in silico Plants, 2023, **5**, 1–16
https://doi.org/10.1093/insilicoplants/diad013
Advance access publication 15 September 2023
Original Research

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Wheat crop traits conferring high yield potential may also improve yield stability under climate change

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Handling Editor: Graeme Hammer

ABSTRACT

Increasing genetic wheat yield potential is considered by many as critical to increasing global wheat yields and production, baring major changes in consumption patterns. Climate change challenges breeding by making target environments less predictable, altering regional productivity and potentially increasing yield variability. Here we used a crop simulation model solution in the SIMPLACE framework to explore yield sensitivity to select trait characteristics (radiation use efficiency [RUE], fruiting efficiency and light extinction coefficient) across 34 locations representing the world's wheat-producing environments, determining their relationship to increasing yields, yield variability and cultivar performance. The magnitude of the yield increase was trait-dependent and differed between irrigated and rainfed environments. RUE had the most prominent marginal effect on yield, which increased by about 45 % and 33 % in irrigated and rainfed sites, respectively, between the minimum and maximum value of the trait. Altered values of light extinction coefficient had the least effect on yield levels. Higher yields from improved traits were generally associated with increased inter-annual yield variability (measured by standard deviation), but the relative yield variability (as coefficient of variation) remained largely unchanged between base and improved genotypes. This was true under both current and future climate scenarios. In this context, our study suggests higher wheat yields from these traits would not increase climate risk for farmers and the adoption of cultivars with these traits would not be associated with increased yield variability.

KEYWORDS: Climate change; climate risk; genetic yield potential; wheat; yield variability.

1. INTRODUCTION

Recent decades have seen wheat yields (Hochman *et al.* 2017; Schauberger *et al.* 2018; Reynolds and Braun 2022) and harvested area (FAO 2022) stagnate globally. Current rates of yield increase associated with genetic improvement (<1 % $year^{-1}$, Dreisigacker *et al.* 2021) are not sufficient to meet the increase in wheat grain demand expected by 2050 particularly considering expected demand growth in Asia (Erenstein *et al.* 2022), challenging effort to achieve food security. Evidence for on-farm conditions suggest that the rate of genetic improvement is even less optimistic when actual farm production conditions are considered (Rife *et al.* 2019). Nevertheless, increasing the genetic yield potential (YP) is considered by many as a cornerstone for an integrated strategy to increase wheat productivity (Foulkes *et al.* 2022). In this context, understanding crop yield physiology can support conventional breeding approaches and increase the current rates of genetic gains (Reynolds and Langridge 2016; Richards *et al.* 2019). While climate change is projected to increase mean wheat yields in many environments due to CO_2 fertilization effects (Webber *et al.* 2018; Jägermeyr *et al.* 2021), it challenges breeding by making target environments less predictable (Zheng *et al.* 2016), altering crop productivity (Abberton *et al.* 2016; Atlin *et al.* 2017; Webber *et al.* 2018), and potentially increasing yield variability (Hernandez-Ochoa *et al.* 2018; Yang *et al.* 2019). Ensuring continuity in yield gains thus requires genotypic adaptation, that is the design and development of novel cultivars with enhanced productivity and stability under future climates (Ramirez-Villegas *et al.* 2020).

Increasing average YP through genetic improvement can be achieved through increasing light interception (LI), radiation use efficiency (RUE) and/or harvest index (HI) (Reynolds *et al.* 2012). The contribution of breeding on the improvement of LI is uncertain (Richards *et al.* 2019), with studies reporting contrasting trends in LI among modern cultivars (Acreche *et al.* 2009; Yang *et al.* 2021). Despite the generally high LI for wheat canopies, there might be scope for further optimizing in-canopy light characteristics via a modified canopy architecture (Richards *et al.* 2019; Slafer *et al.* 2021). Historically, RUE played a minor role in the progress of wheat yields (Reynolds *et al.* 2000), but recent evidence and theoretical considerations suggest it is a promising trait to leverage photosynthesis for increasing biomass production in the future (Mitchell and Sheehy 2018; Asseng *et al.* 2019a; Molero *et al.* 2019). On the other hand, changes in HI have been the main driver of genetic improvement since the green revolution, increasing yields without substantial changes in total biomass production (Slafer *et al.* 2021). Even if the potential for reduced height has been completely exploited, further increases in HI could be reached by optimizing the source-sink ratio and favouring spike fertility (Reynolds *et al.* 2017). In particular, fruiting efficiency (FE, the number of grains produced per unit of spike dry weight at anthesis) is a candidate trait to increase wheat YP, as it does not display trade-offs with spike weight, and the negative relationship observed between FE and average grain weight is likely non-constitutive (Lo Valvo *et al.* 2018; Rivera-Amado *et al.* 2019; Curin *et al.* 2021).

While improving yield levels has been the main target of wheat selection (Fischer 2020), genetic improvement may also affect yield stability (Calderini and Slafer 1999; Sinebo 2005; Vita *et al.* 2010). Yield stability is critical for decisions at different levels of agricultural systems, from farmers' criteria for adopting crop cultivars to the design of policies to support prices, input subsidies, and crop insurance (Macholdt and Honermeier 2016). Both high yield and stability are desirable goals for plant breeding (Calderini and Slafer 1998), with stability considered particularly important for sustainable food systems (Calderini and Slafer 1998). The extent to which these two goals are compatible is conditional to the notion of stability (Becker and Leon 1988). In some settings, stability is regarded as the identical performance of a genotype across all environments (static stability). This might be preferred when selecting a crop for a marginal region where farmers are willing to sacrifice high performance in some years for consistent performance over all years. Conversely, over a large region, various actors in food production value chains may prefer crops that respond well in favourable environments, and to do so in a predictable fashion (dynamic stability) (Walsh and Lynch 2018). Genotypes and environments interact to produce an array of phenotypes, challenging the identification of superior traits and cultivars (Chapman 2008). These interactions are of particular interest when they introduce inconsistencies in the relative rating (of yield levels) in genotypes, measured by changes in the rank (of yield levels) in genotypes (i.e. crossover interactions, (Leon *et al.* 2016)). Crossover interactions play a major role in the development of strategies for crop improvement, providing a discriminating factor for targeting specific or wide adaptation (Gauch 2013). A reduction of static yield stability was observed in response to wheat breeding (Subira *et al.* 2015). This was regarded as a success of breeding, as improved genotypes performed better than predecessors under both favourable environmental conditions as well as in relatively poor environments (Welcker *et al.* 2022). Other studies reported that wheat breeding promoted a reduction of genotype by environment interactions through the selection of genotypes with high and stable yields across a wide range of environments (Vita *et al.* 2010; Voss-Fels *et al.* 2019), pointing at the opportunity to continue to breed genotypes with high yield, wide adaptation and high yield stability.

Despite this, climate change imposes an additional constraint to breeding. Recent evidence suggests that climate change has increased crossover interactions, a critical indicator of changes in the ranking of cultivar performance in different environments (Xiong *et al.* 2021). Breeding efforts for future climates are challenging. In this context, crop models have the potential to support genotypic adaptation (Chenu *et al.* 2017) by providing a way to quantify the interactions between crop traits and climate factors affecting yield under future conditions. Such models have been previously applied in assessing levels of trait expression and trait combinations (Ramirez-Villegas *et al.* 2015; Reynolds and Langridge 2016) as well as of plant ideotypes (Martre *et al.* 2015a, 2015b; Senapati and Semenov 2020). As they decompose yield into a number of underlying simpler traits, crop models are suitable to assist physiological breeding, ultimately allowing predictions about the value of new cultivars in terms of YP, genotypic adaptability and stability.

Against this background, the present study uses process-based simulations to assess (i) the yield stability of lines with high YP and (ii) to what extent the yield benefits from high-yielding trait

combinations are expressed in extreme years, under current and climate change scenarios.

