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ORIGINAL RESEARCH

Designing high-yielding wheat ideotypes for a changing climate

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Abstract

Global warming is characterized by shifts in weather patterns and increases in climatic variability and extreme events. New wheat cultivars will be required for a rapidly changing environment, putting severe pressure on breeders who must select for climate conditions which can only be predicted with a great degree of uncertainty. To assist breeders to identify key wheat traits for improvements under climate change, wheat ideotypes can be designed and tested *in silico* using a wheat simulation model for a wide range of future climate scenarios predicted by global climate models. A wheat ideotype is represented by a set of cultivar parameters in a model, which could be optimized for best wheat performance under projected climate change. As an example, high-yielding wheat ideotypes were designed at two contrasting European sites for the 2050 (A1B) climate scenario. Simulations showed that wheat yield potential can be substantially increased for new ideotypes compared with current wheat varieties under climate change. The main factors contributing to yield increase were improvement in light conversion efficiency, extended duration of grain filling resulting in a higher harvest index, and optimal phenology.

Introduction

Food security has become a major challenge given the projected need to increase world food supply by about 70% by 2050 (FAO 2009). Considering the limitations on expanding crop-growing areas in developed countries such as the United Kingdom, a significant increase in crop productivity will be required to achieve this target. Wheat is the staple food of almost half the world's population and is the most important crop in Europe. Although the world record wheat yield of 15.64 t ha^{-1} was achieved on a farm in New Zealand for cv. Einstein in 2010 (http://www.guinnessworldrecords.com/world-records/1/highest-wheat-yield), the average United Kingdom farm yield has remained slightly above 8 t ha^{-1} for more than a decade (Semenov et al. 2012) and the rate of the yield increase in Europe has flattened (Brisson et al. 2010).

Donald (1968) proposed the approach of "breeding of crop ideotypes" to underpin crop breeding programs, in addition to two existing breeding philosophies of "defect elimination" and "selection for yield". He defined a crop ideotype as an idealized plant, or a plant model (not yet a mathematical one), which is expected to yield a greater quantity or quality of grain when developed as a cultivar. He emphasized that developing new ideotypes will provide a basis for better understanding of crop ecology and physiology and result in progressively more effective ideotypes. In contrast, "selection for yield" has limitations as the desirable combination of traits, which never being considered, can be attained only by chance.

Considering the urgent need to increase wheat yield potential, the Wheat Yield Consortium (WYC) published a programme in 2011 to facilitate and coordinate research in wheat improvement (Foulkes et al. 2011; Parry et al. 2011; Reynolds et al. 2011). In order to develop high-yielding wheat ideotypes, several traits were identified as a key for improvement of wheat yield potential. These traits include increased photosynthetic capacity and efficiency, optimal developmental pattern to maximize spike fertility, optimal partitioning to grain, improved grain filling and potential grain size, lodging resistance and many others. WYC emphasized the importance of mathematical modeling as a powerful tool to understand optimal combinations and trade-offs between proposed traits (Reynolds et al. 2011).

Ecophysiological process-based crop models are commonly used in basic and applied research in the plant sciences and in natural resource management (Passioura 1996; Sinclair and Seligman 1996; Hammer et al. 2002; Rötter et al. 2011; White et al. 2011). They provide the best-known framework for integrating our understanding of complex plant processes and their interaction with climate and environment. Such models are playing an increasing role in guiding the direction of fundamental research by providing quantitative predictions and highlighting gaps in our knowledge (Tardieu 2003; Hammer et al. 2006, 2010; Semenov and Halford 2009; Semenov and Shewry 2011).

Wheat production is highly sensitive to environmental conditions (Porter and Semenov 2005). Global warming is characterized by shifts in weather patterns and increase in frequency and magnitude of extreme events (Semenov 2007; Sillmann and Roeckner 2008; Lobell et al. 2012). Increasing temperature and incidence of drought associated with global warming are posing serious threats to food security. Climate change, therefore, represents a considerable challenge in achieving the 70% increase target in world food production. New wheat cultivars with specific physiological traits will therefore be required for a changing climate. However, the intrinsic uncertainty of climate change predictions poses a challenge to plant breeders and crop scientists who have limited time and resources and must select the most appropriate traits for improvement (Semenov and Halford 2009; Reynolds et al. 2011; Zheng et al. 2012). Modeling provides a rational approach to design and test *in silico* new wheat ideotypes optimized for future environments and climatic conditions (Hammer et al. 2006, 2010; Semenov and Halford 2009; Tardieu and Tuberosa 2010; Semenov and Shewry 2011; Quilot-Turion et al. 2012; Zheng et al. 2012).

