.

Field experiments for model testing

Two field/chamber experiments (INRA, FACE Australia) were used for model testing.

INRA temperature experiment

The response of the winter wheat cultivar Récital to heat shocks (i.e., 2 to 4 consecutive days with maximum air temperature of 38°C) during the grain filling period was studied during three winter growing seasons at INRA Clermont-Ferrand, France (45.8° N, 3.2° E, 329 m elevation) (Majoul-Haddad *et al.*, 2013, Triboi & Triboi-Blondel, 2002). For details see Supplementary Materials and Methods.

FACE Australia experiment (CO_2 × temperature × water)

FACE data were obtained from selected treatments from a designed experiment from Horsham, Australia (36.8°′ S, 142.1° E, 128 m elevation) (Supplementary Table S3). Details presenting the experimental design (Mollah *et al.*, 2009), the experimental data (Fitzgerald *et al.*, 2016), and modelling analyses (O'Leary *et al.*, 2015a) have previously been published. Data were collated from one cultivar (cv. Yitpi) under two water regimes (rain-fed and supplemental irrigation), two nitrogen fertilization regimes (53 or 138 kg N ha^{-1}), and two sowing dates to create two growing season temperature environments for both daytime ambient (365 ppm) and elevated (550 ppm) atmospheric CO_2 concentrations. For details see Supplementary Materials and Methods.

Field experiments for adaptation

Asseng et al. (2015) recently suggested a combination of delayed anthesis with an increased grain filling rate as possible adaptation for wheat to increased temperature. Such trait combination has never been shown yet to exist in the current available genetic material. Therefore, here we first explored a wide range of existing field experiments. We selected field experiments where a number of cultivars were grown across different temperature environments to search for the existence of such trait combination and if such cultivars are indeed better adapted to a warming climate, i.e., these cultivars yield higher than other cultivars under warmer conditions. In these data sets, we looked for pairs of cultivars where one or more had a delayed anthesis in a warmer environment combined with an increased grain filling rate, and yielded higher in the warmer environment than a control cultivar (without these traits). Only the cultivar pairs which fulfilled these conditions are mentioned here. Four field experiments were considered and included experiments from Egypt, Italy, USA and CIMMYT. In each experiment, cultivars were compared under growing environments with increasing temperatures (through delayed sowing or growing at warmer locations). The Egypt experiment included three cultivars grown over three years under full irrigation (and sufficient N) across four temperature environments along the River Nile with two sowing dates. The Italy experiment, included two cultivars grown over two years under full irrigation (and sufficient N) at one location with two sowing dates. In the Italy experiment, the same experiment was repeated with N limitations. The USA experiment included four cultivars (three cultivars were used as a control) grown for one year under full irrigation (and sufficient N) across 11 temperature environments along a transect in the south-east US with one sowing date. The CIMMYT experiment included data from the International Heat Stress Genotype Experiment (IHSGE) (Reynolds *et al.*, 1994), with two cultivars grown over two years under full irrigation (and sufficient N) across six temperature environments (experiments in different countries) with two sowing dates. For details see Supplementary Materials and Methods.

Global impact assessment

The two main scaling methods most commonly used in climate change impact assessment studies are sampling and aggregation (Ewert *et al.*, 2015, Ewert *et al.*, 2011). In sampling, the simulated points are assumed to represent an area (van Bussel *et al.*, 2016, van Bussel *et al.*, 2015), while in aggregation, an area is simulated with grid cells (Porwollik *et al.*, 2017) or polygons assuming a grid cell (or polygon) is equal to a point. Each method differs in uncertainties with respect to input information (high in gridded simulation (Anderson *et al.*, 2015), less in sampling as true point data are used) and representation of heterogeneity (high in gridded simulation, less in sampling which however depends on the sampling strategy (Zhao *et al.*, 2016). We have chosen stratified sampling, a guided sampling method which improves the scaling quality (van Bussel *et al.*, 2016), with several points per wheat mega region (Gbegbelegbe *et al.*, 2017). During the upscaling, a simulation result of a location was weighted by the production a location represents (Asseng et al. 2015). Liu et al. (2016) recently showed that stratified sampling and weighted by the production with 30 locations across wheat mega regions resulted at country and global scale in similar temperature impact and uncertainty as aggregation of simulated grid cells. The uncertainty due to sampling decreases with increasing number of sampling points (Zhao *et al.*, 2016). We therefore doubled the 30 locations from Asseng et al. (2015) to 60 locations (Fig. 1; Supplementary Table S4) covering contrasting conditions across all wheat mega regions. All models provided simulations for thirty high-rainfall or irrigated wheat-growing locations (Locations 1 to 30, simulated with no water or nitrogen limitations), representing about 68% of current global wheat production and 30 low-rainfall wheat-growing locations with wheat yields below 4 t DM ha^{-1} (Locations 31 to 60), representing about 32% of current global wheat production (Reynolds & Braun, 2013). Each location represents an important wheat-growing area worldwide (Fig. 1).

[figure 1 here]

Additional details about the locations 1 to 30 can be found in (Asseng *et al.*, 2015). In contrast to the high-rainfall locations 1 to 30, soil types and N management vary among the low-rainfall locations 31 to 60 (Supplementary Fig. S1-4). For details see Supplementary Materials.

Climate scenarios

There were two steps in global impact simulations. In step 1, six scenarios were simulated for the 60 global locations and 30 years of climate. The six climate scenarios had a baseline climate

(1981-2010) or baseline climate with main daily temperature increased by 2 or 4°C, crossed with two atmospheric CO_2 concentrations, 360 and 550 ppm (Table 1).

The baseline (1980-2010) climate data are from the AgMERRA climate dataset (Ruane *et al.*, 2015a), which combines observations, data assimilation models, and satellite data products to provide daily maximum and minimum temperatures, solar radiation, precipitation, wind speed, vapor pressure, dew point temperatures, and relative humidity corresponding to the maximum temperature time of day for each location. These data correspond to carbon dioxide concentration ([CO_2]) of 360 ppm. The Baseline+2ºC and Baseline+4°C scenarios were created by adjusting each day's maximum and minimum temperatures upward by that amount and then adjusting vapor pressure and related parameters to maintain the original relative humidity at the maximum temperature time of day. Observations and projections of climate change indicate that relative humidity is relatively stable even as this implies increases in specific humidity as temperatures increase (commensurate with the Clausius-Clapeyron equation; (Allen & Ingram, 2002)).

[table 1 here]

In a second step, wheat production in the 60 global locations were simulated under a climate change scenario corresponding to relatively high emissions for the middle of the 21st century (RCP8.5 for 2040-2069, using 571ppm [CO_2] at 2055 from RCP8.5). Projections were taken from five global climate models (GCMs) (HadGEM2-ES, MIROC5, MPI-ESM-MR, GFDL-CM3, GISS-E2-R), with historical conditions modified to reflect projected changes in mean temperatures and precipitation along with shifts in the standard deviation of daily temperatures and the number of rainy days (Supplementary Fig. S7-8). These scenarios were created using the "Enhanced Delta Method" (Ruane *et al.*, 2015b), and GCMs were selected to include models with relatively large and relatively small global sensitivity to the greenhouse gases that drive climate changes to account for the uncertainty of the fifth coupled model intercomparison project (CMIP5) GCMs ensemble (Ruane & McDermid, 2017).

Each scenario was examined with current management as well as under one possible trait adaptation, a cultivar combining delayed anthesis and an increased potential grain filling rate. Therefore, there were 11 treatments and each was simulated for 30 years at each of the 60 locations.

To consider the diversity of model approaches of the 32 participating wheat models and allow all modelers to incorporate their models, we proposed a simple but still physiological-based trait combination. The proposed traits were simulated in full combination only, to quantify the impact of such a trait combination. The aim of this study was not to analyze the contribution of various individual traits, nor to explore the full range of traits that could possibly assist in an adaptation strategy.

The proposed simple trait combination to minimize the impact of future increased temperatures on global yield production included (Supplementary Table S6):

1. *Delay anthesis by about 2 weeks under the Baseline* scenario via increased temperature sum requirement, photoperiod sensitivity, or vernalization requirement. No change in the temperature requirement for grain filling duration was considered.
2. *Increase in rate (in amount per day) of potential grain filling by 20%* (escape strategy).