2. MATERIALS AND METHODS

2.1 Crop model description

A modelling solution developed within the SIMPLACE (Enders *et al.* 2023) modelling framework (www.simplace.net), was used to simulate growth and development of a population of virtual wheat genotypes differing for RUE, FE and light extinction coefficient (KDIF). The solution (SIMPLACE-L5 hereafter) combined the Lintul5 crop growth model (Wolf 2012), a modified version of the soil water balance named SlimWater (Addiscott and Whitmore 1991), the United Nations Food and Agriculture Organization's Irrigation and Drainage Paper 56 (FAO-56) dual crop coefficient procedure for calculating crop evapotranspiration (Allen *et al.* 1998), and modules for estimating the nitrogen demand and supply (Addiscott and Whitmore 1991), hourly canopy temperature (Webber *et al.* 2016) and heat stress (Gabaldón-Leal *et al.* 2016) as described more fully in Webber *et al.* (2018) and Webber *et al.* (2020). SIMPLACE-L5 simulates crop biomass accumulation as a function of RUE and intercepted radiation. RUE is modulated by water and nutrient stress, mean temperature and CO_2 concentration. Incoming radiation is intercepted by the canopy based on the leaf area index and KDIF following Beer's Law. Initial leaf area expansion is exponential as it is assumed to only be limited by radiation capture until leaf area reaches a value of 0.75 or a development stage of 0.2 is reached. After this time, leaf area expansion is limited by dry matter partitioning to leaves as the product of daily biomass increment and a development stage-specific leaf area parameter. Changes in assimilate partitioning to different plant organs (roots, stems, leaves and grains) are driven by phenological development, simulated as a function of accumulated temperature sums, photoperiod and vernalization requirements. Water use is simulated as the maximum of soil plant available water or daily potential crop evapotranspiration. The latter is determined as the product of daily reference crop evapotranspiration (ET0) and the FAO-56 dual crop coefficient estimated using daily simulated leaf area index. Daily plant available soil water is determined with a modified version of SLIM Water and SLIM Roots (Addiscott and Whitmore 1991). Water stress is simulated when daily water uptake is less than daily potential crop evapotranspiration. In this case, a reduction factor equal to the ratio of water uptake to potential crop evapotranspiration reduces RUE, increase partitioning to roots and increases crop canopy temperature, potentially increasing simulated heat stress impacts as described in detail by Webber *et al.* (2016) and Gabaldón-Leal *et al.* (2016). Elevated atmospheric CO_2 concentrations act to increase RUE and reduce stomatal conductance. The later acts to reduce the daily rate of transpiration and also raise canopy temperature, consistent with experimental evidence in wheat (Kimball *et al.* 1999). SIMPLACE-L5 extended the model solution as described in Webber *et al.* (2018) and Webber *et al.* (2020) with a new component to allow for sink-limited grain growth according to the model proposed by Weir *et al.* (1984) and implemented in AFRCWHEAT2 (Porter 1993). Before anthesis, the partitioning scheme was modified to enable ear growth. The ear weight and FE (cultivar-specific parameter) determine the number of grains set at anthesis. Grain growth is modelled by allocating all the net assimilate produced after anthesis to grains. The specific amount of assimilates (20 %) stored in leaves/stems before anthesis translocate to grains which can be boosted to 30 % by increasing drought intensity based on the method developed by Soltani and Sinclair (2012). The assimilate demand for grain filling is determined by the grain number and a temperature-dependent daily maximum growth rate for grain. Grain growth stops when physiological maturity is reached. All yields are simulated on a dry matter basis (assuming 0 % moisture content) and are reported as such throughout this article.

2.2 Global simulations: location and data description

Simulations of wheat growth and development with both current traits and improved traits (described in Section 2.3) were conducted at 34 global sites (see Supporting Information—Table S1 and Fig. 3) as part of the Agricultural Model Intercomparison and Improvement Project(AgMIP) Wheat team study examining potential of improved traits to increase YP for historical and possible weather scenarios, as reported by Guarin *et al.* 2022. Of these sites, 30 were considered in past studies (Asseng *et al.* 2015, 2019b) to represent major wheat-growing regions which collectively produce about 70 % of global wheat (Reynolds and Braun 2013). These sites are either irrigated or characterized by high annual average rainfall, with high average annual yields > 4 t ha^{-1}. Each site was characterized with a representative soil profile considering soil depth and soil horizons described by soil water holding characteristics and texture. The source of the soil data varied (see Supporting Information—Table S1), using published profile descriptions where available and taking profile descriptions from the World Inventory of Soil Emission Potential (WISE) soil database (Batjes 2016). For the first 30, expert information about main wheat cultivars in each region (e.g. photoperiod sensitivity, vernalization sensitivity, observed phenology) was assembled in a previous study (Asseng *et al.* 2015, 2019b) and considered here to define the growing season duration and phenology traits in the simulations for both current and improved traits. For the other four simulated sites, Buenos Aires (Argentina); Leeston (New Zealand); Rots (France); and Valdivia (Chile), detailed datasets including phenology, biomass dynamics and yield components were available for phenology trait calibration (Dueri *et al.* 2022; Guarin *et al.* 2022). Simulations were conducted with historical data for the 1981–2010 harvest years. Future scenario simulations were conducted for 2040–2069 for a moderate and high greenhouse gas representative concentration pathway (RCP), RCP4.5 and RCP8.5 respectively, for five global climate models (GCMs) used by Asseng *et al.* (2019b): Hadley Centre Global Environment Model version 2 (HadGEM2-ES), Model for Interdisciplinary Research on Climate (MIROC5), Max-Planck Institute - Earth System Model version 1.2 at medium resolution (MPI-ESM-MR), Geophysical Fluid Dynamics Laboratory coupled general circulation model (GFDL-CM3) and Goddard Institute for Space Studies General Circulation Model - Russell (GISS-E2_R) (Taylor *et al.* 2015). These climate scenarios were generated using the Enhanced Delta Method (Ruane *et al.* 2015)

which accounts for shifts in both mean and standard deviation (SD) of temperature, mean of precipitation and the number of rainy days. The method has previously been used in the study of Webber *et al.* (2018). Irrigation was simulated to capture the predominant production case as indicated in Supporting Information—Table S1. For the irrigated simulations, irrigations were applied such that the wheat experienced no water stress. Nitrogen limitation was not considered in any of the simulations as these are all high-yielding regions where nitrogen is applied to reach close to YP (irrigated production) or water-limited YP (rainfed conditions). All scenarios under climate scenarios considered elevated CO_2 levels (Toreti *et al.* 2020), with the corresponding levels: baseline: 360 ppm; RCP4.5: 499 ppm and RCP8.4: 571 ppm.

2.3 Simulation of virtual genotypes

For each of the 34 sites, locally adapted cultivars were simulated through site-specific phenology calibration of two parameters (vernal-photothermal times to anthesis; and thermal time from anthesis to maturity) based on sowing, anthesis and maturity dates, as well as vernalization requirement and photoperiod sensitivity typical of each location (Asseng *et al.* 2019b). In addition to the two phenology traits, experimental data were available for three modern varieties which were grown at 5 of the 34 sites, allowed direct calibration of the traits under study to set the baseline trait values ((Dueri *et al.* 2022; Guarin *et al.* 2022); Table 1). For the other 29 sites, the average value of RUE and FE from these three cultivars were denoted as default and used as baseline trait values for the. For these sites, the value of KDIF calibrated in previous studies (0.6, Liu *et al.* 2021) was maintained. From each of these parameterizations at each of the 34 sites for the locally adapted cultivars, 1782 virtual genotypes per site were generated from the combination of trait levels exploring a range from + 0 % to + 34 % for RUE, +0 % to + 20 % for KDIF and −10 % to + 10 % for FE (Table 1) relative to the calibrated baseline values. The maximum value of RUE and KDIF were selected based on observed values from an improved high-yielding doubled haploid (DH) line resulting from a cross between cv. Bacanora and cv. Weebil as compared to the check variety Bacanora. Details are reported in Guarin *et al.* (2022). However, as FE decreased in this DH line, we explored a range of FE both above and below the reference value. The absence of correlations among the traits analysed (Molero *et al.* 2019) supported the adoption of a full factorial design for sampling the trait space. The establishment of the RUE range was corroborated by experimental evidence (García *et al.* 2014). As the link between RUE and grain number is not directly established in crop models as a cultivar-specific parameter, while the increased grain numbers in DH lines indicated a strong regulatory impact on RUE (Bustos *et al.* 2013), we identified a broad variation in RUE in our modelling experiment. Other research findings have also suggested that the advantages of increasing grain numbers on crop yield are reliant on adequate source availability (Zhang *et al.* 2019). Exploration of a wider range for KDIF and FE was supported by the literature (Zhang *et al.* 2014; Slafer *et al.* 2015).

2.4 Stability measures

The stability of virtual genotypes was characterized independently for each location in the baseline climate and for the combinations of location × RCPs × GCMs under climate change. Within each location, stability was evaluated across years.

