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Assessment of drought-related traits for rainfed wheat under current and future climates

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Abstract

Objective: This research aimed to employ crop simulation modeling to identify key traits for improving water-limited yield (Yw) of rainfed wheat (*Triticum aestivum* L.) across Iran's diverse agro-climatic zones under current and projected future climates.

Methods: Using the Global Yield Gap Atlas (GYGA) upscaling protocol and the SSM-iCrop model, simulations were conducted for 32 reference weather stations (RWSs) representing 72% of Iran's national rainfed wheat area. Historical (2000–2015) and future (2041–2060; RCP4.5, +1.9 °C, 500 ppm CO_2) climate scenarios were analyzed to evaluate the impact of modifying physiological traits.

Results: Under the current climate, the national mean simulated Yw was 2.02 t ha^{-1}, ranging from 1.04 to 4.41 t ha^{-1}. Future climate increased mean Yw to 2.87 t ha^{-1} (range: 1.54–5.33 t ha^{-1}), due to CO_2 fertilization and accelerated development, alleviating terminal drought. Trait analysis revealed that increasing the grain-filling duration by 20% was the most effective and consistent strategy, boosting national mean yield by 0.30 t ha^{-1} (current climate) and 0.47 t ha^{-1} (future climate) in high-rainfall Caspian Sea zones. Conversely, shortening the vegetative phase by 20% increased yields by up to 0.1 t ha^{-1} in terminal-drought regions of the Zagros Mountains but reduced yields in eastern and northeastern Iran, with negative impacts intensifying under future climate. Decreasing phyllochron provided modest yield gains (>5% in 7 RWSs) under the current climate, but its benefits diminished under future warming. Increasing radiation use efficiency had a limited impact under both climate conditions. Spatial analysis showed the primary key trait was extending grain-filling for 13 RWSs (current) and 16

RWSs (future), while shortening the vegetative phase was key for 11 and 12 RWSs, respectively. Critically, in 9 RWSs across western/northwestern Iran, the optimal trait shifted with climate change, underscoring strong G×E interactions.
Conclusion: Breeding for enhanced grain-filling duration offers a robust, climate-resilient strategy for most parts of Iran. In contrast, manipulating vegetative growth duration requires precise, region-specific targeting due to its variable and sometimes negative effects. These results provide a spatially explicit blueprint for trait-based breeding to enhance the productivity and climate resilience of Iran's rainfed wheat systems.

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Introduction

Wheat (*Triticum aestivum L.*) is the main source of calories and protein for people in Iran. It directly provides 37% of the food calories and 40% of daily protein (Salehi 2012). It is the most important crop in Iran, so that annually about 43% (~6.2 million ha) of total agricultural and horticultural lands were under wheat cultivation between 2011 and 2016 (Ministry of Agriculture of Iran 2016). During this period, annual wheat production from these lands has been reported about 10.7 million tons per year. Notably, rainfed conditions accounted for 33% of the total wheat production, yet comprised a significant 62% of the overall wheat cultivated area (Ministry of Agriculture of Iran 2016).

The average rainfed wheat yield for Iran is about 0.9 t ha^{-1} (Ministry of Agriculture of Iran 2016) which is lower than other countries with similar mega-environments, including parts of Canada (~3.5 t ha^{-1}; Chapagain and Good 2015), Australia (~2 t ha^{-1}; Anderson 2010; Wang *et al.* 2017), parts of the USA (~2.1 t ha^{-1}; Patrignani *et al.* 2014; Lollato *et al.* 2017), Syria (~2.5 t ha^{-1}; Pala *et al.* 2011), Turkey (~2 t ha^{-1}; Pala *et al.* 2011), and northern India (~2.8 t ha^{-1}; Aggarwal *et al.* 2008). In addition, the rate of increase in rainfed wheat yield in Iran has been lower than in other countries during the last 35 years. For instance, the average yield of rainfed wheat has been increased from approximately 1 t ha^{-1} in the 1980s to 2 t ha^{-1} in the 2000s in western Australia (Anderson 2010). Similarly, in the Southern Great Plains of the USA, average rainfed wheat yield increased from 0.6 t ha^{-1} (1894 - 1955) to 2.1 t ha^{-1} (1955 - 1980) without a significant change in precipitation and an average rainfall of less than 400 mm (Patrignani *et al.* 2014). In contrast, rainfed wheat yield in Iran has persistently remained below 1 t ha^{-1} for a long time.

Breeding for high-yielding cultivars, especially in drought-stressed environments, which are dominant in rainfed conditions, is complicated and challenging (Sinclair 2011). Characterization of desirable traits can be very effective and important in breeding programs (Sedgley 1991; Sinclair and Muchow 2001; Sinclair *et al.* 2005; Ghanem *et al.* 2015). Introducing early maturing chickpea variety named CPI56288 in Australia (Sedgley 1991), producing drought-tolerance soybean variety in the USA (Sinclair *et al.* 2000), and releasing rice varieties in Philippine named "NSIC Rc158" in 2007, and in China named Xieyou9308 (Zhu *et al.* 2002; Peng *et al.* 2008) are some of the successful practical examples of characterizing desirable traits and then using them in breeding programs.

While field experiments (Ray *et al.* 2006) and comparing near-isogenic lines (Moeller and Rebetzke 2017) are the conventional methods for evaluating traits' effect on yield, these approaches are often constrained by the necessity of multi-site and multi-season trials due to significant genotype and environment (G × E) interactions (Anderson 2010). Consequently, experimental approaches can be both costly and time-consuming (Ghanem *et al.* 2015). Mechanistic crop simulation models are effective tools to explore the potential benefit of traits (Martre *et al.* 2015). There are many studies in which crop simulation models have been used to test potentially desirable traits. Tao *et al.* (2017) used eight different mechanistic models to identify the key traits to improve barley yield under current and future climates in Finland. Battisti *et al.* (2017) assessed the effect of water-related traits on soybean yield in southern Brazil using the CSM-CROPGRO-Soybean model under climate change scenarios. Evaluation of desirable traits for wheat in Europe (Semenov and Stratonovitch 2013; Semenov *et al.* 2014), chickpea in Iran (Soltani and Sinclair 2012a, b), soybean in the USA (Sinclair *et al.* 2010), and sorghum in Australia (Sinclair *et al.* 2005) are some examples in which mechanistic models had been used to exploit traits that are effective for yield improvement.