The objective of this paper was to illustrate the capacity of modeling in designing high-yielding wheat ideotypes for a future climate. We used the Sirius wheat model which simulates crop growth and development at a daily time step (Jamieson et al. 1998b; Jamieson and Semenov 2000; Lawless et al. 2005; Semenov 2009). Sirius was calibrated and validated for modern wheat cultivars and was able to simulate accurately crop growth and grain yield in a wide range of environments, including Europe, U.S.A., New Zealand, and Australia, and under climate change (Jamieson et al. 2000; Ewert et al. 2002; Martre et al. 2006; Lawless et al. 2008; He et al. 2012). We define a wheat ideotype as a set of Sirius cultivar parameters. By changing cultivar parameters, we change wheat growth and development in response to climatic and environment variations. In this way, we can assess the performance of new wheat ideotypes for future climates and environments which are not yet available for field experimentations. Local-scale climate scenarios required as input into Sirius were generated by the LARS-WG stochastic weather generator and were based on the Hadley Centre Global Climate Model HadCM3 projections for the A1B emission scenario for the 2050s (Meehl et al. 2007).

Designing High-Yielding Wheat Ideotypes

Nine cultivar parameters considered as most promising for improvement of wheat yield potential were selected for optimization at two contrasting European sites – Rothamsted, United Kingdom (RR) and Seville, Spain (SL) – under future climatic conditions (Table 1). The ranges of possible parameters values are presented in Table 2 and were based on parameters calibrated for existing modern cultivars allowing variations corresponding to the existing wheat germplasm (Semenov et al. 2009; He et al. 2012).

Cultivar parameter space for optimization

Photosynthesis

We assume that a 10% increase in light conversion efficiency could be achieved in the future. Using a model of

Table 1. Characteristics of two European sites.

Site	Lon.	Lat.	Annual precipitation (mm)	Mean temperature (°C) Jan, min.	July, max.	Cultivar	Soil (AWC, mm)	Flowering (1960–1990)
Rothamsted, U.K.	−0.35	51.8	693	0.3	20.8	Mercia	Rothamsted (210)	19 June
Seville, Spain	−5.88	37.42	524	4.3	35.2	Cartaya	Hafren (177)	27 April

AWC, available water capacity.

Table 2. Sirius cultivar parameters with the ranges of values used in optimization of ideotypes.

Parameter	Symbol	Range
Photosynthesis		
Light conversion efficiency	*L*	1–1.10[1]
Phenology		
Phyllochron	*Ph*	70–140 (C° days)[2]
Daylength response	*Pp*	0.05–0.70 (leaf h^{-1} daylength)[3]
Duration of grain filling	*Gf*	500–900 (C° days)[4]
Canopy		
Maximum area of flag leaf	*A*	0.003–0.01 (m^2 leaf m^{-2} soil)[5]
"Stay-green"	*S*	11–14
Drought tolerance		
Response of photosynthesis to water stress	*Wsa*	0.1–0.21
Maximum acceleration of leaf senescence	*Wss*	1.2–1.9
Root water uptake		
Rate of water uptake	*Ru*	1–7[6]

[1]Using a model of canopy photosynthesis, it was shown that 10% increase in *L* could be achieved if Rubisco specificity factor was optimized (Zhu et al. 2010).

[2]Genetic variations of *Ph* up to 20% were observed for wheat (Mossad et al. 1995; Ishag et al. 1998).

[3]Varietal difference in number of days till heading under long and short day conditions varied between 9.74 and 107.40 in a photoperiodic response experiment (Kosner and Zurkova 1996).

[4]Genetic variations of *Gf* up to 40% were observed for wheat (Robert et al. 2001; Charmet et al. 2005; Akkaya et al. 2006).

[5]The reported range of genetic variations for flag leaf area under unlimited water and nitrogen supplies was up to 40% (Fischer et al. 1998; Shearman et al. 2005).

[6]Large genotypic variation in root characteristics and water uptake was reported (Manschadi et al. 2006; Tambussi et al. 2007).

canopy photosynthesis, (Zhu et al. 2004) showed that the value of parameter λ (Rubisco specificity factor that represents the discrimination between CO_2 and O_2) found in current C3 crops exceeds the level that would be optimal for the present CO_2 concentration ([CO_2]), but would be optimal for [CO_2] of about 220 ppm, the average of the last 400,000 years. The simulation results showed that up to 10% more carbon could be assimilated if λ was optimal for the current [CO_2] level.

In Sirius, radiation use efficiency is proportional to [CO_2] with an increase of 30% for doubling in [CO_2] compared with the baseline of 338 ppm, which is in agreement with the recent meta-analysis of field-scale experiments on the effects of [CO_2] on crops (Vanuytrecht et al. 2012). A similar response was used by other wheat simulation models, for example, CERES (Jamieson et al. 2000) and EPIC (Tubiello et al. 2000). However, Long et al. (2006) argued that the results from FACE experiments could show lower effects of elevated [CO_2] on wheat yield (Tubiello et al. 2007; Ainsworth et al. 2008).