Standard deviation (SD) of yield (y) across years was used as a measure of temporal yield variability. The coefficient of variation (CV), contextualizes the variability against yield levels by dividing SD by the mean yield over the same period. As such, SD and CV were used as inverse measures of (static) stability.

The rank and rank variability (RV) were adopted as nonparametric measures of the genotype performance and stability,

Table 1. Trait values used to generate the virtual genotypes in this study. The virtual genotypes (n = 1782) result from the factorial combination of the trait levels, reported as percent change compared to base parameterization.

	Traits			
	Radiation use efficiency (RUE)	**Canopy light extinction coefficient (KDIF)**	**Fruiting efficiency (FE)**	
Units	g MJ^{-1} of PAR	–	grains g^{-1} ear	
Range explored (min/max, relative to base value)	0 %/+34 %	0 %/+20 %	−10 %/+10 %	
Levels (Step)	18 (2 %)	11 (2 %)	9 (2.5 %)	Total = 1782
Cultivar	**Base values**			**Locations**
Apache*	2.6 (pre-anthesis) 2.0 (post-anthesis)	0.6	130	France—Rots
Bacanora*	2.9 (pre-anthesis) 1.9 (post-anthesis)	0.5	154	Mexico—Obregon Chile—Valdivia Argentina—Buenos Aires
Wakanui*	2.79 (pre-anthesis) 2.0 (post-anthesis)	0.52	103	New Zealand—Leeston
Default	2.7 (pre-anthesis) 2.0 (post-anthesis)	0.6	130	Elsewhere

*Calibrated for the Agricultural Model Intercomparison and Improvement Project (AgMIP) Wheat modelling phase 4 exercise.

respectively. Genotypes were ranked from 1 to n (1782) based on decreasing average yield in the time series. RV was measured as the square root of Huehn's S2 index (Eq.1; Huehn 1990), representing the variance of ranks over environments (years):

$$S2_i = \frac{\sum_{j=1}^{q} \left(r_{ij} - \overline{r_i}\right)^2}{q - 1} \quad (1)$$

where r_{ij} is the rank of the ith genotypes in the jth environment, $\overline{r_i}$ the average rank across environments and q the number of environments. The lowest value of the index indicates maximum stability among the genotypes analysed; values > 0 indicate the presence of crossover interactions, that is changes in the rank of genotype i within the time series.

The Finlay–Wilkinson regression approach (Finlay and Wilkinson 1963) was used to assess how the expected yield (y) of a genotype varied as a function of the environmental effects. The two-step ordinary least-square procedure implemented in the R package FW (Lian and Los Campos 2015) estimated the parameters of the model (Eq. 2):

$$y_{ij} = \mu + g_i + (1 + b_i)\, h_j + \varepsilon_{ij} \quad (2)$$

where y is the yield of ith cultivar and jth environment (year), μ is mean yield across cultivars and environments, g_i is the main effect of ith cultivar and h_j is the main effect of the jth environment (year), and e_{ij} is an error term which is equal to zero for the simulated data. The multiplicative term of h_j (b_i + 1, the slope of the regression) is the change of expected cultivar performance per unit change of the environment effect, a measure of the linear sensitivity of a genotype to the environment (also known as responsiveness, e.g. Calderini and Slafer 1999). The values of b_i are obtained by the best fit over all genotypes and environments in the sample. The particular value of b_i is thus a relative measure of sensitivity of a genotype compared to the set of genotypes analysed. Static stability would require a value of b_i near −1, giving a slope near 0. Conversely, genotypes with $b_i > 0$ may perform well in good environments but underperform in bad ones. To identify and quantify these possible trade-offs across environmental conditions, yield gains derived from improved traits (as delta yield between virtual and base genotypes) were regressed on the environment effect. The marginal effect of a given trait on SD, CV, RV and environment sensitivity was analysed by setting the other traits to the respective optimal value, that is the trait value maximizing average yield.

3. RESULTS

3.1 Trait influence on yield, yield stability and genotype ranking under baseline climate

Higher values of any of the traits considered resulted in a yield increase across all sites under baseline climate (Fig. 1A–C). The magnitude of the increase was trait-dependent and differed between irrigated and rainfed environments. RUE had

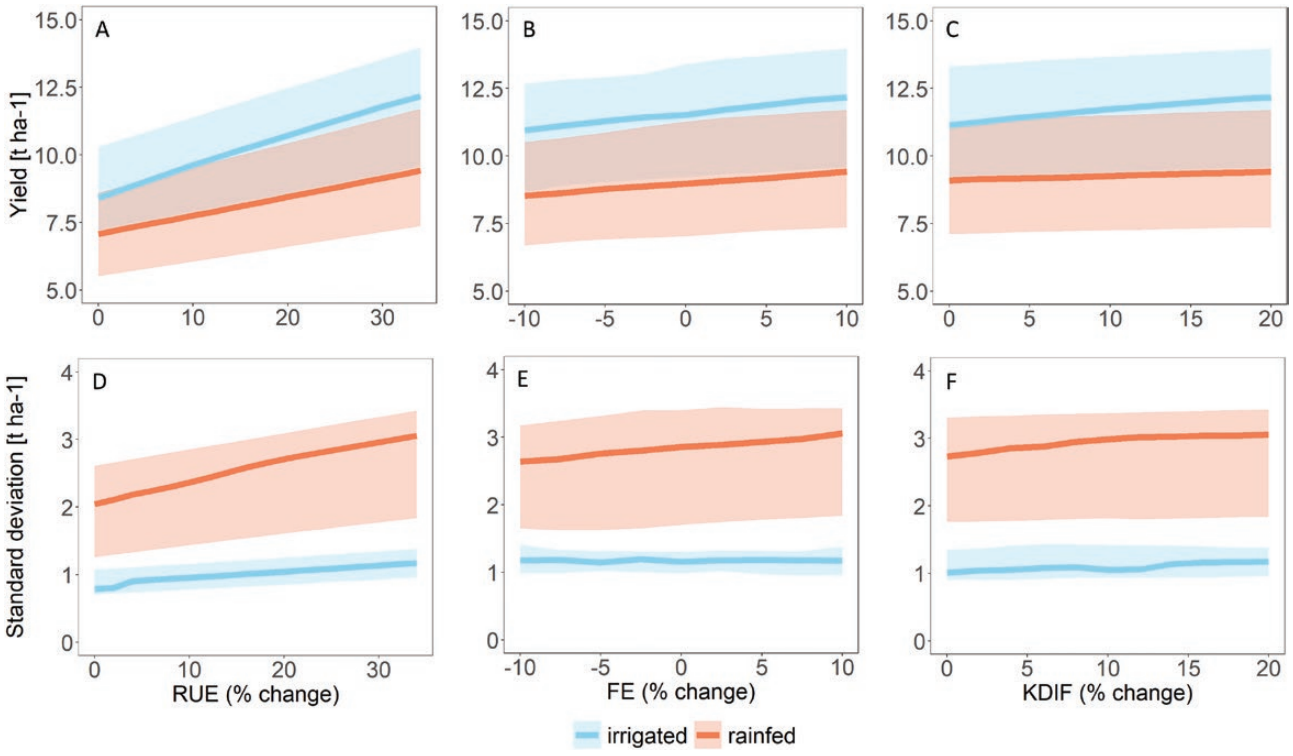

Figure 1. Response of mean yield (A–C) and standard deviation (D–F) to changes in trait values under baseline climate across all sites and years. Trait values are expressed as percentage change compared to the base parameterization. Solid lines and shaded areas represent, respectively, the median and the interquartile range of mean yield (A–C) and standard deviation (D–F) across sites. In each panel, the value of the remaining two parameters is fixed to its value that maximizes yield (A, D: KDIF = +20 %, FE = +10 %; B, E: RUE = +34 %, KDIF = +20 %; C, F: RUE = +34 %, FE = +10 %).

the most prominent marginal effect on yield, which increased by about 45 % and 33 % in irrigated and rainfed sites, respectively, between the minimum and maximum value of the trait, shown in Fig. 1A with other trait values held at value that maximized yield. Changes in FE (Fig. 1B) had a comparatively smaller effect on yield, and total gains across the full range of the investigated trait values for FE were consistent between irrigated (+11 %) and rainfed (+10 %) conditions. The gains from increasing KDIF, on the other hand, were lower and mainly expressed under irrigation (+9 % compared to + 3.5 % in rainfed systems; Fig. 1C). On average, a 1 % increase of RUE was associated with a yield gain of 0.11 t ha^{-1} (irrigated) and 0.07 t ha^{-1} (rainfed). The respective values for FE were 0.06 and 0.04 t ha^{-1}, whereas for KDIF 0.05 and 0.02 t ha^{-1}. Inter-annual variability, measured by SD, was higher in rainfed environments and generally increased with trait values producing higher yield (Fig. 1D–F), with the exception of FE in irrigated environments. In these conditions, the variability was approximately constant across the range of trait values, leading to a slight reduction in CV (see Supporting Information—Fig. S1). In rainfed environments, yield variability increased by 16 % when FE increased within the range of values explored (Fig 1E). The SD across sites responded to changes in RUE increasing by almost 50 % in both irrigated and rainfed conditions (Fig 1D). For KDIF, the increase of SD was relatively larger under irrigation (+16 %) than without (12 %; Fig 1F). Differences across sites in the magnitude of the increase of yield and SD led to small divergences in the response of CV to changes in traits (see Supporting Information—Fig. S1), otherwise consistent within the trait values explored.