Even the most robust mechanistic crop models cannot accurately simulate a cropping system without precise input data on weather, soil, management, and crop characteristics (Ramirez-Villegas and Challinor 2012). Gathering these kinds of data across a country is very difficult, especially in a country like Iran with a high climate diversity. Although real-weather stations data were used in the previous studies carried out at a small scale (Sinclair *et al.* 2005; Soltani and Sinclair 2012a, b), large scale simulation across the whole country has been done using gridded daily weather data, called top-down approach, sometimes with coarse assumptions about soil, weather, and management uniformity within each grid (Sinclair *et al.* 2010; Tao *et al.* 2017). The Global Yield Gap Atlas (GYGA) upscaling protocol has been performed to estimate potential yield, identifying the same agro-climatic zones based on real weather and soil data, and then running the crop models separately within each of these zones. Thus, the GYGA protocol doesn't have the inaccuracy of the top-down approach as it doesn't use the grid, and there is no need for coarse assumptions within homogenous climate zones (Grassini *et al.* 2015; van Bussel *et al.* 2015). Although this approach has been used to estimate the yield gap across various countries (van Bussel *et al.* 2015; Gobbett *et al.* 2017; Liu *et al.* 2017), it has not been applied to evaluate the overall effect of a trait on yield over an entire country so far.

Iran has a very diverse climate due to its topography, with elevation ranging from -300 to 5600 meters above sea level (wheat-cultivated areas: 0 to 2000 meters above sea level), and latitudes ranging from 25^o N and 39.7^o N (wheat-cultivated areas: 28° N to 39.7° N). Climate change would also make the situation more complicated. Owning to genetic × environment interaction, diversity of climates, and climate change effects, various wheat cultivars with different characteristics are needed to achieve high yield in different climates of Iran. For this purpose, effective crop traits must be identified in different agro-climatic zones under current and future climates to exploit them in breeding programs. Thus, the objectives of this study were to: (i) utilize the GYGA protocol to identify rainfed wheat production regions with the highest cultivated areas in Iran (ii) explore the potential benefits of various rainfed wheat traits across the country using the GYGA protocol, and (iii) prepare visualized distribution maps of the key traits across Iran under the current and future conditions.

Materials and Methods

Selection of reference weather stations (RWSs)

The GYGA protocol was used to determine the areas covered by a given weather station (van Bussel *et al.* 2015; Espe *et al.* 2016; Liu *et al.* 2017). At first, the geographical coordinates of the 227 synoptic weather stations across Iran were added on a climate shape file of Iran, extracted from the GYGA website (www.yieldgap.org) within ArcGIS10.3. In this climate map, the similar zones were identified based on three indices: (i) growing degree days (GDD), (ii) temperature seasonality, and (iii) annual aridity index (AI) (www.yieldgap.org/web/guest/cz-ted). As illustrated in Figure 1, circular buffer zones, each with a 100 km radius, were drawn around each weather station and clipped by country and climate zone borders (van Bussel *et al.* 2015; Liu *et al.* 2017). In instances where buffers overlapped into a climate zone, the approach explained by Gobbett *et al.* (2017) was used as depicted in Figure 2.

Then, the areas covered by each synoptic RWS were identified. In this case, the geospatial distributions of harvested areas of rainfed wheat (*Triticum aestivum L.*), provided in a shape file (with 5 arcmin resolution), were added to the shape files of climate and weather stations for which their covered area had been specified by the GYGA protocol as described above. The climate zones with

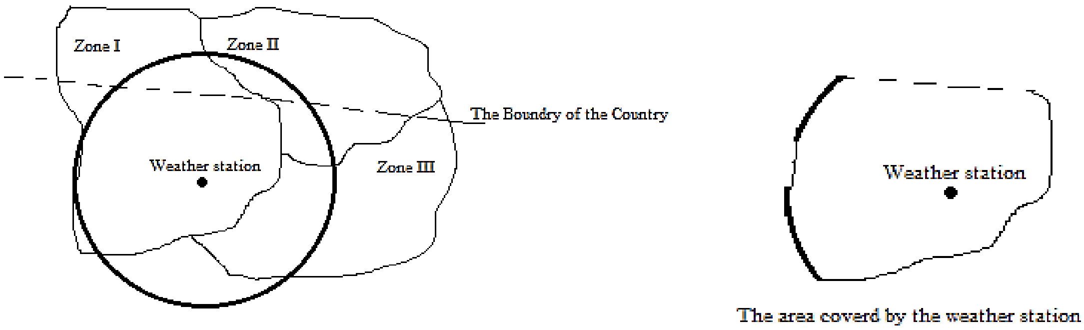

Figure 1. Determination of the area surrounded by a weather station according to the Global Yield Gap Atlas (GYGA) protocol; Left: Before clipping the buffer based on the country and climate zone borders. Right: The final area covered by the given station after clipping by the country and climate zone borders.