Phenology

Three cultivar parameters are directly related to phenological development of wheat, that is, phyllochron *Ph*, daylength response *Pp,* and duration of grain filling *Gf* (Table 2). Modifying the duration of crop growth cycle and its timing in relation to seasonal variations of solar radiation and water availability may have significant effects on yield (Akkaya et al. 2006; Richards 2006). An optimal flowering time has been the single most important factor to maximize yield in dry environments (Richards 1991) and past increases in wheat yield have been associated with shortening of the duration of vegetative development phases (Calderini et al. 1997). The phyllochron *Ph* is the thermal time required for the appearance of successive leaves, and is a major driver of phenological development (Jamieson et al. 1995, 1998a, 2007). Details of the response of final leaf number to daylength could be found in (Brooking et al. 1995; Jamieson et al. 1998b). By modifying phyllochron *Ph* and daylength response *Pp* we alter the rate of crop development and, therefore, the date of flowering and maturity. Increasing the duration of the grain filling period *Gf* has been suggested as a possible trait for increasing grain yield in wheat (Evans and Fischer 1999). In Sirius, *Gf* is defined as a cultivar-specific amount of thermal time which needs to be accumulated to complete grain filling (Jamieson et al. 1998b). During grain filling, assimilates for the grain are available from two sources: new biomass produced from intercepted radiation and water-soluble carbohydrates stored mostly in the stem before anthesis. In Sirius, the labile carbohydrate pool is calculated as a fixed 25% of biomass at

Table 3. Cultivar parameters of the top five wheat ideotypes.

Site	Design #	Ru	Wsa	Gf	Wss	Pp	A	S	Ph
Rothamsted	5	3.96	0.110	900	1.414	0.109	0.01	14	114.2
	9	3.40	0.118	900	1.567	0.118	0.01	14	114.9
	4	4.97	0.149	900	1.692	0.118	0.01	14	114.8
	18	6.88	0.175	900	1.238	0.118	0.01	14	114.8
	11	4.45	0.186	900	1.630	0.110	0.01	14	114.1
Seville	10	6.79	0.10	900	1.253	0.624	0.01	14	82.4
	21	6.90	0.10	900	1.337	0.624	0.01	14	81.2
	16	3.35	0.10	900	1.201	0.128	0.01	14	104.3
	3	4.31	0.10	900	1.202	0.129	0.01	14	104.2
	7	2.92	0.10	900	1.202	0.128	0.01	14	106.0

Definition of parameters are given in Table 2.

anthesis, and is translocated to the grain during grain filling. Increasing *Gf* will increase the amount of radiation intercepted by the crop and, consequently, grain yield. However, in the model, water-soluble carbohydrates accumulated before anthesis are transferred into the grain at a rate inversely proportional to *Gf*. Therefore, any increase of *Gf* will also reduce the rate of biomass remobilization. Under stress conditions, when grain growth could be terminated early as a result of leaves dying before the end of grain filling due to water or heat stress, grain yield will decrease not only because of the reduction in intercepted radiation but also because not all of the labile carbohydrate pool will be translocated to the grain (Brooks et al. 2001; Semenov et al. 2009).

Canopy

Two cultivar parameters to be optimized are related to canopy, that is, maximum area of flag leaf layer *A* and duration of leaf senescence *S*. By varying the maximum area of the flag leaf layer, we change the rate of canopy expansion and the maximum achievable leaf area index (LAI). This in turn will change the pattern of light interception and transpiration and, therefore, will affect crop growth and final grain yield. One of the strategies to increase grain yield is to extend duration of leaf senescence and maintain green leaf area longer after anthesis, so called the "stay-green" trait (Austin 1999; Silva et al. 2000; Triboi and Triboi-Blondel 2002).

Tolerance to drought

Both daily biomass production (photosynthesis) and leaf senescence depend on the drought stress factor *SF* calculated daily as the ratio of actual to potential evapotranspiration. Production of new daily biomass decreases proportionally to the drought biomass reduction factor *Wsa* defined as $Wsa = SF^{\beta}$. By varying β, *Wsa* can change significantly, particularly, for values of $SF < 0.4$.

In Sirius, the rate of leaf senescence requires a cultivar-specific amount of thermal time, and could be accelerated by nitrogen shortage to sustain grain filling or by water or temperature stresses. In the presence of drought stress, the rate of leaf senescence increases, because the daily increment of thermal time is modified by the drought leaf senescence factor *Fs* calculated as $Fs = 2(1-Wss)(SF-0.4) + Wss$ for $SF > 0.4$ and $SF < 0.9$, $Fs = 1$ for $SF > 0.9$, and $Fs = Wss$ for $SF < 0.4$. Earlier leaf senescence will reduce grain yield. Increasing tolerance to drought stress (reducing *Wss*) will make leaves stay green longer under water stress and potentially increase grain yield.

Root water uptake

In Sirius, the soil is represented by 5 cm layers and we assume that only a proportion of available soil water can be extracted from each layer from the root zone by the plant on any day. By default, plants can extract up to 10% of available soil water from the top layer at any single day and only *Ru* (%) from the bottom layer at the maximum root depth. A faster water uptake reduces current stress experienced by the plant in anticipation of additional water coming in the form of precipitation or irrigation later in the season. In dry environments, where there is a low probability of additional water toward the end of the growing season, an alternative strategy that reduces plant water uptake (lower values for *Ru*) is less risky and may achieve, on average, higher yields (Manschadi et al. 2006).