Genotype ranking was largely determined by the value of RUE. Even at high levels of KDIF (+20 %) and FE (+10 %), in all sites the genotype with the lowest (base) RUE values were among the poorest performing, ranked around position 1500 out of 1782, that is below the bottom 20th percentile of the rank of the virtual genotypes by average yield (Fig. 2A). Conversely, genotypes with the highest RUE values ranked above position 250 (85th percentile) and 100 (95th percentile) depending on the value of FE and KDIF, respectively (Fig. 2B and C). The variability of genotype ranking across years was minimal with the trait values that maximized yield levels: changes in the genotype ranking (crossover interactions) were consistently reduced with increased RUE, FE and KDIF (Fig. 2D–F), corresponding to genotypes with rank closer to one (Fig. 2A–C). Ranking variability was highest when FE varied. The highest RV was associated with low values of FE in rainfed environments (Fig. 2F). Compared to the evaluation of genotype performance based on yield level and SD, less pronounced differences were observed between irrigated and rainfed systems on the basis of ranking statistics.

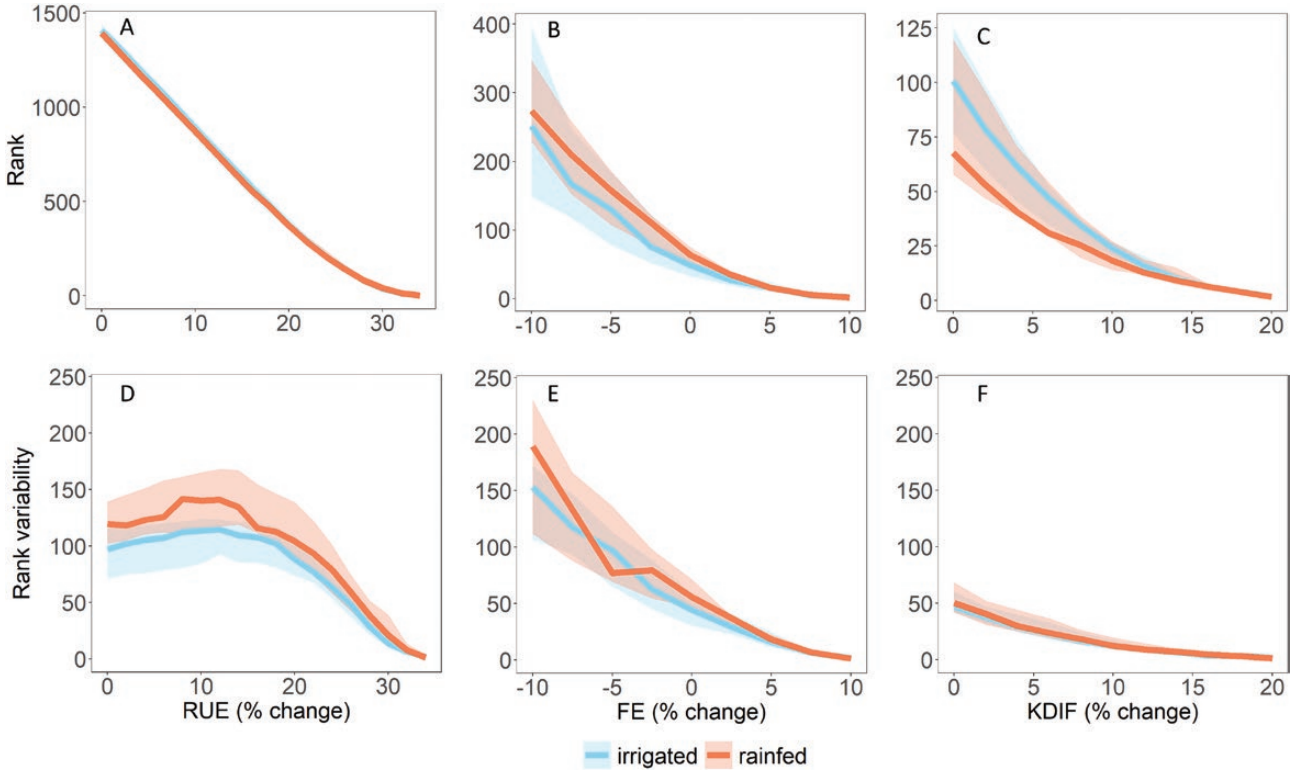

Figure 2. Response of genotype ranking (A–C) and ranking variability (D–F) to changes in trait combination values under baseline climate. Trait values are expressed as percentage change compared to the base parameterization. Solid lines represent the median across sites and shaded areas the interquartile range. While all trait combinations were explored, results are visualized by panel to show the response to changes in radiation use efficiency, RUE (A, D), fruiting efficiency, FE (B, E) and extinction coefficient, KDIF (C, F) keeping the value of the remaining two parameters is fixed at the value which maximized yields (A, D: KDIF = +20 %, FE = +10 %; B, E: RUE = +34 %, KDIF = +20 %; C, F: RUE = +34 %, FE = +10 %). Note a rank near one indicates a best-performing cultivar, while RV near one implies the trait always produces the same ranking.

3.2 Yield, yield stability and genotype ranking under climate change

For the evaluated trait combinations, the sign and magnitude of yield and inter-annual yield variability changes under climate change differed across sites (Fig. 3). Under RCP 4.5 (see Supporting Information for RCP8.5), both average yield and SD increased across genotypes in about half of irrigated sites and one third of the rainfed sites (similarly for Manhattan, Kansas, USA (USMN) in Fig. 3G). With the exception of Buenos Aires, Argentina site (ARBU), this led to a general increase in the CV that, averaged across all the genotypes tested, reached + 4 % in USMN (see Supporting Information—Fig. S2). An increase of yield together with reduced yield variability (e.g. Wageningen, The Netherlands