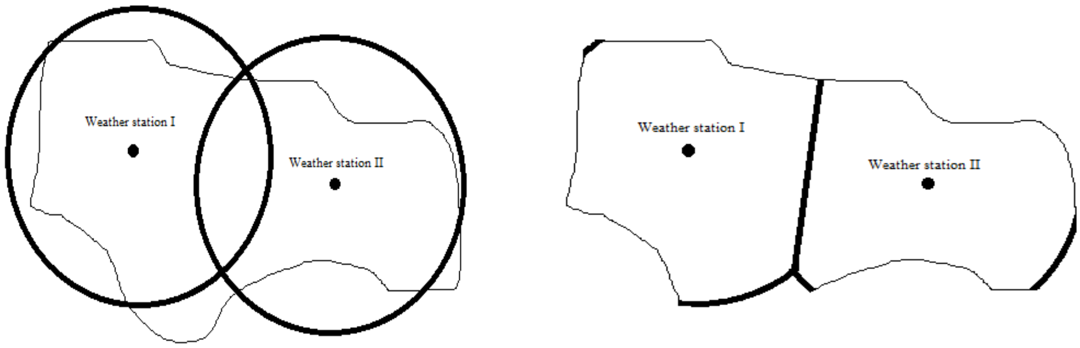

Figure 2. Illustration of the clipping method applied to buffers that overlapped within a given zone; Left: Two overlapped buffers in a given climate zone. Right: The final area covered by the given stations after clipping.

more than 5% of the total national harvested area of rainfed wheat were identified and referred to as designated climate zones (DCZs). All weather stations located within these DCZs that contain >1% of rainfed wheat harvested area were also identified (Grassini *et al.* 2015; van Bussel *et al.* 2015) and were called RWSs. The total rainfed wheat area represented by the selected 19 RWSs was less than 50% of the national harvested rainfed wheat area, whereas according to the GYGA protocol, the selected RWSs should cover more than 50% (van Bussel *et al.* 2015). Thus, the stations within climate zones between 1% and 5% of the national rainfed wheat harvested area were selected as RWS as well. As a result of this selection process, a total of 32 RWSs were identified, collectively representing 72% of the national rainfed wheat harvested area. A summary of the general information of these RWSs is provided in Table 1.

Soil map with functional properties for Iran was obtained from the HC27 soil database (Koo and Dimes 2010). The GYGA protocol was applied to determine the dominant soil (soil type with >50% coverage within each RWS) (Grassini *et al.* 2015; van Bussel *et al.* 2015). In cases where no single soil type exceeded this threshold, all soil types with coverage more than 10% within the RWS were

Table 1. Climatic characteristics during the rainfed wheat growing season of reference weather stations (RWSs), including total precipitation (Pr), average maximum temperature (TMAX), average minimum temperature (TMIN), mean temperature (TEMP), and received solar radiation (SRAD).

RWS code	RWSs	Lat	Long	Altitude (m)*	Pr (mm)	TMAX (°C)	TMIN (°C)	TEMP (°C)	SRAD (Mj m^{-2} season^{-1})	Wheat area covered by the buffer of the RWS (ha)**
1	Hashmabad	36.85	54.27	0-60	298	18	7	12	2265	43473 (1.2%)
2	Maravehtapeh	37.80	55.94	0-500	252	16	8	12	2415	33824 (1.0%)
3	Meshkinshahr	38.38	47.67	1500-2000	315	13	4	8	3599	89267 (2.4%)
4	Germi	39.05	48.06	300-800	208	14	6	10	3023	94837 (2.6%)
5	Gonbad	37.27	55.21	0-500	294	18	7	12	2374	107140 (2.9%)
6	Poldokhtar	33.15	47.72	300-900	278	19	9	14	2139	40588 (1.1%)
7	Bilesavar	39.37	48.32	100-300	235	15	6	10	2807	48186 (1.3%)
8	Manevasamalghan	37.51	56.86	700-1300	262	16	4	10	2972	54037 (1.5%)
9	Ghoochan	37.12	58.45	1200-1700	301	15	2	8	3438	44873 (1.2%)
10	Masjedsoleyman	31.98	49.24	300-500	280	21	10	15	1604	40764 (1.1%)
11	Ravansar	34.72	46.65	1400-2000	424	15	4	10	3381	48331 (1.3%)
12	Mahabad	36.75	45.72	1400-2000	348	14	3	9	3393	75234 (2%)
13	Baneh	36.01	45.90	1400-2000	616	13	4	9	3400	35838 (1.0%)
14	Kermanshah	34.35	47.15	1600-2000	333	17	3	10	3114	171713(4.6%)
15	Aligoodarz	33.10	49.70	1800-2000	385	14	2	8	4045	65990 (1.8%)
16	Mianeh	37.45	47.70	700-1300	233	15	3	9	3163	53340 (1.4%)
17	Nahavand	34.14	48.41	1500-2000	355	15	2	9	3762	86698 (2.3%)
18	Mahneshan	36.74	47.68	1600-2000	226	15	3	9	3282	83159 (2.3%)
19	Bostanabad	37.85	46.84	1800-2000	286	12	0	6	4226	42310 (1.1%)
20	Fariman	35.65	59.83	1200-2000	248	15	2	8	3456	37596 (1.0%)
21	Khodabandeh	36.14	48.59	1700-2000	357	12	2	7	3964	60652 (1.6%)
22	Avaj	35.57	49.22	1900-2000	379	13	2	7	4253	45441 (1.2%)
23	Tabriz	38.12	46.24	1300-2000	217	14	3	9	3319	61007 (1.7%)
24	Ghorveh	35.18	47.79	1300-1800	302	13	2	8	4049	32152 (1.0%)
25	Saghez	36.22	46.31	1300-1800	390	15	0	7	4153	97433 (2.6%)
26	Bijar	35.89	47.62	1600-2000	293	12	2	7	3925	410651 (11.1%)
27	Eslamabadgharb	34.12	46.47	1400-2000	401	17	1	9	3994	127701 (3.5%)
28	Hamedan	34.87	48.53	1800-2000	295	15	1	8	3910	108308 (2.9%)
29	Komijan	34.71	49.31	1600-2000	237	15	1	8	3930	126594 (3.4%)
30	Saveh	35.08	50.37	1500-1800	164	16	5	11	2706	41998 (1.1%)
31	Takab	36.40	47.10	1800-2000	286	13	0	7	4375	120248 (3.3%)
32	Qargabad	35.11	49.83	1600-2000	234	14	2	8	3571	119969 (3.2%)