Optimization set-up

An evolutionary search algorithm was incorporated in Sirius 2010, which allows optimization of cultivar parameters for the best performance of wheat ideotypes in a target environment. Sirius employs an evolutionary algorithm with self-adaptation (EA-SA) which is shown to be applicable for solving complex optimization problems in a high-dimensional parameter space (Beyer 1995; Schwefel and Rudolph 1995; Back 1998; Meyer-Nieberg and Beyer 2007). EA-SA was used in the past by the authors for calibration of cultivar parameters by minimizing difference between simulated and observed data (Stratonovitch and Semenov 2010).

In the current study, each ideotype was represented by nine cultivar parameters described in the previous section. For the remaining cultivar parameters, default values for cv. Claire for RR or cv. Cartaya (SL) were used. EA-SA optimized cultivar parameters by randomly perturbing (mutating) their values and testing performance in a target environment. At every step, 16 candidates (new wheat ideotypes) were generated from a "parent" by perturbing parent's cultivar parameters. For each of 16 new candidates, 100-year mean yield was calculated for a future climate scenario. The candidate with the highest 100-year mean yield was selected as a "parent" for the next step. In EA-SA, so-called "control" parameters, which control the degree of variation in cultivar parameters and are assigned to individual ideotypes, are also used. Control parameters are "inherited" from a parent and are subject to random variations. Although selection only depends on values of cultivar parameters, which determine 100-year mean yield, control parameters tend to coevolve and converge to 0 when cultivar parameters reach their optimal state. General conditions of convergence of EA-SA are given in (Semenov and Terkel 2003). The main advantage of EA-SA, compared with genetic algorithms, is that they do not require tuning control parameters during the search, where predefined heuristic rules are unavailable or difficult to formulate in a high-dimensional space with a complex optimization function (Semenov and Terkel 1985; Beyer 1995; Back 1998).

In our example, we optimized wheat ideotypes at two European sites with contrasting climates. The selected sites were Rothamsted in the United Kingdom and Seville in Spain, which represent wheat-growing areas in these countries (Table 1). Local-scale climate scenarios, named as 2050 (A1B), were based on climate projections from the HadCM3 global climate model for the A1B emission scenario for 2050 (Nakicenovic and Swart 2000). One hundred years of site-specific daily weather were generated at each site by the LARS-WG weather generator (Semenov and Stratonovitch 2010). Monthly mean precipitation and monthly mean maximum temperature for 1960–1990 and the 2050 (A1B) climate scenario at RR and SL are presented in Figure 1. The objective for optimization was to maximize the 100-year mean yield. Ideotypes with the coefficient of variation (CV) of yield exceeding 15% were excluded from the selection process. In the past 50 years the yield increase was largely a result of increase in harvest index (HI). However, there has been no systematic improvement of HI since the early 1990s from values of 0.50–0.55. There are several estimations of maximum possible HI for wheat: Austin et al. (1980) estimated this value as ~0.62 and more recent analysis by Foulkes et al. (2011) suggested using ~0.64. Unkovich et al. (2010) used a value of 0.65 as a maximum HI when they fitted the BetaGeneral distribution to a sample of 194 estimates of HI for rainfed wheat in Australia, which was constructed by averaging across data-source × site × year for over 1200 HI. During optimization we discarded from selection ideotypes with the 90th percentile of HI exceeding 0.65.

The stopping rule for optimization was (1) no further improvement was possible (the search found a local optimum, or EA-SA prematurely converged) or (2) the 95th percentile of yield (Y^{95}) exceeds 20 t ha^{-1}. All simulations were assumed to be water-limited, but no N limitation was considered.

EA-SA is a local search algorithm which converges to one of the local maxima in a multidimension parameter space. To avoid convergence to a local maximum and to explore fully the parameter space, we used multiple "parents" to initiate a search algorithm. For each site, RR or SL, we used 25 parents randomly scattered in the parameter space (Table 2) except one parent which has the same cultivar parameters as cv. Claire at RR or cv. Cartaya in SL calibrated previously using experimental data (Wolf et al. 1996). For each of 25 initial parents, EA-SA converged to one of the local maxima or found a wheat ideotype with the 95th percentile of yield exceeding 20 t ha^{-1}.

The optimization function, that is, 100-year mean yield with additional constrains, is a complex function, which could have very different sensitivity to variations in cultivar parameters and belongs to the class of valley functions. EA-SA will converge quickly to an optimal value of the most sensitive cultivar parameter (or several parameters) at the bottom of the "valley," leaving other parameters in a state not fully optimized, a phenomenon known as premature convergence (Back et al. 2000). To overcome premature convergence, we adopted the following procedure. When we observed convergence of a parameter (or several parameters) to a single value for the majority of ideotypes, we assumed that the optimal value for this parameter is found and we repeated optimization assigning this optimal value to a parameter and excluding it from the optimization process. In this way, we were able to continue optimization of the remaining cultivar parameters improving wheat yield potential. We repeated this procedure until no single optimal parameter value was found for the majority of the 25 parents.