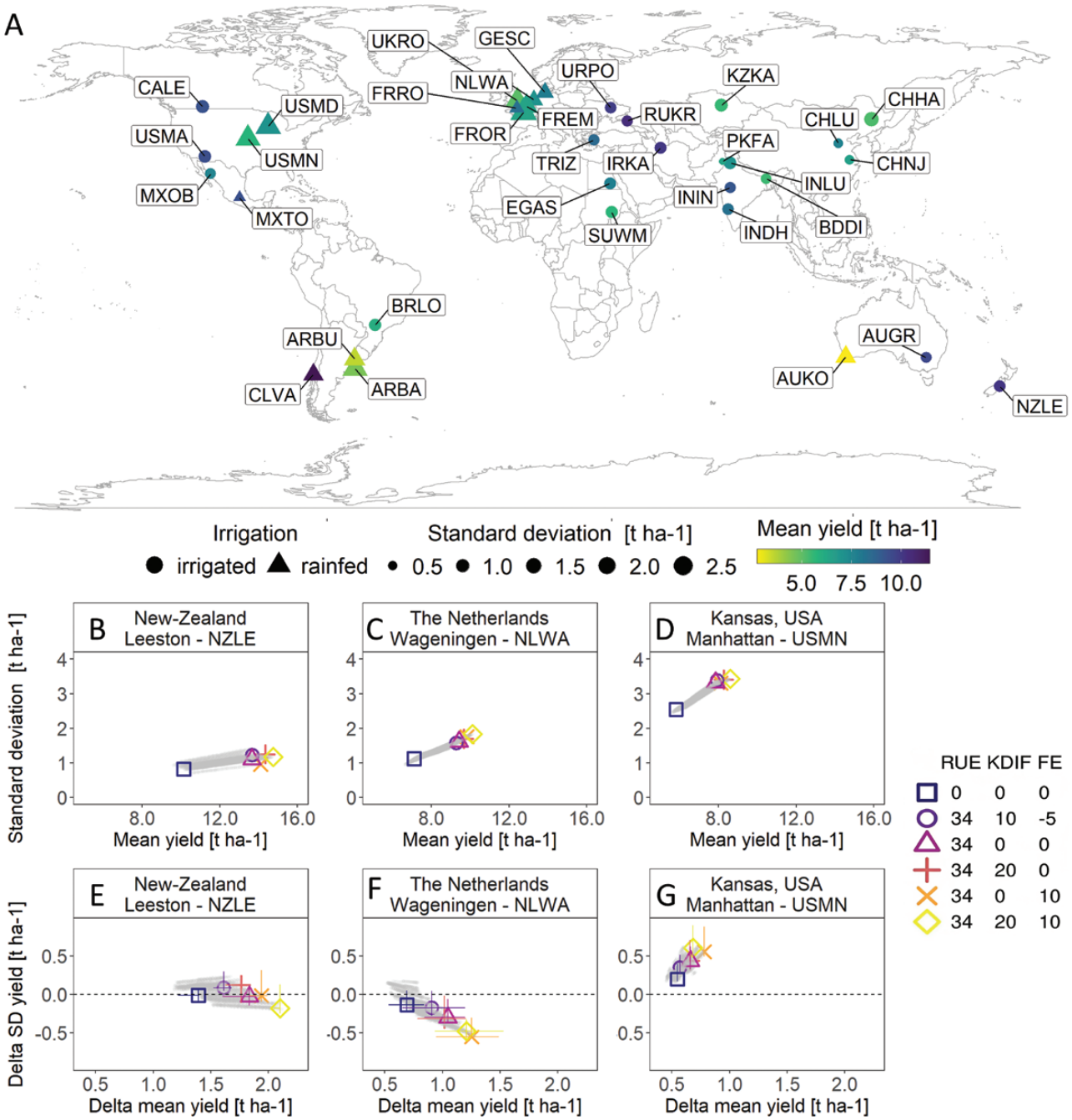

Figure 3. Spatial distribution of the study sites with their mean yield and standard deviation (SD) for base with unchanged trait values (A) and virtual genotypes exploring combinations of improved trait values (B–G) under baseline climate (A–D) and their changes under climate change scenario RCP 4.5, (E–G). Full names of each site are provided in Supporting Information—Table 1. Changes are reported as deltas between future and baseline values. Three sites are selected to illustrate different responses to climate change. In panels B–G, selected genotypes (including the base trait values, squares) are highlighted, with error bars representing the interquartile range across the five GCMs. Small dots represent the rest of the virtual genotypes tested. All rainfed environments are considered as having on average high, adequate rainfall and N supply to allow high yields levels.

(NLWA) in Fig. 3F), and a consequent reduction of CV resulted in almost half of the rainfed sites (up to about −20 % change in CV) and only 3 out of 21 irrigated ones (up to −4 % change in CV; see Supporting Information—Fig. S2). An increase of CV derived from the concurrent reduction of yield and increase of SD was observed in four irrigated sites (up to + 17 % change in CV) and one rainfed (+1 % change in CV). In the remaining sites (four irrigated and two rainfed), SD of yield either decreased (associated with a reduction of yield) or displayed a variable response across the genotypes (as in Leeston, New Zealand—NZLE, Fig. 3E), resulting in a variable effect on CV. Despite the differences in the magnitude of the change in mean yield and SD, the changes in CV were generally consistent between base (unchanged) trait values and improved trait values (see Supporting Information—Fig. S2).

Under baseline climate, genotypes at the opposite ends of the rank (i.e. lowest- and highest-yielding ones) displayed the highest ranking stability, with RV greatly increasing for cultivars in the middle of the ranking (Fig. 4A–C). This pattern was consistent across locations and RCPs (see Supporting Information—Fig. S3). The influence of climate change on the ranking variability differed among genotypes. While for most the change was site-dependent, the highest-ranked genotype identified in the baseline almost always remained the best genotype across all sites (Fig. 4D–F and see Supporting Information—Fig. S3). In addition to the higher yield gains obtained under climate change compared to the population of virtual genotypes (Fig. 4D–F), this indicated that these genotypes (yellow diamond in Fig. 4) remained stable at the top of the ranking. The base genotype (blue square in Fig. 4) which was among the lowest yielding, generally displayed minor changes in ranking variability under climate change (Fig. 4D–F and see Supporting Information—Fig. S3).

A single trait combination (RUE + 34 %, FE + 10 %, KDIF + 20 %, at the upper simulated end of all three trait changes, 'best genotype' hereafter) outperformed all the virtual genotypes in terms of average yield in 32 of the 34 sites under baseline climate. In the remaining two sites, the highest average yield was achieved by trait combinations differing from the best genotype only for KDIF. In Buenos Aires, Argentina (ARBA), the genotype with KDIF value of + 12 % out-yielded the best one by only 0.01 t ha^{-1}, whereas in Harbin, China (CHHA) the difference obtained with KDFI + 16 % was more marked (0.15 t ha^{-1}). Under future climate scenarios, the 'best genotype' outperformed all the others in each site, including ARBA and CHHA. This response was consistent across almost all (332/340) combinations of site × RCP × GCM. The very few exceptions occurred mostly under RCP8.5, where the difference in average yield compared to the overall 'best genotype' reached almost 3.0 t ha^{-1}. The changes in yield and SD of the best genotype (summarized in Fig. 5A) were in line with those observed for the rest of the virtual genotypes. Changes in ranking and ranking variability under future scenarios (Fig. 5B) indicated changes in the frequency of crossovers between years in the 'best genotype'. Even in the presence of crossover, however, the difference in yield was negligible in almost all cases, with few extreme exceptions (see Supporting Information—Fig. S4). The positive association between changes in ranking and in stability for the 'best genotype' (Fig. 5B) pointed to an increased (decreased) RV associated with a worse (better) position in the rank under climate change.

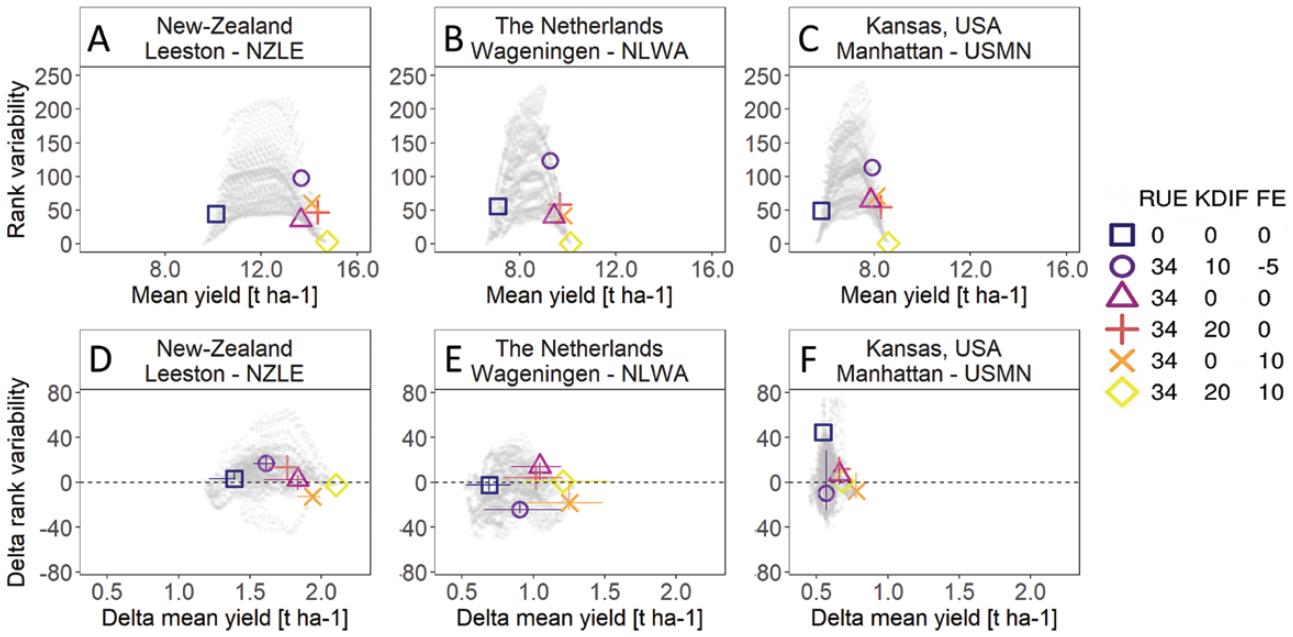

Figure 4. Ranking variability of base trait values (squares) and virtual genotypes under baseline climate (A–C) and the change in RV under climate change scenario RCP 4.5 (D–F). Changes are reported as deltas between future and baseline values. Selected genotypes (including the base one, blue squares) are highlighted, with error bars representing the interquartile range across the five GCMs. Small dots represent the rest of the virtual genotypes tested.