Testing the climate change response of models without N dynamics

Simulation results from all 32 models were used in the grain yield impact analysis. When analyzing the impacts on grain protein yield and protein concentration, only 18 crop models were used that had routines to simulate crop N dynamics leading to grain protein and had been previously tested with field measurements. The yield distributions and yield impacts simulated with the 32 models and the 18 models used in protein analysis were similar (Supplementary Fig. S10-11).

We also applied the Kolmogorov–Smirnov two-sample test to test the differences of the distributions of simulated yield impacts from the 18 models (used in the protein analysis) and the 32 models. The distributions of climate change impacts on grain yields were different for the two multi-model ensembles for the climate change scenarios with genetic adaptation, but not without the genetic adaption and for the trait effect (Supplementary Table S7).

Aggregation of local climate change to global wheat production impacts

Before aggregating local impacts at 60 locations to global impacts (Fig. 1), we determined the actual production represented by each location. The total wheat production for each country came from FAO country wheat production statistics for 2014 (www.fao.org). For each country, wheat production was classified into three categories (i.e., high rainfall, irrigated, and low rainfall). The ration for each category was quantified based on the Spatial Production Allocation Model (SPAM) dataset (https://harvestchoice.org/products/data). For some countries where no data was available through the SPAM dataset, we estimated the ratio for each category based on the country-level yield from FAO country wheat production statistics. The high rainfall production and irrigated production in each country were represented by the nearest high rainfall and irrigated locations (Location 1-30). Low rainfall production in each country was represented by the nearest low rainfall locations (Location 31-60).

The global wheat grain and protein production impact was calculated using the following steps:

1) Calculate the relative simulated mean yield (or protein yield) impact for climate change scenarios for 30 years (1981-2010) per single model at each location.
2) Calculate the *median across 32 models* (or 18 in case of protein simulations) *and five GCMs per location (multi-model [CMs and GCMs] ensemble median)*. Note that CMs and GCMs simulation results were kept separate only for calculating the separate CM and GCM uncertainties (expressed as range between 25th and 75th percentiles).
3) Calculate the absolute regional production loss by multiplying the relative yield (or protein yield) loss from the multi-model ensemble median with the production represented at each location (using FAO country wheat production statistics of 2014 from www.fao.org, the latest reported yield statistics available at the time of the study). Calculate separately for high rainfall/irrigated and low input rainfed production. This assumes that the selected simulated location is representative of the entire wheat-growing region surrounding this location.
4) Add all regional production losses to the total global loss.
5) Calculate the relative change in global production (i.e., global production loss divided by current global production).
6) Repeat the above steps for the 25th and 75th percentile relative global yield (or protein yield) impact from the 32 (or 18 in case of protein simulations) model ensemble.

The 18-model ensemble used for protein simulations simulated similar yield impacts compared to the 32-model ensemble (Supplementary Table S7), but small yield differences between the two ensembles made it necessary to normalize the simulated impacts from the two ensembles for the calculation of impacts on grain protein concentration. The reported impacts on grain protein concentration are therefore the normalized numbers. The 32-model ensemble yield impacts and the simulated 18-model ensemble relative grain protein yield impacts are directly reported (i.e., without this normalizing). The calculation of changes in grain protein concentration is shown with equations below.

Yield change (y_c), due to climate change or the introduction of a trait, was calculated as:

$$y_C = \tilde{y}^{(32)}_{future} / \tilde{y}^{(32)}_{baseline} \tag{1}$$

where $\tilde{y}^{(32)}_{future}$ and $\tilde{y}^{(32)}_{baseline}$ are respectively future (with or without adaptation) and Baseline yield as simulated by the median of 32 models. Grain protein yield change (p_c) is calculated as:

$$p_C = \tilde{p}^{(18)}_{future} / \tilde{p}^{(18)}_{baseline} \tag{2}$$

where $\tilde{p}^{(18)}_{future}$ and $\tilde{p}^{(18)}_{baseline}$ are respectively future (with or without adaptation) and baseline protein yield as simulated by the median of 18 models.

Impact on grain protein concentration uses global mean grain yield in 2014 as a baseline, reported as 3.31 t DM ha^{-1} (FAO, 2016) and a mean grain protein percentage of 13% (based on dry matter grain weight), which is a weighted average of the simulated results. While there are no global statistics on grain protein, the simulated global grain protein concentration appears reasonable, considering the protein content in the USDA World Wheat Collection has been reported to range from 7% to 22% of the dry weight (Vogel *et al.*, 1976), but generally varies from about 10–15% of the dry weight for wheat cultivars grown under field conditions (Shewry & Hey, 2015). Observed grain protein content in temperate regions, like the Netherlands has been reported to range from 10 to 15% (Asseng *et al.*, 2000)). An average of 13.2% (ranging from 10.5 to 16.3%) grain protein concentration has been reported across 330 wheat varieties from China grown during 2010-2011 (Yang *et al.*, 2014) and an average of 13.4% was reported across wheat fields in Finland during 1988-2012 (Peltonen-Sainio *et al.*, 2015).

In the simulated weighted average, the mean of the high rainfall/irrigated locations 1 to 30 has a weight of about 2/3, and the mean of the low rainfall/low input locations 31 to 60 has a weight of about 1/3, according to their contribution to global production. The impact on grain protein concentration ($\Delta GP\%$) was calculated as follows:

$$\Delta GP\% = \frac{p_C \times 3.31 \times 0.13}{y_C \times 3.31} - \frac{3.31 \times 0.13}{3.31} = 0.13\left(\frac{p_C}{y_C} - 1\right) \quad (3)$$

This results in a change in grain protein concentration of -0.59 percentage point when using the changes in grain yield from 32 crop models as used in the analysis. Alternatively, using the changes in yield from the 18 crop models would result in a change in grain protein concentration of -0.36 percentage point (not used here).

Results

Model testing

Results of crop model simulations were compared to observations from outdoor chamber and free-air CO_2 enrichment (FACE) experiments with increased temperature, heat shocks, and elevated CO_2 combined with increased temperature and drought stress. A statistical analysis on model ensemble performance for grain yield, grain protein yield and grain protein content is given in Table S4, showing RMSE for yield from 0.4 to 1.9 t ha^{-1}, with reasonable skill (EF) to simulate the variability for observed yield. RMSE for protein concentration ranged from 0.8 to 3.2% with poor skill due to the low variability in the observed protein concentration data (Table S4). Median predictions from this multi-model ensemble reproduced observed grain yields well including those affected by heat shock, high temperature or elevated CO_2 concentration (Fig. 2A-C). Continuous high temperature conditions during the grain filling period (the period when the grain grows) reduced observed and simulated biomass growth and yield more than a 4-day heat shock, applied at different times during the same growth period, but elevated CO_2 increased biomass growth and yield in the observations and simulations. In addition, changes in grain protein yield and protein concentrations were captured well (i.e. similar response in simulations and observations) even under conditions where effects of temperature interacted with effects of CO_2 concentration and water (Fig. 2D-I). The multi-model ensemble median and at least 50% of the simulation results for growth dynamics, final grain and protein yield, and protein concentration were generally within the uncertainty intervals of the measurements (Fig. 2).

[figure 2 here]

Observed adaptation traits for climate change

Using datasets from observed field experiments (not simulations) at different locations in the world (in USA, Mexico, Egypt, Sudan and Italy), we found in these observations that existing genotypes with a trait of an extended growing period to delay anthesis (also called flowering), combined with a trait with a higher rate of grain filling (i.e. potential grain filling rate which is met when assimilates are available from photosynthesis and/or remobilization), are effective in countering some of the yield declines occurring in non-adapted cultivars when grown in warmer locations or during a warmer part of a season (Fig. 3A). Other cultivars which had a delayed anthesis but not an increase grain filling rate (not shown here), did not yield higher than the non-adapted cultivars. For some locations, where observed grain protein data were available, the combination of delayed anthesis and higher rate of grain filling traits also increased grain protein yield in one cultivar compared to another cultivar (but for several cultivar pairs) when grown under warmer growing conditions, although these traits were not fully expressed under cooler conditions (Fig. 3B).

[figure 3 here]

Observed grain and protein yield increased with this trait combination in warmer climates, but not when N supply was limited (Fig. 4).

[figure 4 here]

However, the relative change in observed grain yield was positively correlated with the change in grain protein concentration, even under limited nitrogen supply (Fig. 5).