*: It shows the range of elevation of the rainfed wheat lands within the RWSs; **: The value in parentheses shows the fraction of whole rainfed wheat cultivated land area in Iran; Lat: Latitude, Long: Longitude, Alt: Altitude.

selected and used as dominant soils. In this study, the model was run for each selected soil type within the RWS separately, and then the weighted average of the results of the simulation based on the area coverage with each soil type within the RWS was calculated (van Bussel *et al.* 2015).

Weather data of RWSs

Daily weather data for each RWS, including precipitation, sunshine hours, and minimum and maximum air temperatures, were obtained from the Iran Meteorological Organization. To address missing data points and to estimate received solar radiation based on recorded sunshine hours, the Weatherman tool, embedded within the DSSAT model, was employed (www.dssat.net). Weather data from 2000 to 2015 were prepared and used as the baseline climate dataset for crop simulation analyses.

To create future climate data, delta values representing the mean differences between projected future and baseline temperature and precipitation were applied to the historical dataset. The delta values were derived from the CMIP5 global models for the year 2055 (2041-2060), representing an increase of +1.9 °C in temperature and no change (0%) in precipitation compared to the baseline period (2000-2015). These values are based on the average of 42 global circulation models (GCMs) under the RCP4.5 Scenario for West Asia, which includes Iran (Christensen *et al.* 2013). Atmospheric CO_2 concentrations under the RCP4.5 Scenario were projected to reach 500 ppm by 2055 (van Vuuren *et al.* 2011). For the baseline period (2000–2015), a median CO_2 concentration of 385 ppm was adopted, corresponding to the level recorded in 2007 (www.esrl.noaa.gov/gmd/ccgg/trends). Since a comprehensive analysis of future climates was not a primary objective of this study, only the RCP4.5 climate change scenario was considered. This scenario was included solely to offer a concise indication of how the studied crop traits might respond under a plausible future climate. Further research is needed to explore this aspect more thoroughly.

Crop model

The SSM-iCrop model was used in this study (Soltani and Sinclair 2012c; Soltani *et al.* 2013). This model can incorporate the effects of key environmental factors (temperature, photoperiod, vernalization, and water deficit) on wheat phenology and growth. In the model, water deficit influences leaf area development, biomass, and grain yield. It also accounts for the adverse effects of extreme temperatures, such as heat and frost, on leaf area development and yield. Furthermore, the impact of vapor pressure deficit (VPD) on dry matter production was calculated. The model simulates daily phenology development, leaf area development and senescence, dry matter production and partitioning, yield formation, and soil balance. It also accounts for the termination of crop growth under severe drought based on VPD and the severity of soil water deficit (Soltani and Sinclair 2011; Soltani and Sinclair 2012c; Soltani *et al.* 2013). Phenological development in the model was predicted using biological day requirements between growth stages (Soltani *et al.* 2013).

The robustness of the SSM-iCrop model in simulating soil water content, phenological development, and growth and yield production has been demonstrated under different conditions (Soltani *et al.* 2013; Soltani and Sinclair 2015; Lollato *et al.* 2016; Moeinifard *et al.* 2017). In a comparative study conducted at Gorgan, located in northeastern Iran, Soltani and Sinclair (2015) reported that the coefficient of variation (CV) in simulated wheat yield was 8.2% using the SSM model. This performance was notably superior to that of other widely used crop models, including CropSyst (CV = 14.3%), APSIM (CV = 15.0%), and DSSAT (CV = 18.5%). SSM model resulted in a normalized root mean square error of less than 12% for the soil plant available water capacity prediction in Oklahoma, USA (Lollato *et al.* 2016). In a recent study in Iran, the SSM-iCrop simulation model was employed to parameterize and evaluate its capability in predicting phenological stages, leaf area expansion, biomass and grain yield, and nitrogen dynamics of wheat across various regions (Abidi *et al.* 2025). The assessment was conducted using datasets collected from multi-year and multi-location experiments. Their findings showed that the model provided accurate estimations of phenological stages (r = 0.99, CV = 7.8%), biomass (r = 0.79, CV = 11.3%), and grain yield (r = 0.84, CV = 12.6%). Thus, the SSM-iCrop model was regarded as a reliable tool for simulating wheat growth and yield under diverse environmental conditions (Abidi *et al.* 2025).

The weather data required by the model were minimum and maximum daily temperature (°C), daily precipitation (mm), and daily incident solar radiation above the canopy (MJ m^{-2}). The soil data required for the model were soil water limits (volumetric soil water content at saturation, drained upper limit, and lower limit), soil albedo, soil depth, fraction of coarse material in soil, the drainage factor, curve number for runoff, and soil bulk density (Soltani and Sinclair 2012c). Some of the crop parameters in the model are indicated in Table 2. There was a slight difference between phenological development of the wheat cultivars, which resulted from differences in the vernalization parameter. Thus, the crop parameters, except the parameter for vernalization, basically were those of the wheat cultivar Tajan, extracted from trials across the whole country under different conditions and different years.

In this study, simulations were conducted under rainfed conditions, assuming non-limiting nitrogen conditions. Thus, date of sowing, soil water content at sowing time, and plant density were the only management data needed for each RWS. Sowing date for each RWS was obtained from a previous study (Farshi *et al.* 1998). To validate these sowing dates, the typical rainfed wheat sowing date for some RWSs was gathered from the experts of local offices of the AREEO[1] Based on the

[1]Agricultural Research Education and Extension Organization

Table 2. The crop parameters information used in the SSM-iCrop model for the current, standard cultivars.