Simulation results

Figure 2 illustrate progress in optimization for RR and SL. For all simulations the light conversion efficiency was

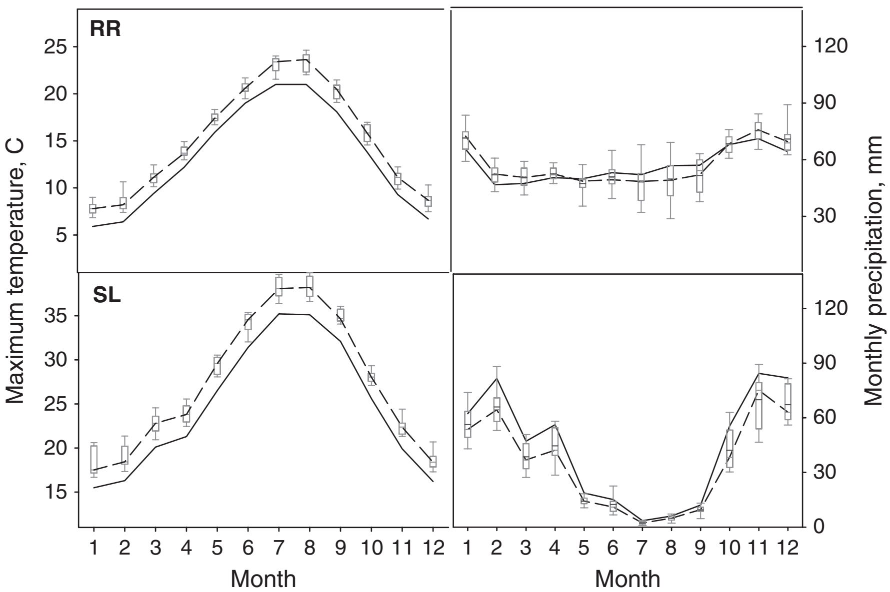

Figure 1. Monthly weather statistics. Monthly mean maximum temperature (left column) and mean monthly precipitation (right column) for 1960–1990 (solid) and the 2050 (A1B) scenario (dashed) at Rothamsted (RR) and Seville (SL). Box plots represent uncertainty in predictions from 15 global climate models (GCMs) from the Coupled Model Intercomparison Project (CMIP3) ensemble, which includes the HadCM3 climate models. Box boundaries indicate the 25th and 75th percentiles; the line within the box marks the median; whiskers below and above the box indicate the 10th and 90th percentiles. Note that the scales for temperature are different, but the range is the same, 30°C.

set as a constant: $L = 1.1$. At first stage, stage 1, eight parameters were optimized at both sites (Table 1). When optimization process stopped at RR, duration of grain filling *Gf* and maximum area of flag leaf *A* converged to near-maximum values of 900 and 0.01, respectively, for almost all ideotypes (Fig. 2, RR stage 1, Table 2). In SL, parameters *Gf, A,* and "stay-green" *S* converged to near-maximum values (Fig. 2, SL stage 1). Ideotypes with a longer duration of grain filling *Gf* can potentially produce higher grain yield if green leaf area is maintained during grain filling, which could be a problem in SL because of severe drought stress at the end of grain filling. Ideotypes with maximum values of *A* and *S* intercept more solar radiation during the growing season because of earlier establishment of canopy at the beginning of the growing season and later senescence of leaves at the end of grain filling.

At stage 2 at RR, parameters *Gf* and *A* were set to their maximum values and the remaining six parameters were optimized. One cultivar parameter, the "stay-green" parameter *S*, converged to near-maximum values of 14 for all ideotypes (not shown on Fig. 2). At stage 3 at RR, three parameters *Gf, A,* and *S* were set to their optimal values and five remaining cultivar parameters were optimized. Convergence was observed for two cultivar parameters, phyllochron *Ph* and daylength response *Pp*. Both of these parameters control wheat phenology including flowering date and were responsible for placing grain filling in the most favorable part of the season, maximizing intercepted solar radiation and minimizing the effect of water limitation on grain yield (Fig. 2, RR stage 3). Remaining cultivar parameters controlling water stress tolerance, *Wss* and *Wsa*, and water uptake, *Ru*, were randomly scattered in the parameter space, because water stress had a small effect on grain yield at this location. At RR the best wheat ideotype achieved 17.6 t ha^{-1} 100-year mean grain yield with 95th percentile of yield exceeding 18.7 t ha^{-1} for the 2050 (A1B) climate scenario (Fig. 4A).

At stage 2 in SL, parameters *Gf, A,* and *S* were set to their maximum values and the remaining five parameters were optimized. Due to more severe weather constrains, that is, high maximum temperature and low precipitation during summer (Fig. 1B), all remaining cultivar parameters, except for root water uptake *Ru*, converged to their optimal values. Root water uptake *Ru* did not converge in SL, because there is no a clear single optimal strategy of extracting soil water during the season. In SL, the best wheat ideotype achieved 14.1 t ha^{-1} 100-year mean grain yield with 95th percentile of yield exceeding 15.3 t ha^{-1} (Fig. 4B).