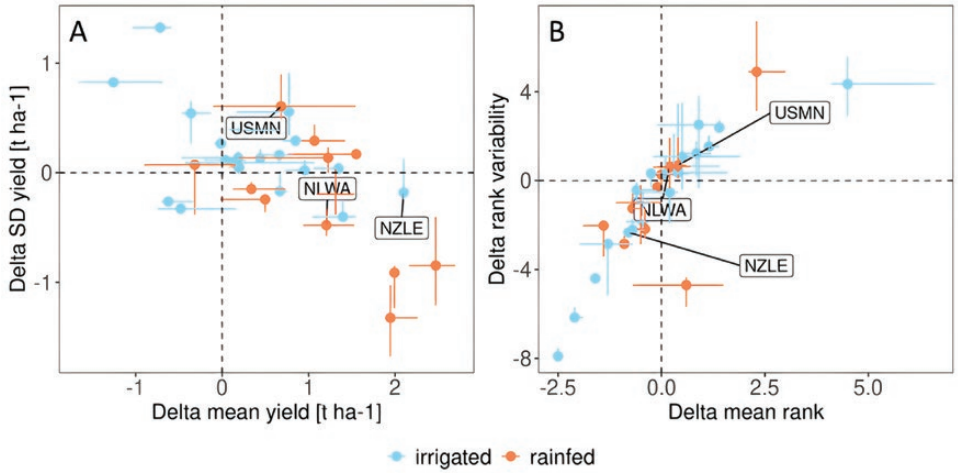

Figure 5. Changes in yield and yield stability between RCP4.5 and baseline climate scenarios for the highest yielding genotype (RUE + 34 %, KDIF + 20 %, FE + 10 %) across the 34 test locations. Changes are assessed both in terms of absolute yields (mean yield and standard deviation; panel A) and genotype ranking (mean rank and RV; panel B). A negative delta mean rank indicates better genotype ranking under future climate. For reference, the three sites investigated in more details (NLWA: Wageningen, The Netherlands; NZLE: Leeston, New Zealand; and USMN: Manhattan, United States) are indicated in the figure.

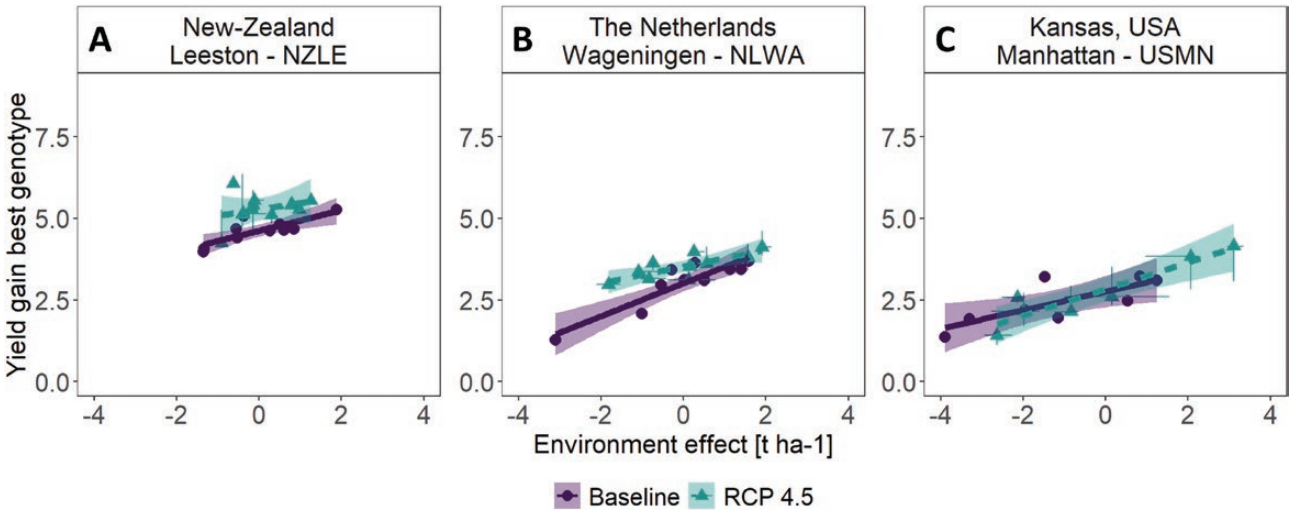

Figure 6. Gains of best genotype across environmental conditions (i.e. years in the time series) as delta yield compared to the base genotype under baseline (circles) and RCP 4.5 (triangles) climate scenarios. The environment effect measures the linear sensitivity of a genotype to the environment explained in Section 2.3.

3.3 Yield gains from improved crop traits across environments

The increased inter-annual variability displayed by the highest yielding genotype compared to the base parameterization was associated with yield gains along all environmental conditions (i.e. years within a site; Fig. 6). Across all year × location combinations explored, the 'best genotype' was never outperformed by the base one (data not shown). Under baseline climate, gains were higher in irrigated sites (average of 4.1 t ha^{-1} for the 'best genotype' across locations) than under rainfed ones (average 3.2 t ha^{-1}). Across locations, yield gains from improved crop traits were more variable in rainfed sites (spanning from an average of 1. 2 t ha^{-1} in Kojonup, Australia (AUKO) to 6.7 t ha^{-1} in Valdivia, Chile (CLVA)) than in irrigated sites (from 2.9 t ha^{-1} in Nanjing, China (CHNJ) to 5.2 t ha^{-1} in Ludhiana, India (INLU)). Yield gains were consistently smaller in relatively worse years (corresponding to negative environment effect) than under favourable (positive environmental effect) conditions (Fig. 6). The gains ranged from 0.04 t ha^{-1} (worst year) to 2.4 t ha^{-1} (best year) in AUKO, whereas the respective values for CLVA were 4.6 and 7.7 t ha^{-1} (rainfed sites). In CHNJ and INLU (irrigated), the gains ranged respectively from 2.4 to 3.4 t ha^{-1} and from 4.0 to 6.0 t ha^{-1} between the worst and best year of the time series. Across sites and environmental conditions, yield gains of the 'best genotype' were distributed around 49% (rainfed) and 53% (irrigated) of the yield achieved by the base genotype. The advantage from improved traits displayed in the baseline was preserved under climate change, with only minor differences across locations (Fig. 6). On average, yield gains for the best genotype increased under RCP4.5 by 0.06 t ha^{-1} in irrigated conditions and 0.34 t ha^{-1} in rainfed sites. The respective values for RCP8.5 were 0.2 t ha^{-1} and 0.6 t ha^{-1}.

The slope of the Finlay–Wilkinson regression highlighted an increased sensitivity to changes in environmental conditions for improved genotypes. This was mostly driven by changes in RUE: with the other traits being at their optimal value (i.e. FE = +10 % and KDIF = +20 %), the slope of the regression ranged from 0.86 to 1.15 for irrigated sites and from 0.89 to 1.23 for rainfed sites under baseline climate across the range of trait variation explored (Fig. 7A). Genotypes with the highest RUE (+34 %) displayed higher environment sensitivity than the base genotype regardless the value of the other traits (slope always > 1 in Fig. 7B and C). The marginal contribution of KDIF to genotype sensitivity was comparatively smaller than RUE (Fig. 7C). Also in this case, the slope of the regression increased with increasing values of KDIF, and genotypes displayed a lower sensitivity in irrigated sites than in rainfed ones, likely due to the wider range of drought stress conditions explored in the latter. Higher FE values determined an increasing sensitivity only under rainfed conditions, whereas with irrigation the slopes were consistent within the range of FE explored. With irrigation, therefore, changes in FE did not alter the environmental sensitivity of the genotypes. Under climate change, the sensitivity of the genotypes to environmental conditions was either comparable or reduced across the trait space compared to baseline climate (Fig. 7). Effects of elevated CO_2 reducing transpiration rates implemented in the model reduced the effects of marginal drought under irrigated conditions under a moderate climate change scenario (RCP4.5, result not shown).