[figure 5 here]

Global climate change impact

Availing of a robust predictor with a multi-model ensemble (Fig. 2) and evidence from field experiments for the existence for traits to counteract detrimental effects from raising temperature on crops (Fig. 3-5), we assessed with crop models what impact climate change would have on overall wheat grain and protein yield and on protein concentration at other locations and globally (Fig. 1). The 32 tested crop models were applied with five bias-corrected global climate models (GCMs) for the representative concentration pathway 8.5 (RCP8.5) for the 2050s. The multi-model median (crop models plus GCMs) impact of climate change and the variation across crop models and GCMs is shown for 60 locations around the globe representing major wheat producing regions and climate zones (Fig. 6). In general, low and mid-latitude locations show negative yield impacts from climate change, while high-latitude locations show some positive yield impacts. Negative impacts on protein yields were predicted at many locations, including high-latitude locations (Fig. 6A).

Effect of adaptation

The field-identified trait combination of delayed anthesis and increased grain filling rate was introduced into the crop models (Supplementary Table S6). Simulated yields did not improve in many of the low-rainfall/low-input locations due to a combination of terminal drought and N limitation (Fig. 4). Protein yields that increased with the introduced trait combination were negatively affected by climate change for many locations, including those at high latitudes (Fig. 6). But grain yields were improved in most locations with the trait combination of delayed anthesis and increased grain filling rate (Fig. 6B).

[figure 6 here]

The impact of climate change on grain protein concentration, which varies with both grain yield and protein yield, was more variable. Grain protein concentration varied between growing seasons and locations as did the response to climate change and the impact of the adapted trait combination (Fig. 7). While the combined impact of increased temperature, elevated CO_2 concentration, and change in rainfall for RCP8.5 indicates that grain yield would increase for many seasons and locations, protein yield increase would not keep pace. This would result in a reduction in grain protein concentration for many situations (Fig. 7). However, climate change and the adapted trait combination could lead to an increase in grain protein concentration for low-rainfall locations, particularly for those locations where yield is projected to decline (Fig. 7).

[figure 7 here]

We scaled the simulated impacts up from fields to globe by weighting each location with reported country wheat production data. Despite the stimulating effect of elevated CO_2 on crop growth, global wheat production would only increase by 2.8% (-7.4 to +14.0%, 25th to 75th percentile range combining crop model and GCM uncertainty) by 2050 under RCP8.5. Most of the gains from elevated CO_2 on crop growth will be lost due to increasing temperature. Simultaneously introducing the trait combination of delayed anthesis and increased grain filling rate could increase global yield to 9.6% (-7.8 to 27.0%) by 2050, with the impact from traits being 6.8%.

The growth stimulus from a 100-ppm increase in atmospheric CO_2 concentration is lost with an increase of about 2 °C (increase of 1.0 to 4.2 °C, 25th to 75th percentile range of crop model uncertainty) according to the simulated multi-model ensemble median (Fig. 8).

[figure 8 here]

However, when N limited growth, as is common for low-rainfall environments with low-fertilizer inputs, the growth stimulus was reduced. The multi-model ensemble median, averaged over 30 years, shows a CO_2 effect of 8.4% global yield increase (5.7 to 12.8% for 50% of crop models, weighted by production) per 100 ppm increase in CO_2 (Fig. 8). Protein yields were estimated to change by -1.9% (-9.6 to +5.5% change, 25th to 75th percentile range combining crop model and GCM uncertainty) at the global scale with climate change, with many regions expected to be affected. Crop models account for a dilution of crop N and grain protein concentration at elevated CO_2 concentration (Fig. 9). When the trait combination of delayed anthesis and increased grain filling was introduced, simulated global protein yield changed to -0.2% (-12.1 to +12.0% change) by 2050, with the impact from traits being 1.7%. Similarly, while extremely variable between locations and seasons (Fig. 7), protein concentration is estimated to change by -0.6 percentage points, representing a relative change of -4.6% (-0.3 to -1.0 percentage points, representing a relative change of -2.4 to -7.5%) by 2050 at the global scale. Greater losses in protein concentration would occur in many regions and seasons, amounting to -1.1 percentage points, representing a relative change of -8.6% (-0.6 to -1.5 percentage points, representing a relative change of -4.7 to -11.8%), with the impact from traits being -0.5 percentage points, representing a relative change of -4.1%.

[figure 9 here]

Impact uncertainty

For the simulated impact estimates, the share of uncertainty from crop models was often larger than from the five bias-corrected GCMs (Fig. S12). Uncertainties tended to increase with adaptation and were larger for impact estimates for protein yield than for grain yield. The largest crop model uncertainties were for low and mid-latitude areas (Fig. S12).

Discussion

Model testing

Median predictions from this multi-model ensemble reproduced observed grain yields well, consistent with other multi-model ensemble studies (Asseng *et al.*, 2013, Bassu *et al.*, 2014, Li *et al.*, 2015, Martre *et al.*, 2015), but here including those affected by heat shock, high temperature and elevated CO_2 concentration, a critical pre-request for simulating climate change impacts. Heat shock and high temperature interaction with elevated CO_2 concentration have never been tested with any impact model before. Multi-model ensemble simulations were recently compared with historical yields and showed that simulated yield impacts from temperature increase were similar to statistical temperature yield impact trends based on historical sub-country, country and global yield records (Liu *et al.*, 2016). This result suggests that interactions between climate and crop models can be insensitive to the methods chosen, thus further supporting the use of the state-of-the-art multi-model ensembles such as the one used for this study.

Grain protein concentration is suggested by the simulation to decline globally by -1.1 percentage points, representing a relative change of -8.6%, due to the simulated yield increase (for most locations) from elevated atmospheric CO_2 and the yield-improving trait adaptation. Attributing changes in observed protein trends is often hindered by many confounding factors in the field.

For example, a study across fields in Finland from 1988 to 2012 showed a decline in grain protein concentration over this period of up to -0.7 grain protein % during the last third of this period (Peltonen-Sainio *et al.*, 2015). Some of this declined has been attributed to plant breeding for higher yields and a declining response over time of grain protein concentration to N fertilizer (Peltonen-Sainio *et al.*, 2015). In contrast, despite yield increases (by 51%) with variety releases since 1968 in North Dakota, USA, grain protein concentration has not changed during this time (Underdahl *et al.*, 2008).

Depending on the target market, required protein concentrations vary from 8% for pastries to >14% for pasta and bread, farmers grow specific wheat categories for specific markets. In addition, farmers might also attempt to manage N applications towards protein outcomes, but their effectiveness is often hampered by in-season variability in growing conditions (Asseng and Milroy 2006). Recent trends in N fertilizer application (total amount of N fertilizer applied in agriculture) in the 20 major wheat producing countries, including China, India, Russia, USA and several European countries have leveled off or even declined like in France and Germany (FAO, 2018) and might further reduce wheat grain protein concentrations in the future.

Adaptation traits for climate change

Rising temperatures are the main driver of projected negative climate change impacts on wheat yields (Porter *et al.*, 2014). The shortening of the growing period (the time from sowing to maturity) with increasing temperatures has been identified as the main yield-reducing factor in another study, but not implemented (Asseng *et al.*, 2015). In a warmer climate, the growing period is shorter so there is less time to intercept light for photosynthesis resulting in less biomass accumulation and lower yields. To adapt crops to a warmer climate, the growing period could be extended by delaying anthesis. However, grain filling generally occurs during the relatively hot period of the season in most wheat growing regions (Asseng *et al.*, 2011), so yield might be reduced due to the negative effect of even higher temperatures on the sensitive processes of grain set (time when the number of grains is set) and grain filling. Therefore, combining traits for delayed anthesis and higher rate of grain filling, as shown in our study, is an effective adaptation strategy for yield. While grain and protein yield increased with the newly introduced trait combination in warmer climates, grain protein concentration still declined in some cases when other growth restricting factors such as limited N supply also suppressed expression of these traits in a warmer climate. Applying additional N fertilizer application might not be a simple solution for climate change adaptation as major wheat-producing countries, such as France have been reducing N fertilizer application rates since the late 1980s (Brisson *et al.*, 2010).