Parameter	Description	Unit	Value
Phyl	Phyllochron	°C $leaf^{-1}$	90.25
PLAPOW	A coefficient (exponent) in power relationship between plant leaf area and main stem node number	For 300 plants m^{-2}	2.34
FrzTh	Leaf destruction critical frost temperature	°C	-5
FrzLDR	Fraction leaf destruction below the critical by each degree centigrade	m^2 m^{-2} $°C^{-1}$	0.01
HeatTH	Leaf destruction critical heat temperature	°C	30
HtLDR	Leaf destruction coefficient above the critical temperature	-	0.1
IRUE	Radiation use efficiency under optimal growth conditions	gr Mj^{-1}	2.2
TBRUE	Base temperature for dry matter production	°C	0
TP1RUE	Lower optimum temperature for dry matter production	°C	15
TP2RUE	Upper optimum temperature for dry matter production	°C	22
TCRUE	Ceiling temperature for dry matter production	°C	35
MEED	Maximum effective depth of water extraction from soil by roots	mm	1000
GRTDP	Biological daily increase (growth) in root depth	mm biological day^{-1}	30
WSSG	FTSW threshold when dry matter production starts to decline	-	0.3
WSSL	Water stress factor for leaf area development	-	0.4
WSSD	A coefficient that specifies acceleration or retardation in development in response to water deficit	-	0.5
vsen	Vernalization sensitivity coefficient	-	0.00089 or 0.0015*
ppsen	Photoperiod sensitivity coefficient	-	0.001467
bdSOWEMR	Biological days from sowing to emergence	Biological day	4
bdEMRTIL	Biological days from emergence to first-tiller	Biological day	4.95
bdTILSEL	Biological days from first-tiller to first-node (stem-elongation)	Biological day	11.4
bdSELBOT	Biological days from first-node to booting (ligule of flag leaf visible)	Biological day	6
bdBOTEAR	Biological days from booting to ear emergence	Biological day	2
bdEARANT	Biological days from ear emergence to anthesis	Biological day	8
bdANTPM	Biological days from anthesis to physiological maturity	Biological day	34

*The value 0.0015 was used for the typical, standard cultivar in RWSs with cold winters (The RWSs where the sum of growth degree days (GDD) over the year based on 0 °C as the base temperature was less than 5000 GDD), and 0.00089 was used for the typical, standard cultivar in warmer RWSs (The RWSs where the sum of GDD over the year based on 0 °C as the base temperature was more than 5000 GDD).

collected data, an algorithm was found to describe the actual sowing date very well. The comparison of the simulated sowing dates derived from this algorithm with the observed sowing dates confirmed that the algorithm provides a reliable and sufficiently accurate estimation of the wheat sowing date (Figure 3). The algorithm defined the sowing date as the fifth day of a rain-free 5-day period following October 7 (day 280 of the year), during which the mean daily temperature remained below 15 °C. An exception was made for Masjedsoleyman (RWS No. 10), where the temperature threshold was adjusted to 18 °C (data not shown).

To determine soil water content at sowing, the model was run well before a probable sowing date, i.e., from 22 August (Soltani *et al.* 2013; Lollato *et al.* 2016). For simulations under future climate conditions, the sowing dates were assumed to remain unchanged from the baseline scenario. The plant density was set at 250 plants m^{-2} at all RWSs.

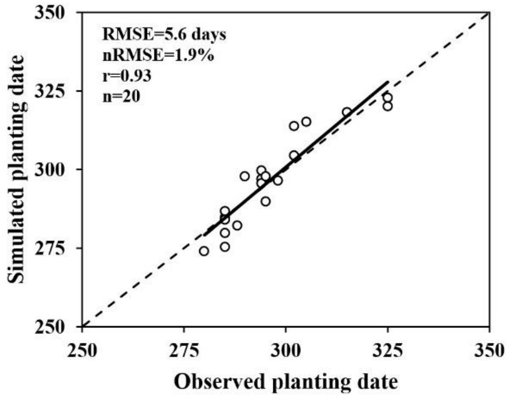

Figure 3. One-to-one plot comparing simulated planting dates generated by the planting-date algorithm versus typical planting dates, based on day of the year across 20 reference stations for winter wheat. The points on the plot correspond to the regions of Abadan, Ahvaz, Aligoodarz, Arsanjan, Dezful, Eslamabadgharb, Garmsar, Ghoochan, Gorgan, Jahrom, Komijan, Meshkinshahr, Nahavand, Karaj, Saqqez, Sepidan, Tabriz, Yasuj, Torbatejam, Zabol, Bilesavar, and Gonbad). For additional details, refer to Alimagham *et al.* 2019.

Crop traits

Initial simulations were conducted using the baseline crop parameters presented in Table 2 to estimate grain yield under both current and future climate conditions for each RWS. Simulations were repeated by modifying each trait as shown in Table 3 to explore their putative benefit under current and future climates. Each trait was individually adjusted by ±20% relative to its baseline value, except PLAPOW (a coefficient in the power relationship between plant leaf area and main stem node number) and Phyl (Phyllochron), which changed by ±5 and ±10%, respectively. The selection of percentage changes for the traits in this study was based on their known impact on wheat yield improvement and the reported genetic diversity of these traits in domestic and international sources. For example, numerous domestic sources report about 20% diversity for phenological traits such as days to maturity. However, for some traits like radiation use efficiency and phyllochron, the amount of variation (for instance, 10% for phyllochron) is based on the diversity reported in international studies, assuming that the use of foreign genetic resources is feasible.