4. DISCUSSION

4.1 Implications for breeding for YP in a changing climate

This study used a crop simulation model to evaluate the relationship between crop traits conferring high yield and yield stability as this varied across major wheat-growing areas and climate scenarios. The model was tested against experimental data from modern cultivars grown in high-yielding environments (Dueri *et al.* 2022; Guarin *et al.* 2022) where it demonstrated its suitability for the simulation of wheat YP under favourable conditions while displaying a coherent response to changes in crop traits values (Bustos *et al.* 2013). In particular, the model was specifically extended to account for sink-limitations during grain growth for an appropriate description of the influence of FE on yield formation. The simulation results confirmed the importance of constitutive traits conferring high yields across environments for achieving wide adaptation. Regardless of the location or environmental conditions, increased RUE led to higher simulated yields, and the highest-yielding genotype identified was stable in terms of ranking. In particular, among the traits considered, improved RUE was the most effective in raising YP, thus supporting the idea of prioritizing increased photosynthetic efficiency for future breeding efforts (Reynolds *et al.* 2012; Zhao *et al.* 2015; Slattery and Ort 2021). FE also appeared as a relevant target trait for breeding (Slafer *et al.* 2015). On the one hand, increasing the value of this trait produced consistent yield gains under irrigated and rainfed locations while, on the other hand, lower FE values were associated with a reduced ranking stability of the genotypes.

Higher yields from improved traits were generally associated with increased inter-annual yield variability (measured by SD), but the relative yield variability (as CV) remained largely unchanged between the base traits and improved genotypes. In this context, improved wheat would remain a low-risk crop for farmers (Cernay *et al.* 2015), and the adoption for high-yielding cultivars should not be hindered by their yield variability, mainly in high-yielding environments. Such trait combination leading to simultaneous improvement in yield stability and high yield across environments is also captured for other crops such as oilseed rape (Du *et al.* 2020). Additionally, optimum crop management has been shown to counteract variability associated with GxE, such that increasing yields through using higher-yielding cultivars with more modern farming systems does not appear to necessarily decrease yield stability (Calderini and Slafer 1998). However, in other studies, improved crop traits led to a greater sensitivity to changes in environmental conditions. For instance, there was a trade-off between yield increase and yield stability of soybean under non-optimal management across environments (Zhang *et al.* 2022). Under the conditions explored here,

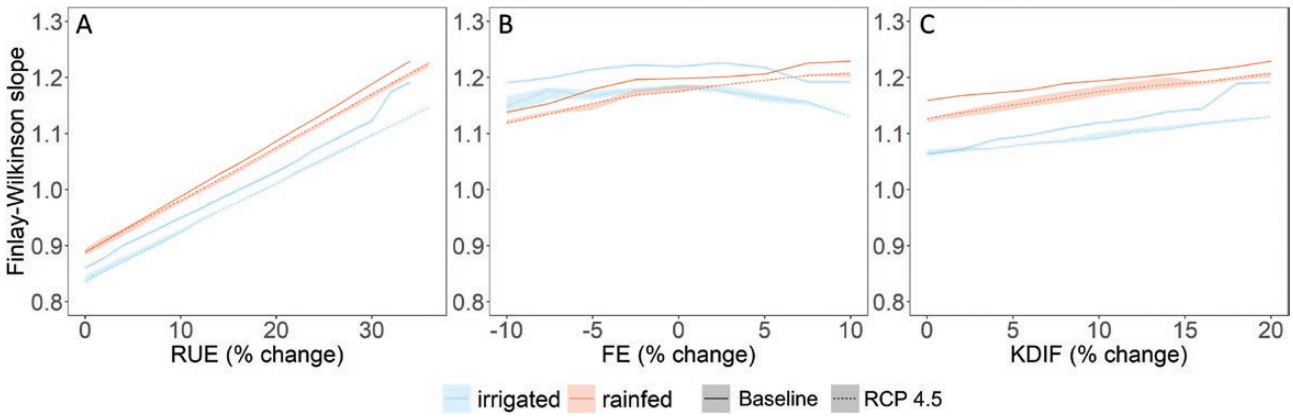

Figure 7. Sensitivity to environmental conditions (slope of the Finlay–Wilkinson regression, see Section 2.4) as influenced by changes trait values. Trait values are expressed as percentage change compared to the base parameterization. Solid and dashed lines represent the mean across sites under baseline and climate change (RCP4.5) conditions, respectively. The shaded areas represent the variation of such mean (interquartile range) across the five GCMs. To aid visualization, in each panel, the value of the remaining two parameters is fixed to an optimum value (A: KDIF = +20 %, FE = +10 %; B: RUE = +34 %, KDIF = +20 %; C: RUE = +34 %, FE = +10 %).

however, no trade-offs in yields were observed for improved genotypes, that is the genotype with the best average performance did not underperform in relatively worse environments. Conversely, higher yields in optimal environments (i.e. good years within a site) translated into yield spillover in relatively more marginal conditions (unfavourable years). Simmonds (1991) argued that lines selected for high performance in high-yielding environments may often underperform in low-yielding environments. Despite the higher sensitivity to environment conditions, however, improved genotypes still outperformed the base genotype over the range of the environments tested. While such result may be influenced by the sampling of the locations for the current study (high yielding, either irrigated or characterized by high rainfall), this is in line with previous findings confirming that the trend described by Simmonds (1991) has yet to become an issue. In Argentina, Australia, Italy and the UK, modern cultivars have consistently out-yielded older ones, even in the lowest-yielding conditions and despite the increased environmental sensitivity associated with increased YP (Del Pozo *et al.* 2021), as well as in high-yielding environments. In general, constitutive traits maximizing productivity sustained a significant yield improvement also under moderate stress (Vita *et al.* 2010), thus making modern elite cultivars genetically more suitable than older wheat cultivars to increase productivity in low-input production systems (Voss-Fels *et al.* 2019).

This results of this simulation study suggest a limited prospect for targeted breeding for YP when informed only by simulation modelling capturing these traits in response to climate and soil and no other limiting factors. Importantly, we must stress that our study also assumed phenology adapted to each environment and as such identified a combination of traits, not a genotype. With this in mind, these study results suggest that there are the best combination of these traits are largely constant across mega-environments (Gauch 2013). In our study, the changes in the genotype ranking based on average yield were minimized while approaching the top of the ranking, and a single genotype consistently outperformed all the others across all locations. We realize that this is largely an artefact the fact that in this simulation limiting factors were not considered, and this phenomenom is rarely observed under actual production conditions. This is nevertheless an interesting result as it suggests observed RV in experiments may not be related to the traits associated with high yield and rather adaptation to yield-limiting factors. In the simulations, the lack of variability in the top-ranked trait combination thus prevented the subdivision of the sites into sub-regions for targeted breeding (Atlin *et al.* 2000) to leverage narrow adaptation for increasing YP. This finding is consistent with literature analysing both real-world and simulated data. Reynolds and Langridge (2016) observed that lines characterized by the best physiological traits expressed the highest average yields across all study sites. In a simulation study covering the UK and New Zealand environments, Senapati *et al.* (2019) found that some of the cultivar parameters were subject to a strong selection pressure and converged to a single optimal value for all the locations. Also in our study, a global optimum for combined trait values was found, corresponding to the combination of the highest RUE, FE and KDIF within the range explored. The consistency of this outcome across non-stressed environments suggests that genotype selection in a few optimal environments could be a successful strategy for developing superior lines for increasing YP. From there, local breeders must adapt them to reflect the local phenology, diseases resistance, quality and stressor exposure. Indeed, root ideotypes are different for irrigated and rainfed conditions according to several studies (Schmidt and Gaudin 2017; Rezzouk *et al.* 2022), though in our study, ideotypes for both irrigated and rainfed conditions are almost the same with our focus on only aboveground traits (Schmidt and Gaudin 2017; Rezzouk *et al.* 2022).