A key message from our study is that, our results suggest that the combination of two simple traits through breeding can be used to overcome the antagonism between grain yield and grain protein concentration. That antagonism has continuously reduced the nutritional and end-use value of wheat since the 'green revolution' in the 1960ies with strongly increasing grain yields through the introduction of semi-dwarf genotypes combined with irrigation and fertilizers (Triboi *et al.*, 2006). The field-observed positive correlation in field experiments between grain yield and protein concentration could be due to an increase in crop N accumulation at anthesis related to the extended duration of the vegetative phase and a more efficient translocation to grains during grain filling. But, it could also be due to a higher nitrogen remobilization rate and earlier leaf senescence. Hence, there is a need to improve the understanding of the physiological basis for the field-based observed positive correlation between grain yield and protein concentration through new targeted field experiments.

Global climate change impact

While field experiments are critical for developing and testing hypotheses, these are limited to just a few sites and seasons. The application of a multi-model ensemble, combined with evidence from field experiments for the existence for traits to counteract detrimental effects from raising temperature on crops, enabled us to assess what impact climate change would have on overall wheat grain and protein yield and on protein concentration at other locations and globally. By applying the 32 tested crop models with five bias-corrected global climate models (GCMs), we covered a wide range of available GCM outputs (McSweeney & Jones, 2016). The chosen representative concentration pathway 8.5 (RCP8.5) for the 2050s is a high greenhouse gas concentration scenario with emissions continue to increase at current rates. Low and mid-latitude locations show mostly negative yield impacts from climate change, while high-latitude locations show some positive yield impacts, consistent with other global studies and other crops (Rosenzweig *et al.*, 2014), but negative impacts on protein yields were predicted at many locations, including high-latitude locations.

Effect of adaptation

The combined impact of increased temperature, elevated CO_2 concentration, and change in rainfall for RCP8.5 indicates that grain yield would increase for many seasons and locations, but protein yield increase would not keep pace and would result in a reduction in grain protein concentration for many situations. However, climate change and the adapted trait combination could lead to an increase in grain protein concentration for low-rainfall locations, particularly for those locations where yield is projected to decline.

Most of the gains from elevated CO_2 on crop growth will be lost due to increasing temperature consistent with other simulation and field experimental studies (Asseng *et al.*, 2015, Wheeler *et al.*, 1996). Simultaneously introducing the trait combination of delayed anthesis and increased grain filling rate could increase global yield. About a third of the impact on grain yields (2.1%) from this trait combination could be achieved globally by introducing the adaptation in the baseline climate, although yield would be reduced for many of the rainfed locations subject to terminal drought.

A simulated growth stimulus from a 100-ppm increase in atmospheric CO_2 concentration is suggested by our study to be lost with an increase of about 2 °C according to the simulated multi-model ensemble median and is consistent with field experiments (Wheeler *et al.*, 1996). Higher yield responses to elevated CO_2 have been reported in field experiments for wheat subject to drought stress compared to well-watered controls (Kimball, 2016, O'Leary *et al.*, 2015b). This did not hold true, however, when N limited growth (Kimball, 2016), as is common for low-rainfall environments with low-fertilizer inputs. The multi-model ensemble median here, averaged over 30 years, shows a CO_2 effect of 8.4% global yield increase per 100 ppm increase in CO_2. By comparison, observations from open top chamber and FACE field studies have shown 10-20% increases in wheat yield per 100 ppm elevated CO_2 (Ainsworth & Long, 2005, Kimball, 2016, O'Leary *et al.*, 2015b), but less or even nil yield change when N is limiting (Kimball, 2016). Additional N supply for crop uptake could therefore become more important in the future. However, acceleration of soil organic matter turnover by higher temperature depletes soil carbon and N stocks, a process captured by some models. Crop models also account for the dilution of crop N and grain protein concentration at elevated CO_2 concentration, giving results similar to experimental wheat data (Pleijel & Uddling, 2012), but do not consider that nitrate assimilation in crops could be inhibited (Bloom *et al.*, 2010), so likely underestimate the reduction in grain protein with climate change.

Other processes, like a possible effects of elevated CO_2 via stomata closure on canopy temperature (Kimball *et al.*, 1999), not considered in the current models might also add to under- or overestimation of simulated impacts. The same applies to the poor understanding of genotype and CO_2 interactions that are hence not included in the models (Myers *et al.*, 2014). Other factors not included might also become important for future crop performance, such as rising ground-level ozone exposures, e.g. in southern and eastern Asia (Tao *et al.*, 2017a) and diming of light for photosynthesis in areas with high aerosol pollution.

Our analysis of the multi-location field trials suggests that crops with traits of delayed anthesis time and increased grain filling rate could be combined in wheat genotypes to combat the negative effects of increasing temperature on yield. The genetics of wheat anthesis time is determined by known genes so adaptations can be made through breeding or cultivar choice (Griffiths *et al.*, 2009, Le Gouis *et al.*, 2012). Although grain filling results from interactions between multiple physiological processes, some relevant major quantitative trait loci have been identified, and grain filling rate can be increased efficiently through breeding (Charmet *et al.*, 2005, Wang *et al.*, 2009). Some studies also showed that the rates of dry mass and N accumulation have common genetic determinisms (Charmet *et al.*, 2005), so breeding for a higher rate of grain filling could improve both grain yield and protein concentration. Importantly, anthesis time and grain filling rate are mostly controlled by different loci (Wang *et al.*, 2009) suggesting that these two traits can be improved concomitantly. The impact on yield and protein from this potential adaptation depends on the availability of nitrogen during the post-anthesis period (Bogard *et al.*, 2011) and might require additional nitrogen remobilization into the grains (Avni *et al.*, 2014, Uauy *et al.*, 2006).

Impact uncertainty

The share of uncertainty from crop models was often larger than from the five bias-corrected GCMs, suggesting a need for more research investments into impact models to reduce climate change impact uncertainty estimates, although the chosen GCMs only represent part of the overall available GCM uncertainties (McSweeney & Jones, 2016). The crop model uncertainty varied across locations, while the GCM uncertainty showed less spatial variation. Uncertainties tended to increase with adaptation and were larger for impact estimates for protein yield than for grain yield, partly because fewer crop models were available for the former. The largest crop model uncertainties were for low and mid-latitude areas.

Conclusions

Our simulation results demonstrate that climate change adaptations that benefit grain yield are not necessarily positive for all aspects of grain quality for human nutrition (Myers *et al.*, 2014), particularly in rainfed and low-input cropping regions. Many of the regions likely to be negatively affected are low and mid-latitude regions that are less resilient to climate change, where populations are growing (Roser & Ortiz-Ospina, 2017) and food demand is increasing rapidly (Godfray *et al.*, 2010).

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Figure captions

Fig. 1. The thirty locations representing high rainfall and irrigated wheat regions (blue) and thirty locations representing low rainfall/low input regions (red) of the world used in this study. Wheat area from (Monfreda *et al.*, 2008).

Fig. 2. Measurements and multi-model simulations of total above ground wheat biomass, grain yield, grain protein yield and grain protein concentration for wheat treated with heat shocks, higher temperature, elevated atmospheric CO_2 concentration, and different sowing times or irrigation. (**a, b** and **c**) Total above-ground biomass (circles, continuous lines) and grain yields (triangles, dashed lines) for wheat for three different experiments grown in control conditions or with (**a**) heat shocks of 38°C for 4 h on 4 consecutive days during grain filling; (**b**) continuous +10°C/+5°C (day/night) temperature increase during endosperm cell division/early grain filling; and (**c**) elevated CO_2 (550 ppm). Multi-model ensemble medians (lines) and 25th to 75th percentile intervals (shaded areas) based on 32 simulation models are shown. Symbols indicate medians and error bars the 25th to 75th percentile intervals of measurements. **(d** to **i)** Percent changes in grain yield (**d** and **g**) and protein yields (**e** and **h**) and absolute changes in grain protein concentration (**f** and **i**) in response to chronic high temperature or heat shocks at different developmental stages (**d, e** and **f**) and different combinations of atmospheric CO_2 concentration, drought and sowing dates (**g, h** and **i**). Data are medians of measured or simulated changes and error bars show 25th to 75th percentile intervals. In all panels, simulations are the median of the 32 (grain yield) or 18 (grain protein) wheat model ensembles.