Given that the maximum effective depth of water extraction from soil (MEED) is correlated with the daily increase in root depth (GRTDP), GRTDP was also increased along with MEED. Similarly, the parameters WSSD (a coefficient that specifies acceleration or retardation in development in response to water deficit) and WSSL (threshold of fraction transpirable soil water when leaf area development starts to decline) were modified.

Table 3. The crop traits that had been modified in the SSM-iCrop model and the assumptions behind them to improve yield by their modifications.

Trait	General effect of the trait	Assumption behind the modification of the trait
1. bdEMRTIL 2. bdTILSEL 3. bdSELBOT 4. bdANTPM	Phenology matching with growth season	Escaping from late-season drought stress by decreasing the vegetative growth period. Using resources such as radiation and late-season rainfall is more effective by increasing vegetative growth or grain filling period.
5. IRUE	Dry matter production	Decreasing radiation use efficiency (RUE) results in decreasing water use rate and potentially an avoidance or delay in the development of water deficit. Increasing RUE results in the effective use of resources such as rainfall and radiation.
6. Phyl 7. PLAPOW	Leaf area development	Slower leaf area development causes less water use during the vegetative period. Faster leaf area development increases radiation capturing and dry matter production; also, it shades the soil surface, thereby reducing evaporation of water from the soil surface and increasing water availability for the crop.
8. WSSG and WSSL 9. CVPD (Critical VPD to limit on maximum transpiration rate)	Response to soil and air water deficit	A lower amount of WSSG and WSSL makes the plant drought-tolerant. A higher amount of WSSG and WSSL causes less water use during the vegetative period. Limitation on maximum transpiration rate prevents excessive water loss under conditions of high atmospheric vapor pressure deficit and results in conserved soil water for later use by the crop.
10. MEED and GRTDP 11. GRTDP	Root growth	An increase in the rate of depth of water extraction may increase dry matter production. An increase in the rate of water extraction may make the crop more vulnerable to drought at the end of the season.

Results

Model evaluation

The findings showed that the simulated outputs closely matched the observed measurements. The model performed well in estimating the number of days to physiological maturity (r = 0.99, nRMSE = 4%, RMSE = 6 days), leaf area index (r = 0.25, nRMSE = 18%, RMSE = 0.8), biomass (r = 0.82, nRMSE = 21%, RMSE = 268 g m^{-2}), and grain yield (r = 0.84, nRMSE = 20%, RMSE = 103 g m^{-2}) (Figure 4). Overall, the results verify the robustness of the SSM-iCrop model in forecasting wheat growth and development. Consequently, the model appears to be a suitable and reliable tool for analyzing wheat growth, estimating potential yields, and assessing the impacts of climate change across diverse environmental conditions in Iran.

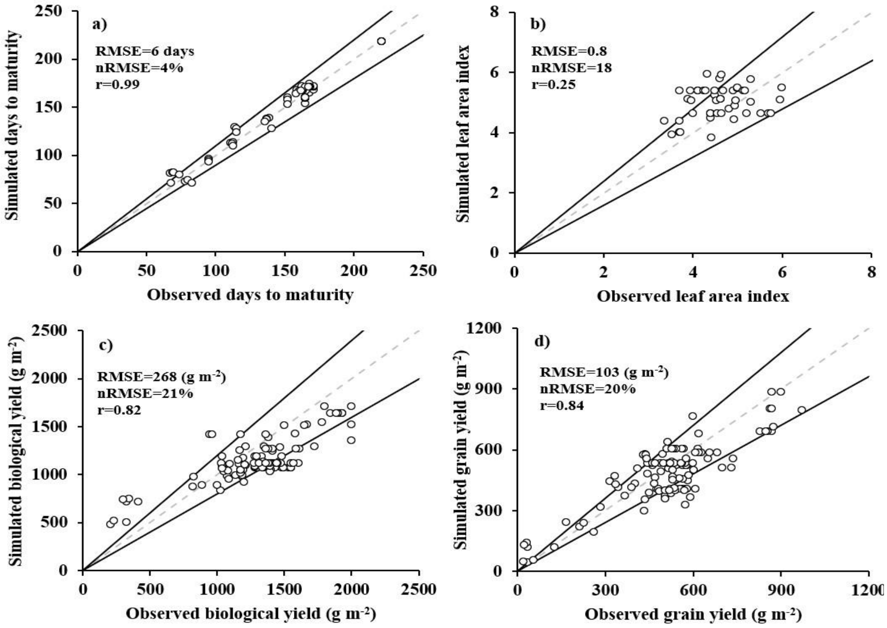

Figure 4. Evaluation results of the SSM-iCrop model for wheat based on simulated data and observed data from field experiments conducted across different regions of Iran for: a) days to physiological maturity, b) leaf area index, c) biomass, and d) grain yield. The solid lines indicate the ±10% range compared to the 1:1 line (dashed line). For additional details, refer to Alimagham *et al.* 2019.

Yield of present cultivars under current and future climates

Figure 5 illustrates the distribution of simulated water-limited potential yield (*Yw*) of wheat across Iran, using present cultivars, under both current and future climates. The mean yield across the country was estimated at 202 g m^{-2} under the current climate and 287 g m^{-2} under the future climate (all yields were reported on a dry weight basis). There was a large variation for grain yield across the country as well as over years in each RWS under both current and future climates (Figures 5 and 6). Under the current climate conditions, Yw ranged from 104 to 441 g m^{-2}, whereas under future climate conditions, this range increased to 154 - 533 g m^{-2}. The highest-yielding RWSs were located in the northern region of Iran, along the Caspian Sea coast and behind the Alborz Mountain range, characterized by a moderate and humid climate. Specifically, RWSs No. 1 (441 g m^{-2}), 2 (439 g m^{-2}), 3 (432 g m^{-2}), 4 (358 g m^{-2}), and 5 (342 g m^{-2}) resulted in the greatest yields under current climatic conditions. These RWSs also had the highest yield under future climate conditions, ranging from 429 to 533 g m^{-2} (Figures 5 and 6).