In Figure 3, we compared the cultivar parameters for two cultivars, Claire at RR and Cartaya in SL, with cultivar parameters of the top five ideotypes at RR (Fig. 3A) and Seville (Fig. 3B) optimized for the 2050 (A1B) climate scenario. Substantial changes will be needed for

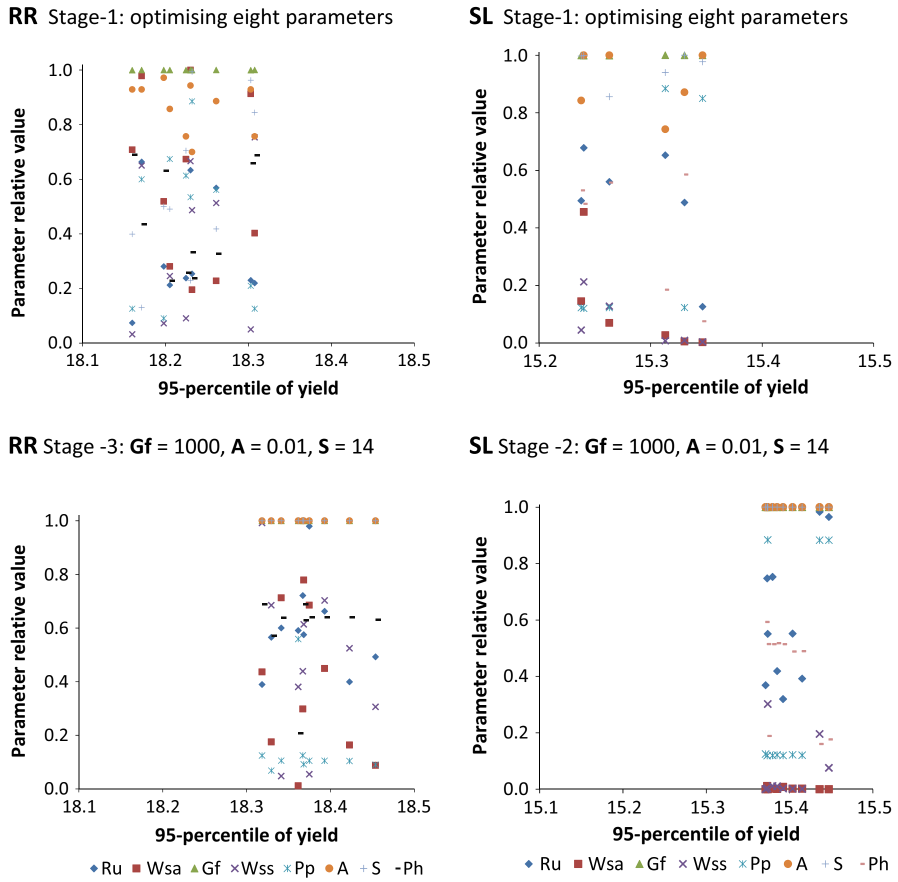

Figure 2. Optimization stages at Rothamsted (RR) and Seville (SL) for the 2050 (A1B) climate scenario. All parameters were normalized in order to present their values at a single graph with 0 set for a minimum value and 1 for maximum value from the range of possible values defined in Table 2. Ten ideotypes with the highest 95th percentile of yield are shown.

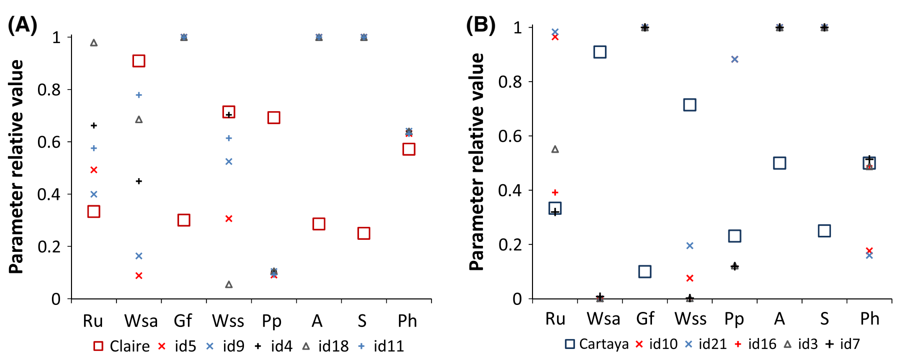

Figure 3. Cultivar parameters for the top five wheat ideotypes at Rothamsted (A) and Seville (B) optimized for the 2050 (A1B) climate scenario. Cultivar parameters for cv. Claire and cv. Cartaya are shown as open squares. Numerical values of cultivar parameters of these ideotypes are given in Table 3.

currently available wheat cultivars to deliver high yields in the climate of 2050 (Table 3). To realize high yield at RR for 2050 (A1B), duration of grain filling *Gf*, maximum area of flag leaf *A*, and "stay-green" *S* have to increase, as well as phylochron *Ph* and daylength response *Pp* have to be adjusted to achieve optimal phenological development and flowering time (Fig. 3A). To realize high yields in SL, in addition to *Gf*, *A*, and *S*, maximum acceleration of leaf senescence *Wss* and response of photosynthesis to water stress *Wsa* have to be improved to minimize the effect of water stress during the growing season (Fig. 3B). It is interesting to note that cv. Cartaya has phenology (*Ph* and *Pp*) that is nearly optimal for the future 2050 (A1B) climate scenario.