Fig. 3. Comparison of the relative performance of measured wheat genotypes with or without both delayed anthesis and accelerated grain filling traits grown under field conditions at different temperatures. Changes in measured grain yield (**a** and **b**), grain protein yield (**c** and **d**), and grain protein concentration (**e** and **f**) versus changes in traits. Symbol colors indicate mean temperatures during the growing season (from sowing to maturity) at each location in increasing order from deep blue, light blue, to red. The advanced wheat lines VA12W-72 and GA06493-13LE6 were compared to the standard cultivars AGS2000, Jamestown, and USG3120 in experiments at 10 locations in the U.S.A.. Mean values for AGS2000, Jamestown and USG3120 were used as the control to calculate changes in yield and protein. The modern cultivar Bacanora 88 and the standard cultivar Debeira were grown at one location in Mexico over two consecutive seasons, and at one location in Egypt and one in Sudan both for one season. The cultivars Creso and Claudio were grown at one location in Italy for two consecutive growing seasons. The modern elite cultivars Misr1 and Misr2 and the standard cultivar Sakha93 were grown at four locations in Egypt. Grain protein data were available for Italy and Egypt experiments only. Solid lines are standardized major axis regressions (all $P < 0.001$).

Fig. 4. Comparison of cultivars with delayed anthesis and accelerated grain filling rate to standard cultivars in different temperature environments in Italy with limited nitrogen (60 kg N ha^{-1}). Relationship of observed (**a** and **b**) grain yield and (**c** and **d**) protein yield to (**a** and **c**) anthesis and (**b** and **d**) to grain filling rate. Green (< 13^{o}C), dark red (13 to 15^{o}C) and red (> 15^{o}C).

Fig. 5. Comparison of wheat genotypes with delayed anthesis and accelerated grain filling rate compared to standard genotypes grown in the field in different temperature environments. Relative change in measured grain protein yield (**a**) and absolute change in grain protein concentration (**b**) against the relative change in grain yield. Symbol colors refer to mean temperature during growing season (planting to maturity) in increasing order from deep blue, light blue, to red for average temperatures at each location. The cv. Creso and the cv. Claudio were grown at one location in Italy for two consecutive growing seasons, and the modern elite cultivars Misr1 and Misr2 and the standard cultivar Sakha93 were grown at four locations in Egypt. Dashed line is 1:1 and solid lines are standardized major axis regressions.

Fig. 6. Simulated multi-model ensemble projection under climate change of global wheat grain yield (left half) and protein yield (right half), **(a)** without genotypic adaptation and **(b)** with genotypic adaptation. Relative climate change impacts for 2036-2065 under RCP8.5 compared with the 1981-2010 baseline. Impacts were calculated using the medians across 32 models (or 18 for protein yield estimates) and five GCMs (circle color) and the average over 30 years of yields using region-specific soils, cultivars and crop management.

Fig. 7. Multi-model impact of climate change with and without cultivar adaptation on the relationship between grain yield and protein concentration. Projections of annual wheat grain yield and grain protein concentration are shown for baseline period 1981-2010 (black) for RCP8.5 climate change impact in 2036-2065 with current cultivars (orange) or with genetic adaptation, i.e. combined delayed anthesis with increased rate of grain filling (cyan) for 30 individual years across 60 locations using region-specific soils, cultivars and crop management. **(a)** Grain yield versus grain protein concentration for individual years and locations. Medians across GCMs and 18 crop models are plotted. The ellipses capture 95% confidence levels of data in each treatment. Distributions of values for grain protein concentration **(b)** and grain yield **(c)** for 30 low-rainfall locations (dashed lines) and 30 high rainfall or irrigated locations (solid lines). **(d)** Absolute changes in crop model ensemble medians for grain yield versus grain protein concentration.

Fig. 8. Simulated impacts of increasing temperature on global wheat grain production with 100 ppm increase in atmospheric CO_2 concentration. Relative grain yield impacts were calculated from simulated impacts of 550 ppm versus 360 ppm CO_2 (linearly interpolated) and weighted by production. Center line shows crop model ensemble median of 32 crop models and mean of 30 years using region-specific soils, cultivars, and crop management. The shaded area indicates the 25th percentile and 75th percentile across crop models. Dashed lines are linear extensions to +5°C beyond simulated temperature range impacts. Equations show linear regression for before and after cross-point at 2°C.

Fig. 9. Simulated response to elevated CO_2. In (**a**) relative crop N response versus relative crop biomass response to elevated CO_2. In (**b**) relative protein yield response versus relative grain yield response to elevated CO_2. In (**c**) relative grain protein concentration response versus relative grain yield response to elevated CO_2. Data are multi-model (18 models) ensemble median for 30 individual years during baseline period (1981-2010) across 60 global locations with 360 ppm (baseline) and 550 ppm (elevated) CO_2.

Table 1. Outline of the baseline and climate change scenarios simulated in this study.

Period	Scenario / GCM	CO_2 (ppm)	Adaptation
1981-2010	Baseline	360	None
1981-2010	Baseline	360	2-traits combination
1981-2010	Baseline +2°C	360	None
1981-2010	Baseline +4°C	360	None
1981-2010	Baseline	550	None
1981-2010	Baseline +2°C	550	None
1981-2010	Baseline +4°C	550	None
2040-2069	HadGEM2-ES	571	None
2040-2069	MIROC5	571	None
2040-2069	MPI-ESM-MR	571	None
2040-2069	GFDL-CM3	571	None
2040-2069	GISS-E2-R	571	None
2040-2069	HadGEM2-ES	571	2-traits combination
2040-2069	MIROC5	571	2-traits combination
2040-2069	MPI-ESM-MR	571	2-traits combination
2040-2069	GFDL-CM3	571	2-traits combination
2040-2069	GISS-E2-R	571	2-traits combination