The results showed that, among all the traits evaluated in this study, the modified traits that resulted in the highest increase in yield of rainfed wheat across Iran under both current and future climates were increasing biological days from anthesis to physiological maturity (+20bdANTPM), decreasing phyllochron (-10Phyl), increasing radiation use efficiency (+20IRUE), and decreasing biological days from first tiller to first node (-20bdTILSEL) (Figure 7). The spatial distribution of these traits was analyzed across the entire country. Both -10Phyl and +5PLAPOW resulted in increased leaf area development, particularly during early growth stages. Under current climate conditions, the yield gain in the whole country was 10 g m^{-2} for increasing grain filling duration, 8 g m^{-2} for decreasing phyllochron, 7 g m^{-2} for decreasing growth stage period, and 7 g m^{-2} for increasing radiation use efficiency. Under future climate conditions, the yield gains were 16 g m^{-2} for increasing grain filling duration, 9 g m^{-2} for decreasing phyllochron, 6 g m^{-2} for decreasing growth stage period, and 9 g m^{-2} for increasing radiation use efficiency.

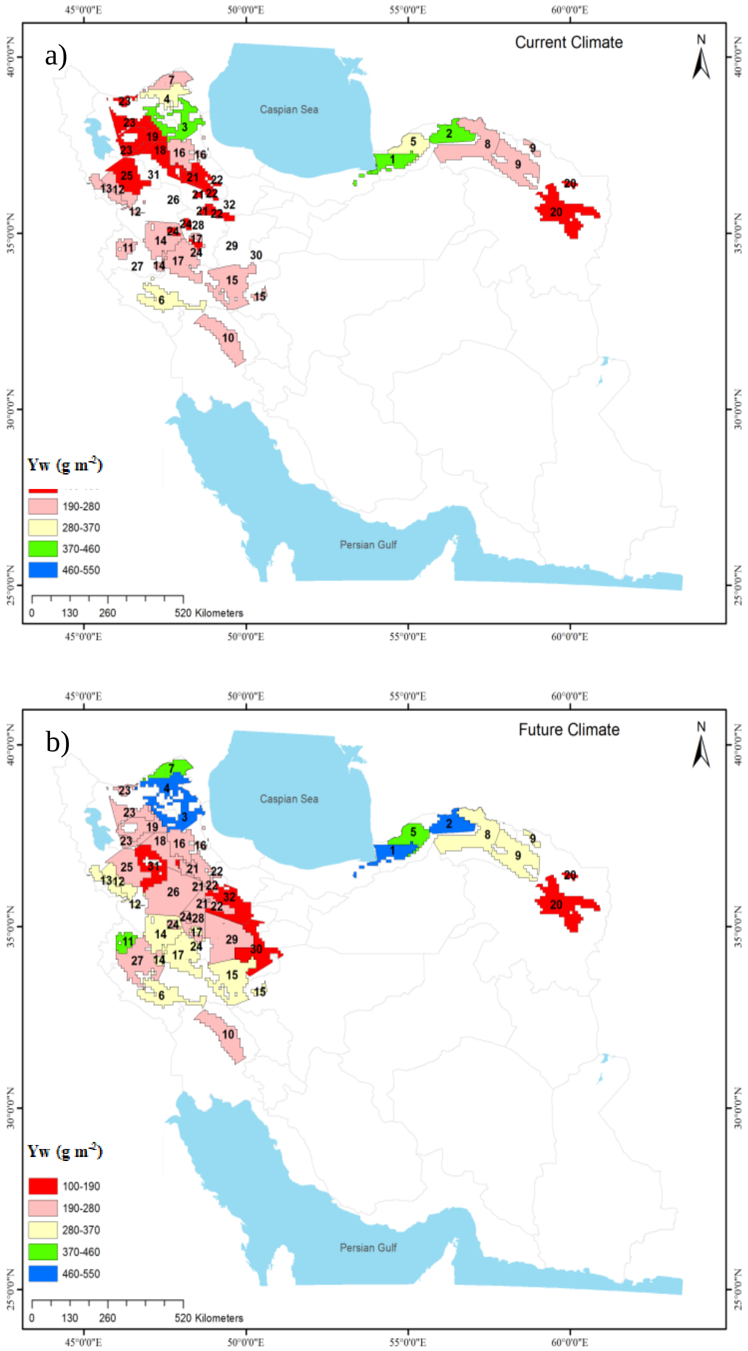

Figure 5. Simulated water-limited potential yield (Yw) of current cultivars in the important rainfed wheat production regions in Iran under current (a) and future (b) climate conditions. Climatic characteristics and codes of the RWSs are presented in Table 1.