In Figure 4, box-plots of grain yield for the top five wheat ideotypes at RR (Fig. 4A) and Seville, Spain (Fig. 4B) for the 2050 (A1B) climate scenario are presented. Simulated grain yields for cv. Claire at RR and Cartaya at SL were 17% and 9% higher for the 2050 (A1B) climate scenario compared with the yields for the 1960–1990 scenario mainly due to increase in [CO_2] to 534 ppm. But these yields were substantially lower compared with the yields simulated for five best ideotypes at these locations for the 2050 (A1B) scenario. Dates of anthesis and maturity are shown for RR (Fig. 4C) and for SL (Fig. 4D), and the HI is shown for RR (Fig. 4E) and for SL (Fig. 4F). Wheat ideotypes optimized for the 2050 (A1B) climate scenario can potentially deliver 52% and 78% increase in yield compared with yields of cv. Claire and Cartaya for 2050 (A1B), respectively. The main factors contributing to yield increase were improvement in light conversion efficiency, extended duration of grain filling resulting in a higher HI, and optimal phenology. At RR duration of grain filling for the top five ideotypes increased on average by about 14.5 days due to earlier anthesis and later maturity. In SL duration of grain filling increased by about 11.9 days, mostly due to later maturity, which was possible because all ideotypes had improved tolerance to water stress during leaf senescence. At both locations flowering time was positioned to

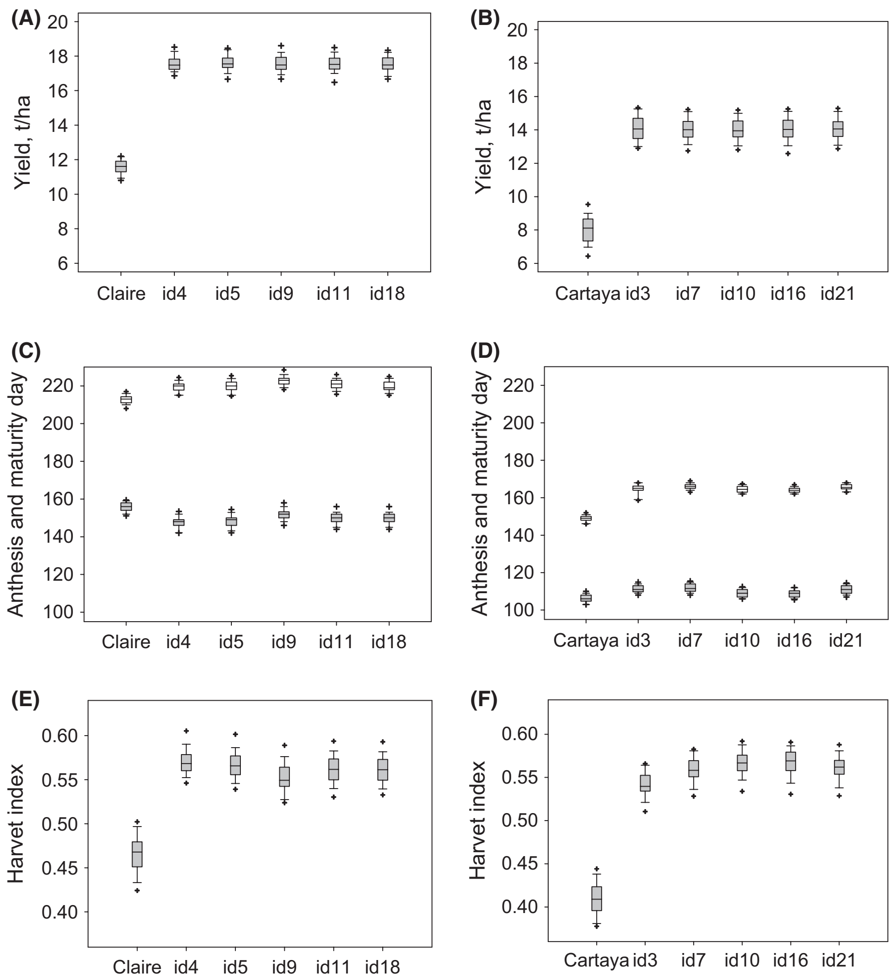

Figure 4. Box plots for the five best-yielding wheat ideotypes optimized for the 2050 (A1B) climate scenario at Rothamsted (left panels) and Seville (right panels) for grain yield (A and B), anthesis (gray boxes) and maturity (open boxes) (C and D) and harvest index (E and F). Box plots for yield, anthesis and maturity and harvest index for cv. Claire and Cartaya are also shown. Box boundaries indicate the 25th and 75th percentiles, the line within the box marks the median, whiskers below and above the box indicate the 10th and 90th percentiles, and crosses mark the 5th and 95th percentiles.

maximize the amount of intercepted solar radiation and avoid the effect of late-season water stress.