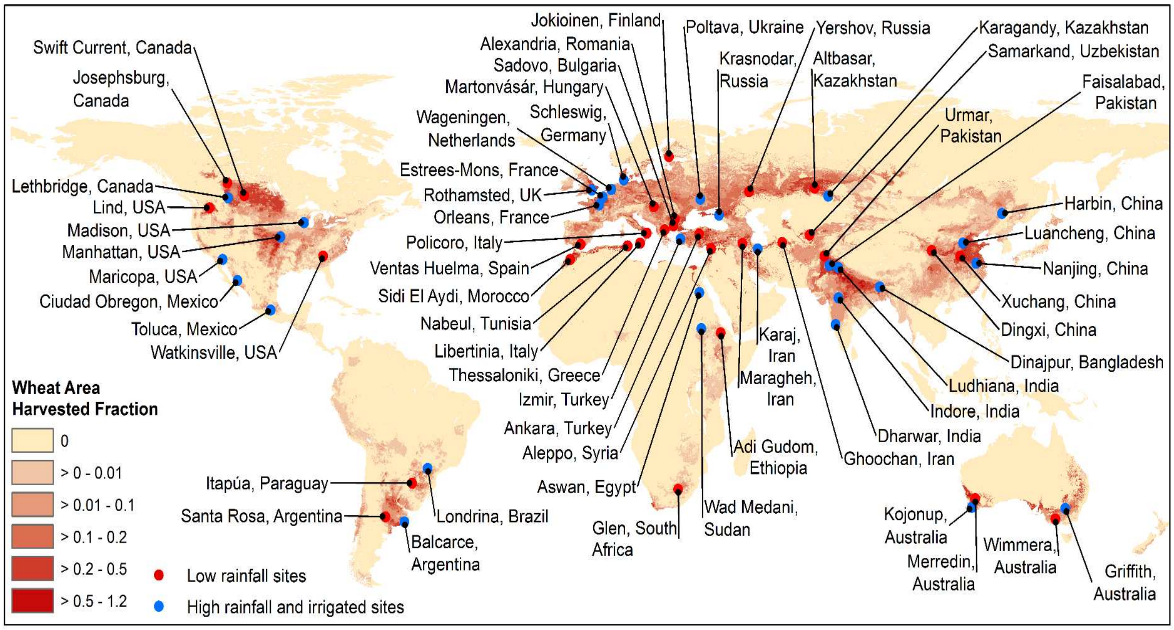
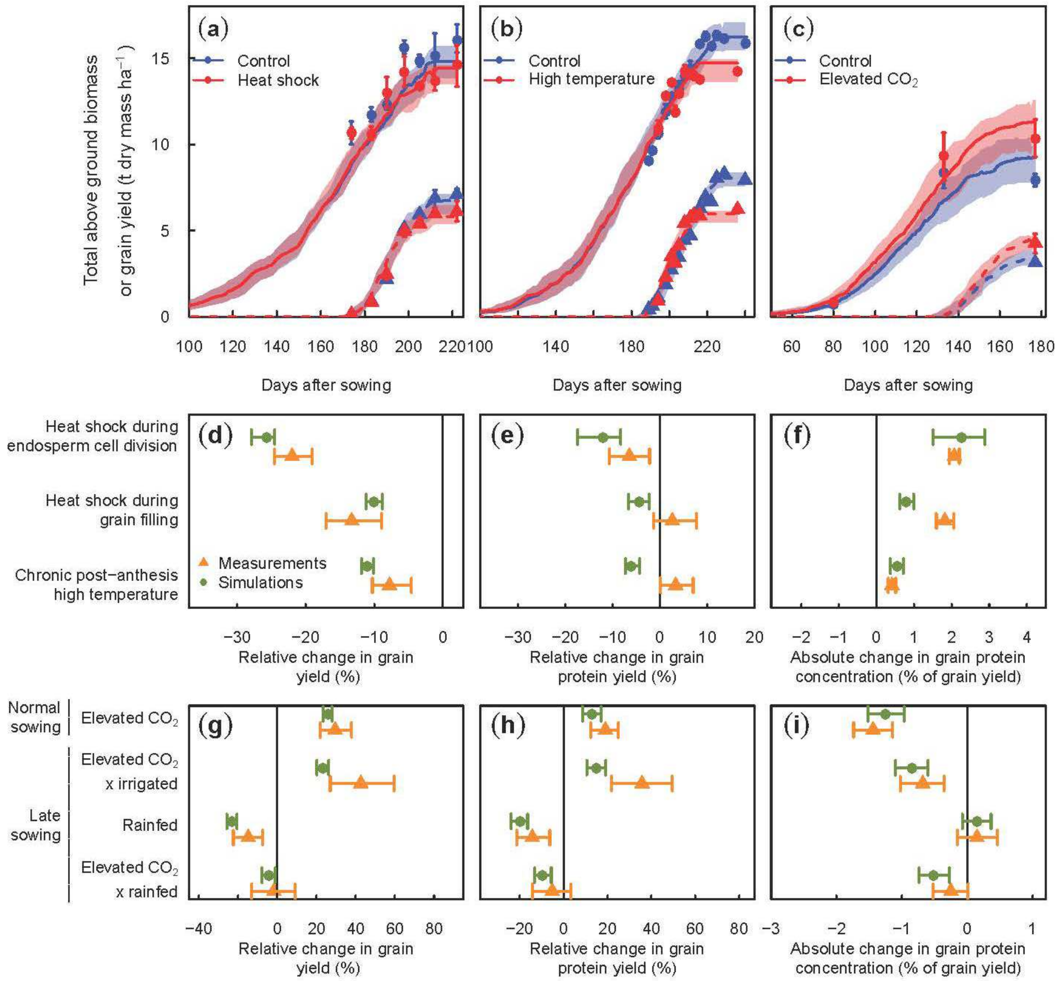
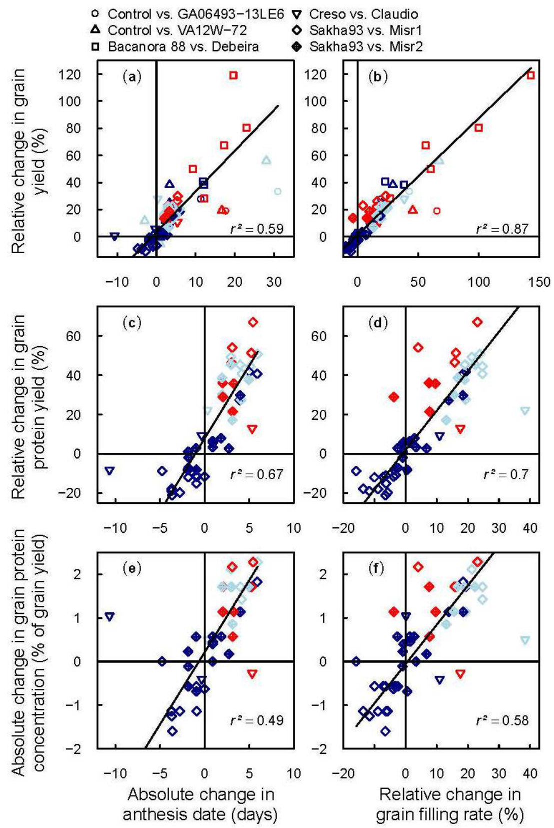

Swift Current, Canada
Josephsburg, Canada
Lethbridge, Canada
Lind, USA
Madison, USA
Manhattan, USA
Maricopa, USA
Ciudad Obregon, Mexico
Toluca, Mexico
Watkinsville, USA
Jokioinen, Finland
Alexandria, Romania
Sadovo, Bulgaria
Martonvásár, Hungary
Wageningen, Netherlands
Schleswig, Germany
Estrees-Mons, France
Rothamsted, UK
Orleans, France
Policoro, Italy
Ventas Huelma, Spain
Sidi El Aydi, Morocco
Nabeul, Tunisia
Libertinia, Italy
Thessaloniki, Greece
Izmir, Turkey
Ankara, Turkey
Aleppo, Syria
Aswan, Egypt
Poltava, Ukraine
Krasnodar, Russia
Yershov, Russia
Altbasar, Kazakhstan
Karagandy, Kazakhstan
Samarkand, Uzbekistan
Faisalabad, Pakistan
Urmar, Pakistan
Harbin, China
Luancheng, China
Nanjing, China
Xuchang, China
Dingxi, China
Dinajpur, Bangladesh
Ludhiana, India
Indore, India
Dharwar, India
Ghoochan, Iran
Karaj, Iran
Maragheh, Iran
Adi Gudom, Ethiopia
Wad Medani, Sudan
Glen, South Africa
Itapúa, Paraguay
Londrina, Brazil
Santa Rosa, Argentina
Balcarce, Argentina
Kojonup, Australia
Merredin, Australia
Wimmera, Australia
Griffith, Australia
Wheat Area Harvested Fraction
0
> 0 - 0.01
> 0.01 - 0.1
> 0.1 - 0.2
> 0.2 - 0.5
> 0.5 - 1.2
Low rainfall sites
High rainfall and irrigated sites

Fig. 1



(a)
Control
Heat shock
(b)
Control
High temperature
(c)
Control
Elevated CO2
Total above ground biomass or grain yield (t dry mass ha−1)
Days after sowing
(d)
(e)
(f)
Heat shock during endosperm cell division
Heat shock during grain filling
Chronic post−anthesis high temperature
Measurements
Simulations
Relative change in grain yield (%)
Relative change in grain protein yield (%)
Absolute change in grain protein concentration (% of grain yield)
(g)
(h)
(i)
Normal sowing
Elevated CO2
Late sowing
Elevated CO2 x irrigated
Rainfed
Elevated CO2 x rainfed
Relative change in grain yield (%)
Relative change in grain protein yield (%)
Absolute change in grain protein concentration (% of grain yield)

Fig. 2



Control vs. GA06493−13LE6
Control vs. VA12W−72
Bacanora 88 vs. Debeira
Creso vs. Claudio
Sakha93 vs. Misr1
Sakha93 vs. Misr2
(a)
(b)
(c)
(d)
(e)
(f)
r² = 0.59
r² = 0.87
r² = 0.67
r² = 0.7
r² = 0.49
r² = 0.58
Relative change in grain yield (%)
Relative change in grain protein yield (%)
Absolute change in grain protein concentration (% of grain yield)
Absolute change in anthesis date (days)
Relative change in grain filling rate (%)