Climate change was responsible for changes in both productivity and inter-annual yield variability, with changes being location-dependent. This however, did not alter the picture outlined under baseline climate: the best-performing trait combination in the baseline was confirmed successful under climate change and such best genotype was consistently the best across environmental conditions (see Supporting Information—Fig. S4). This allows us to cautiously suggest that current breeding efforts aimed at increasing YP through the traits studied here may not likely be jeopardized by climate change for the high-yielding environments explored. However, our results are based on simulations from one model only in which the effects of elevated atmospheric CO_2 largely counteract the yield losses associated with accelerated phenology with warmer temperatures (Webber *et al.* 2018). Previous modelling studies predicted the possibility of substantial increase in genetic YP of wheat under climate change in high productive countries (Senapati *et al.* 2019). Our study confirmed such projection for most of the sites analysed, with few exceptions where a decrease in yield was associated with an increased inter-annual variability under climate change (see Supporting Information—Fig. S2). In these cases, genetic improvement showed little potential for adaptation, with all the virtual genotypes within the trait space explored displaying a similar response.

Globally, increased yield stability has tended to be a minor breeding objective despite its potential (Annicchiarico 2002). Conducting such experiments to evaluate interactions between genotype and environment are complex, challenging to interpret and expensive. In order to ensure the reliability of yield stability by direct selection, time and resources are used extensively to replicate such experiments over several locations and years, which is continually insufficient covering all genotype × environment interactions (Banterng *et al.* 2006). Variability in observed yield of the genotypes echoes not only the responses of the genotypes to different soil and climatic conditions at different sites, which are of the main target of breeding programs, but also results from the effects of other variables, including pests and diseases or measurement errors (Falcon *et al.* 2020). Implementing new traits such as higher RUE in modern genotypes that we projected up to 45 % yield improvement coupling with higher yield stability represent important advances in a range of efforts needed to achieve food security over contrasting environments assuming optimal management. However, yield improvement in natural conditions (not a modelling framework) would come with potential hidden costs that could undermine future food security. Higher biomass accumulation would demand to maintain synthetic fertilizers rate and increase the pesticide application to ensure productivity (Hawkesford 2014) and control pests and diseases (Bilsborrow *et al.* 2013), projected to more frequent outbreaks associated with climate change (Bajwa *et al.* 2020).

Those factors would have long-term negative environmental and economic consequences on sustainability of cropping systems (Cook 2006).

The economic significance of releasing high-yielding, more stable genotypes from the scale of farmers' income to global wheat market volatilities are considerably more challenging to predict (Shiferaw *et al.* 2013). Supply and demand balance and oil price (as a primary substance of synthetic fertilizers) are the most influential drivers of fluctuations in food price (Tadesse *et al.* 2014). Here is where economic scenario analysis comes into play to evaluate whether the modern genotypes can revert the global wheat market to an age of over-supply or an increase in food demand is consistently larger than supply (Fuss *et al.* 2015; Le Mouël and Forslund 2017).

4.2 Role and limitations of the modelling study in supporting breeding

Crop models can be employed to support breeding efforts for overcoming such challenges to measure the yield stability and gain of the genotypes over the environments, separately controlling the effects of other influencing variables (e.g. pests and diseases, environmental heterogeneity, or measurement errors) and testing the performance of the genotypes across an unlimited number of environments (Suriharn *et al.* 2008; Chenu *et al.* 2011; Salmerón *et al.* 2017; Clarke *et al.* 2019). Comparing the results of yield stability analysis from multi-environment experiments and crop model outcomes showed that simulated yield is overestimated as expected; however, the crop model captured the relative mean yield change across the environments for study genotypes (Banterng *et al.* 2006). Modelling genotype × environment interactions can support breeding programs in raising YP by testing virtual genotypes well before a resource-intensive and time-consuming selection takes place (Chapman 2008; Chenu *et al.* 2011; Robert *et al.* 2020). Moreover, in a changing climate, models can provide timely assessments of the productivity of current elite genetic material, as well as of the potential for genetic adaptation to anticipated climate change (Lopes *et al.* 2015; Hammer *et al.* 2020). However, the accurate prediction of genotype performance across multiple environments is conditional to the availability of crop models accounting for the necessary physiological processes at an appropriate level of complexity, the development of a well-constrained parameter set and the quality of the input data to drive the model (Ramirez-Villegas *et al.* 2020).

The methods and model used in this specific study also suffered a number of limitations. While baseline default cultivars were locally adapted by calibration of thermal times and considering photoperiod sensitivity and vernalization requirement typical in each region, the study considered only three improved modern varieties in defining baseline trait values which is clearly a simplification. As for the model used in this study, again it was tested against experimental data from modern cultivars grown in only a few high-yielding environments (Dueri *et al.* 2022; Guarin *et al.* 2022). While it demonstrated its suitability for the simulation of wheat YP under favourable conditions where it displayed a coherent response to changes in crop traits values (Bustos *et al.* 2013), we did not test it across all sites studied. Furthermore, we acknowledge that the model does not include all the relevant interactions among the traits studied. For example, the possibility that RUE may be indirectly influenced by sink limitation (Liang *et al.* 2018) is ignored in the implementation used in this study, though the current state of understanding for source-sink interactions—recently published as a wiring diagram—supports the possibility to do so (Reynolds *et al.* 2022). Moreover, model improvements are necessary to include the effects of drought (Ratjen *et al.* 2012) and heat stress (Maiorano *et al.* 2017) on spike fertility. While this was not a critical issue for the current study due to the focus on high yielding, either irrigated or high-rainfall locations, such improvements will become necessary for extending the analysis to low-yielding environments characterized by a more frequent occurrence of stresses. The present study outlined the possibility for improved crop traits to raise YP with no trade-offs in terms of yield stability under current climate and climate change scenarios, but such outcome was supported by the results of a single crop model. However, as the crop model structure is a main source of uncertainty in modelled response to changes in crop traits and climate conditions (Martre *et al.* 2015c), a next step to extend this study would be to apply a multi-model ensemble to quantify the uncertainty bracketing these outcomes. However, it will be challenging to understand and explain the behaviour of a multi-model median without investigating individual models where there is a genotype by climate-year by model interaction.

The determination of crop model parameters is crucial for the model to correctly capture genotype behaviour across different environments. The trait space explored—represented by the range of model parameters—was supported by both experimental data (Bustos *et al.* 2013) and the literature on the traits considered (Reynolds *et al.* 2007; Furbank *et al.* 2015; Slattery and Ort 2021). Despite being focussed on relevant traits and levels of expressions for breeding, the results of our analysis were constrained by the specific trait space explored. A global optimum of trait combinations may lay beyond these boundaries, and it may require to take into account additional traits. In our relatively simple parameter space, we could assume no correlation among the traits selected (Molero *et al.* 2019). This choice was consistent with other model-based ideotyping studies (Casadebaig *et al.* 2016; Senapati *et al.* 2019), but such approach could be inadequate when considering a more complex landscape of trait combinations. In any case, moving from a set of prescribed changes in model parameters to a range of phenotypic screens that are measurable and can be selected for in breeding trials remains a challenging process (Ramirez-Villegas *et al.* 2020).

Finally, this study focussed by design on high-yielding environments. Despite the sampling of favourable sites, the analysis of bad years provided an indication of a yield spillover effect improving yields under relatively marginal conditions, outlining breeding for high YP as a win-win situation across environments both in terms of productivity and yield stability. However, further study is required to explore the benefits of improved traits for YP in more marginal environments, to confirm the absence of trade-offs under limiting growing conditions (Reynolds *et al.* 2011; Zhao *et al.* 2015; Slattery and Ort 2021).

5. CONCLUSIONS

This study has addressed the question as to whether higher potential yields could possibly jeopardize efforts towards food security by introducing higher yield variability and possibly yield failures in the face of climate change. The results of simulation study using a single crop model suggest that such trade-offs are not likely to appear under average climate change conditions for high-yielding traits in high-yielding wheat regions. However, potential environmental costs and risks associated with higher nitrogen fertilization rates required to achieve high yields, particularly in the face of increasingly variable and extreme climate were not included in our study. The study provides some promise of the possibility to increase YP across environments without increasing relative yield variability.

SUPPORTING INFORMATION

The following additional information is available in the online version of this article –

ACKNOWLEDGEMENTS

The study was supported by the International Wheat Yield Partnership (IWYP, grant IWYP115), through funding the International Maize and Wheat Improvement Center (CIMMYT) and by the Agricultural Model Intercomparison and Improvement Project (AgMIP). P.M. acknowledges support from the metaprogram Agriculture and forestry in the face of climate change: adaptation and mitigation (CLIMAE) of the French National Research Institute for Agriculture, Food (INRAE). A.C.R. received support via NASA Earth Sciences funding for the GISS Climate Impacts Group.

CONFLICT OF INTEREST STATEMENT

We have no conflicts of interest.

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