The HI for the top five wheat ideotypes optimized for the 2050 (A1B) climate scenario is presented in Figure 4E for RR and Figure 4F for SL. Mean HI of the five best ideotypes at RR was 0.56 compared with HI=0.47 for cv. Claire, and mean HI in Seville was 0.56 compared with HI=0.41 for cv. Cartaya, which are in the range of values considered theoretically possible (Foulkes et al. 2011).

Concluding Remarks

1 Our results demonstrated that the substantial increase in simulated wheat yield is possible by optimizing cultivar parameters for a future climate predicted by the HadCM3 climate model under the A1B emission scenario for the 2050s at both locations, Rothamsted and Seville. We assumed that at least 10% improvement in light conversion efficiency would be possible in wheat by tuning the C3 photosynthetic mechanism for a higher level of [CO_2] (Zhu et al. 2010). Inefficiency of carbon fixation in wheat can also be improved by introducing the C4 mechanism, which shows up to 50% greater radiation use efficiency compared with the C3 mechanism at the current [CO_2] (Parry et al. 2011). However, in field and chambers experiments, C4 crops showed lower response to increase in [CO_2] compared with C3 crops reducing a comparative advantage of C4 mechanism for the future [CO_2] (Ainsworth and Long 2005; Vanuytrecht et al. 2012).

2 A major contributing factor in increasing wheat yield potential is extended duration of grain filling, resulting in an increase of HI. This can only be possible if wheat can maintain green area index until the end of grain filling. In water-limited environments such as Seville, improvement in drought tolerance, which delays leaf senescence, will be essential.

3 We did not consider nitrogen (N) limitation in our simulation, assuming plentiful supply of N. However, postanthesis N uptake and redistribution could be a serious constraint in achieving greater wheat yield potential. Grain demand for N during grain filling is satisfied from three sources (Jamieson and Semenov 2000). The first is excess of N in the stem including N released by natural leaf senescence. If this amount is insufficient, then soil N is taken. Should these combined sources be insufficient then N is remobilized from leaves reducing their photosynthetic capacity and accelerating leaf senescence (killing leaves). As a result, grain filling duration can be shortened and grain yield potential can be reduced. One of the strategies to prevent this from happening is to increase the capacity to store N in nonphotosynthetic organs, such as internodes, that allows the translocation of N to grains without reducing wheat photosynthetic capacity (Dreccer et al. 1998; Martre et al. 2007; Bertheloot et al. 2008; Bancal 2009). Another strategy would be to improve N uptake from the soil in the postanthesis period. However, the ability of roots to take up N could decline during grain filling (Oscarson et al. 1995; Andersson et al. 2004; Martre et al. 2006). Moreover, if the end of grain filling coincides with low water availability (a typical situation in SL), then soil N available for uptake could be substantially reduced due to water shortage (Semenov et al. 2007).

4 We assume that wheat ideotypes were tolerant to high temperatures around anthesis (maximum daily temperature above 30°C), because the current version of Sirius does not include cultivar parameters for tolerance to heat stress around anthesis. The wheat yield could be limited by the grain number and the grain size, which are established to a large extent at the period around anthesis, a stage in development known to be sensitive to high temperature stress (Porter and Semenov 2005). The grain number and the grain size can be substantially reduced if a cultivar, sensitive to heat stress, is exposed to a short period of high temperature around flowering, limiting the capacity of grains to store newly produced biomass and substantially reducing wheat yield (Tashiro and Wardlaw 1989; Wheeler et al. 1996). Semenov and Shewry (2011) demonstrated that the risk of heat stress around flowering will increase in Europe with climate change, potentially resulting in substantial yield losses for heat-sensitive cultivars commonly grown in northern Europe (Semenov and Shewry 2011).

5 In our simulation experiments, we assume that cultivar parameters could be changed independently from each other. This might not be always the case. For example, a high value for maximum area of flag leaf *A* may require a higher value for phylochron *Ph* to provide sufficient time for larger leaves to grow. Dependencies between parameters, when known, can be effortlessly incorporated in the current modeling framework in the same way that we accounted for restrictions on the maximum value of HI.

6 Sirius is one of many wheat simulation models available. Potentially, ideotypes designed using a different crop model might look different from those presented. In the recent study on uncertainty analysis of simulated crop responses to climate change based on multimodel ensemble of crop models, it was shown that even when models are able to simulate observed yields accurately under a range of environments for the current conditions, simulated climate change impacts could vary across models due to differences in model structures and parameter values (Asseng et al. 2013). Rötter et al. (2011) suggested that further improvements of crop models will be needed to meet future challenges and a more rigorous approach based on multimodel ensembles of crop models will be required for robust predictions.

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Conflict of Interest

None declared.

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