Fig. 3

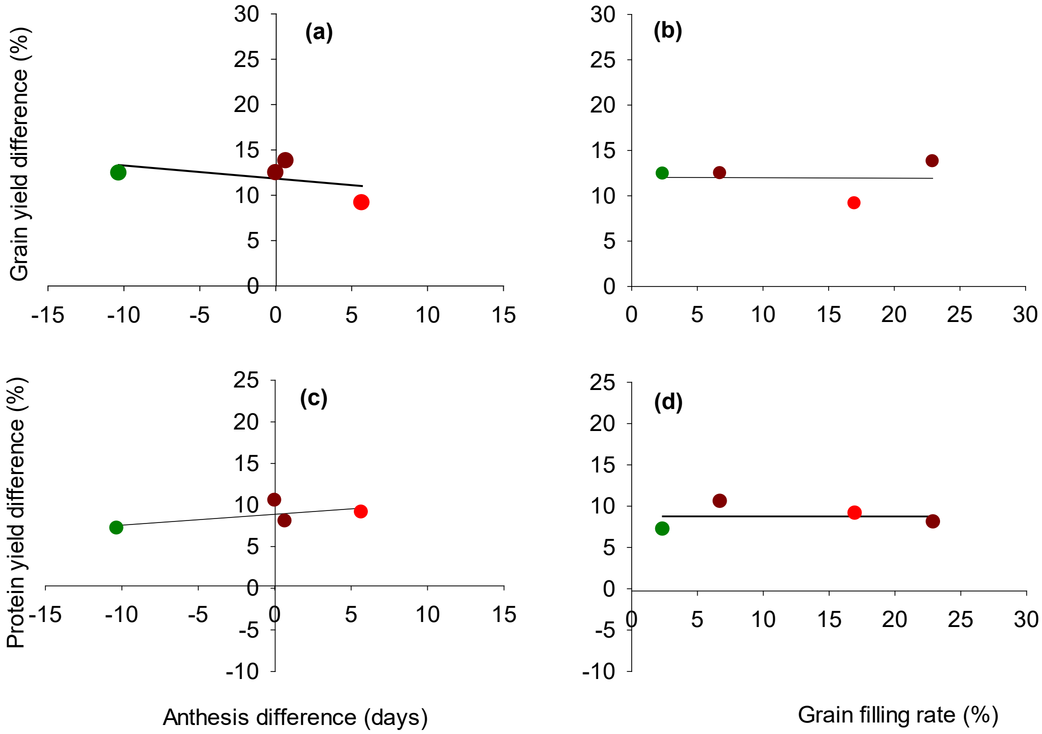

(a)
(b)
(c)
(d)
Grain yield difference (%)
Protein yield difference (%)
Anthesis difference (days)
Grain filling rate (%)

Fig. 4

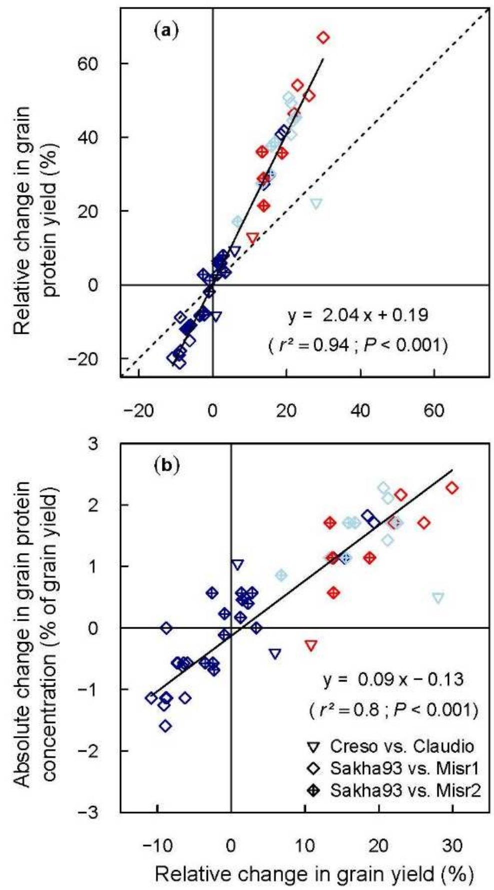
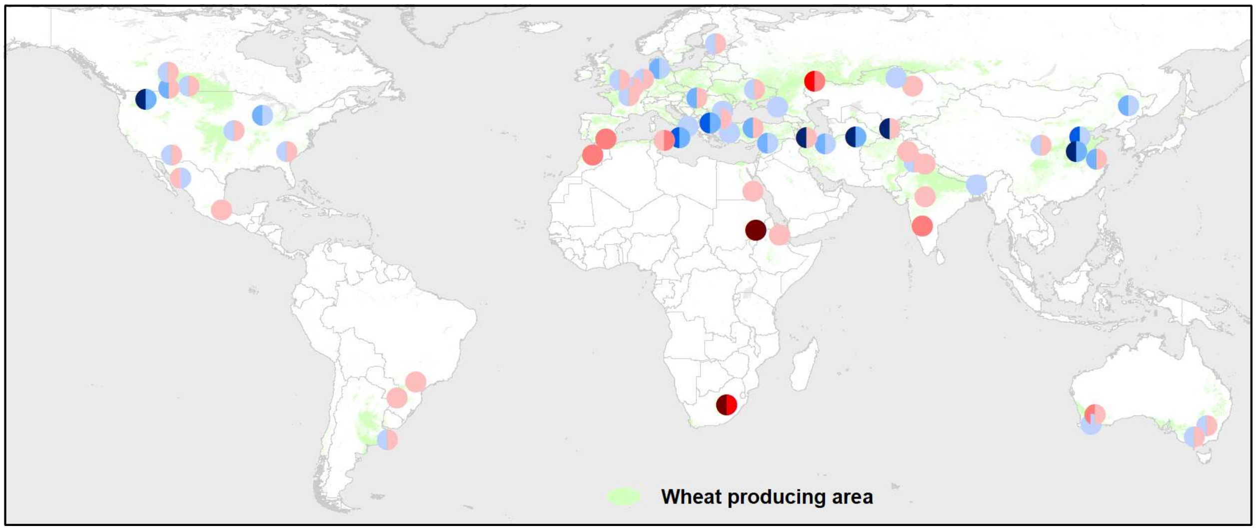
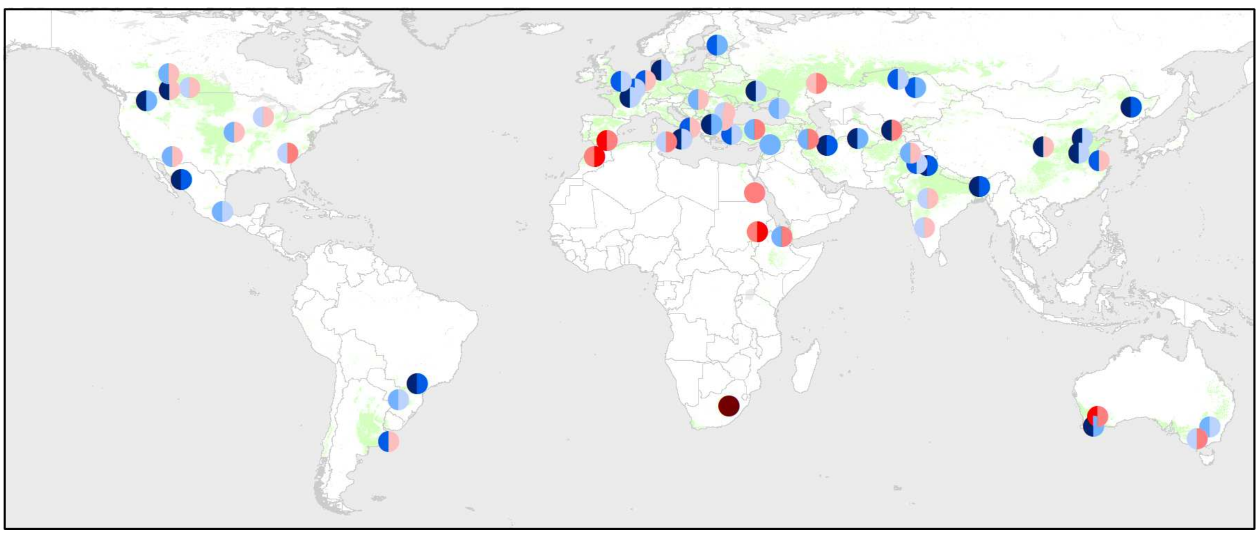

(a)
Relative change in grain protein yield (%)
y = 2.04 x + 0.19
(r² = 0.94 ; P < 0.001)
(b)
Absolute change in grain protein concentration (% of grain yield)
y = 0.09 x − 0.13
(r² = 0.8 ; P < 0.001)
Creso vs. Claudio
Sakha93 vs. Misr1
Sakha93 vs. Misr2
Relative change in grain yield (%)

Fig. 5

(a) Change in grain and protein yield for current cultivars



(b) Change in grain and protein yield for adapted genotypes



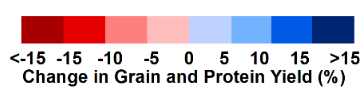


Fig. 6

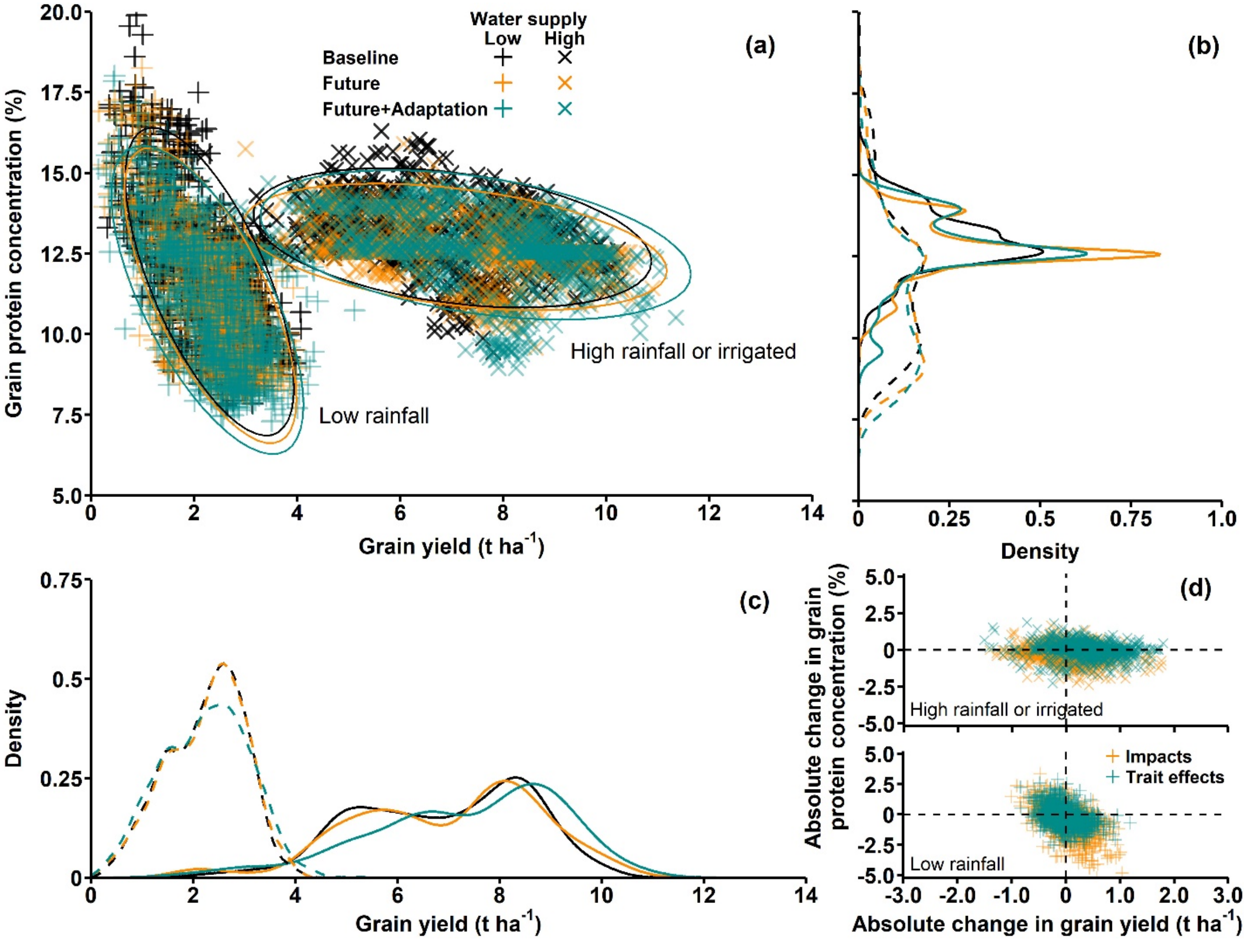

Grain protein concentration (%)
Grain yield (t ha-1)
Water supply
Low
High
Baseline
Future
Future+Adaptation
(a)
High rainfall or irrigated
Low rainfall
(b)
Density
(c)
Density
Grain yield (t ha-1)
(d)
Absolute change in grain protein concentration (%)
High rainfall or irrigated
Impacts
Trait effects
Low rainfall
Absolute change in grain yield (t ha-1)

Fig. 7

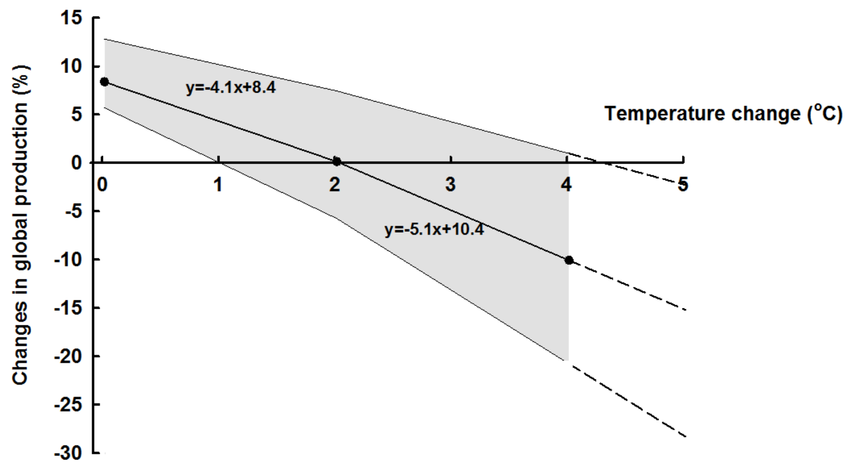

Changes in global production (%)
Temperature change (°C)
y=-4.1x+8.4
y=-5.1x+10.4
15
10
5
0
-5
-10
-15
-20
-25
-30
0
1
2
3
4
5

Fig. 8

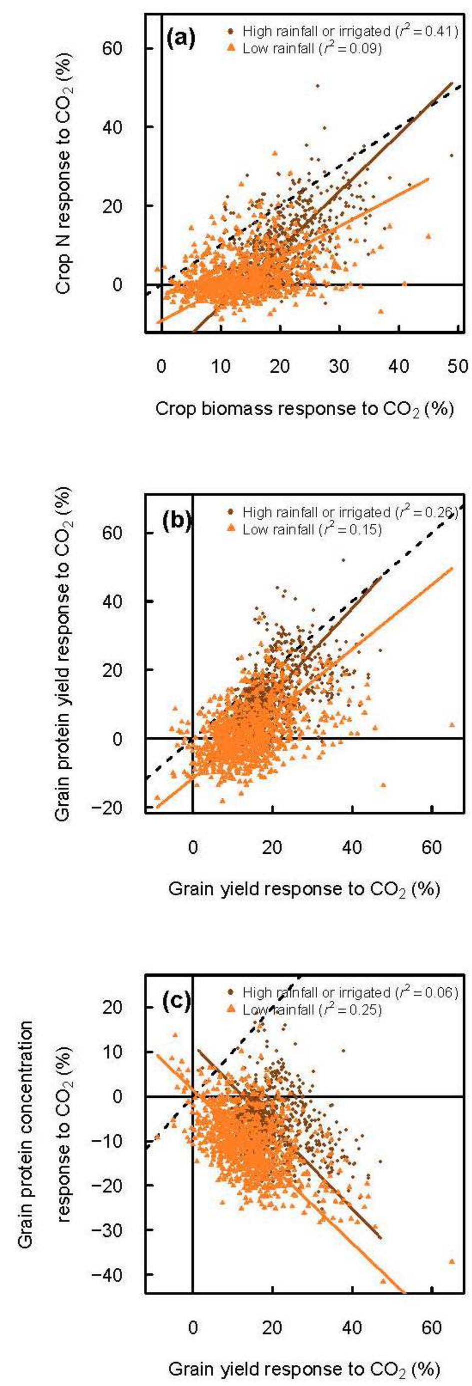

(a)
High rainfall or irrigated ($r^2 = 0.41$)
Low rainfall ($r^2 = 0.09$)
Crop N response to CO_2 (%)
Crop biomass response to CO_2 (%)
(b)
High rainfall or irrigated ($r^2 = 0.26$)
Low rainfall ($r^2 = 0.15$)
Grain protein yield response to CO_2 (%)
Grain yield response to CO_2 (%)
(c)
High rainfall or irrigated ($r^2 = 0.06$)
Low rainfall ($r^2 = 0.25$)
Grain protein concentration response to CO_2 (%)
Grain yield response to CO_2 (%)

Fig. 9