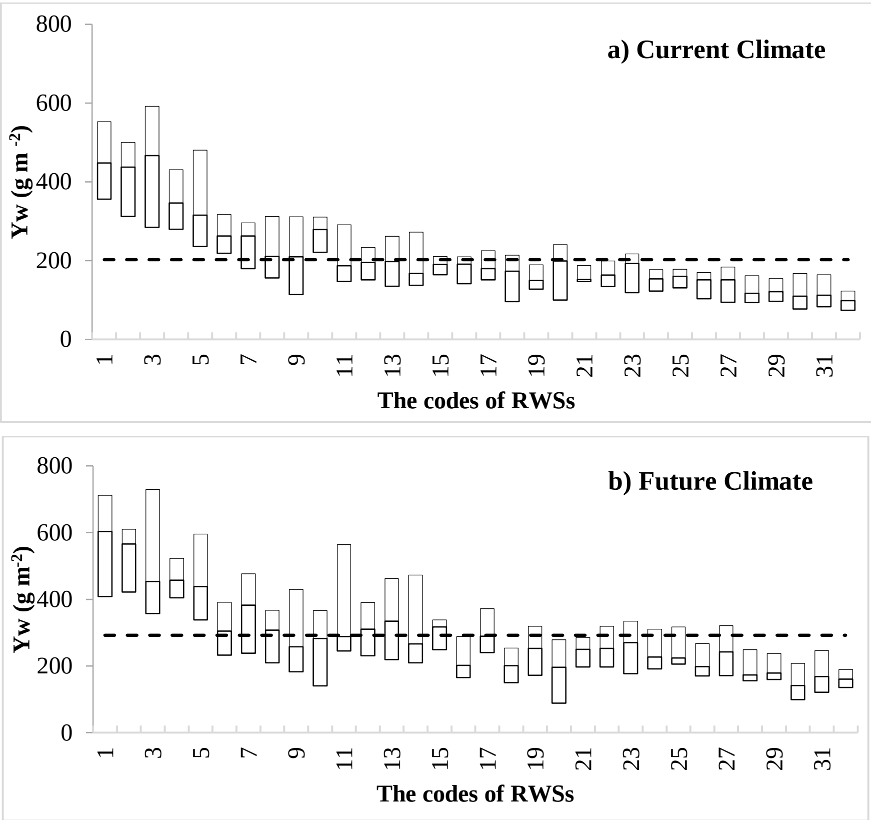

Figure 6. The box plot of simulated water-limited potential yield (Yw) for standard cultivars in each RWS under current (a) and future (b) climates. The information on each RWS is shown in Table 1. The top line, middle line, and bottom line at each box represent the 75%, 50%, and 25% quartiles, respectively, for each RWS among all years. Climatic characteristics and codes of the RWSs are presented in Table 1.

Decreasing biological days from first tiller to first node (-20bdTILSEL)

Escaping from late-season drought stress by decreasing the vegetative growth period is a mechanism that can enhance yield by reducing the total crop growth duration. Some wheat genotypes possess a shorter growth stage duration (Flohr *et al.* 2018). All the RWSs that benefited from this trait were located in the Zagros Mountain range, except for RWS Bilesavar, No. 7, which is situated near the Caspian Sea coast, under both current and future climate conditions (Figure 8). However, this trait negatively affected yield in four RWSs under the current climate and 12 RWSs under the future climate. The impact of this trait was negative in all RWSs located in the eastern and northeastern regions, except for RWS Maravehtapeh, No. 2, under the future climate (Figure 8). An interesting finding was that the yield gain resulting from reduced growth duration at RWS Kermanshah, No. 14, was 8.4 g m^{-2}, identifying it as a key trait at this station under the current climate. However, under the future climate scenario, this trait had a negative effect on crop yield (Figure 8).

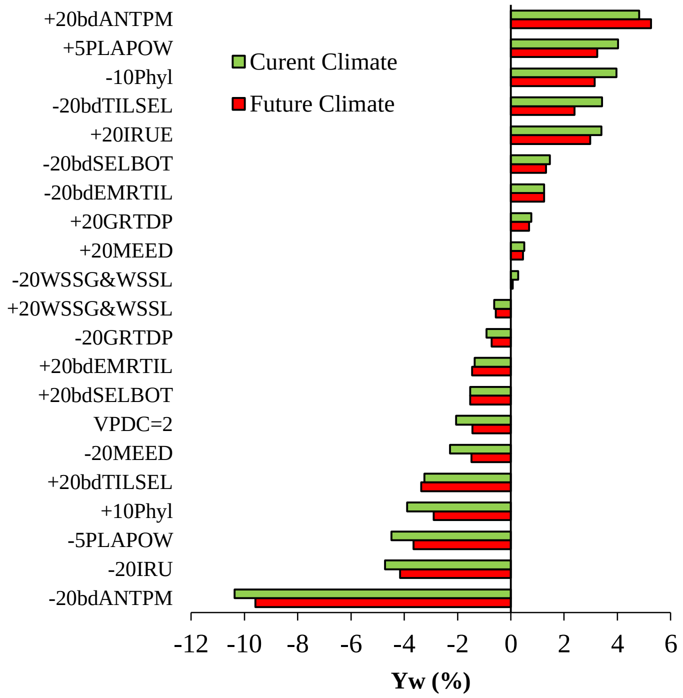

Figure 7. The simulated effect of different traits, as a percentage of standard cultivars, on water-limited potential yield (Yw) at the whole country level (Iran) under current and future climate conditions. For a description of the traits, refer to Table 3.

Increasing biological days from anthesis to physiological maturity (+20bdANTPM)

Using resources such as radiation and late season rainfall is more effective by increasing the grain filling period, and an approach to increase yield. Although the grain filling duration has remained largely unchanged among cultivars released over the past five decades (Rahemi *et al.* 2015), some modern cultivars in certain European countries exhibit variations in this trait (Ceglar *et al.* 2018). Compared to Iranian cultivars, which typically require about 935 temperature units (°C) for grain filling, cultivars in some European regions have been reported to need about 1100 temperature units (Ceglar *et al.* 2018).

Simulation results based on increasing grain filling duration showed a 100% yield improvement across all RWSs under both current and future climate (Figure 9). RWSs located near the Caspian Sea coast benefited more from this modification compared to other RWSs. The average yield gain resulting from increased grain filling duration was 30 g m^{-2} for Caspian Sea coast RWSs, rising to 47.3 g m^{-2} under future climate conditions. In contrast, the corresponding yield gain for other RWSs was limited to 7 g m^{-2} under the current climate and 12.8 g m^{-2} under the future climate. If there was available water for transpiration during the grain filling period, the trait would lead to increased yield. The RWSs near the Caspian Sea coast usually received around 20% of annual rainfall during April, May, and when the wheat grain filling stage occurred.

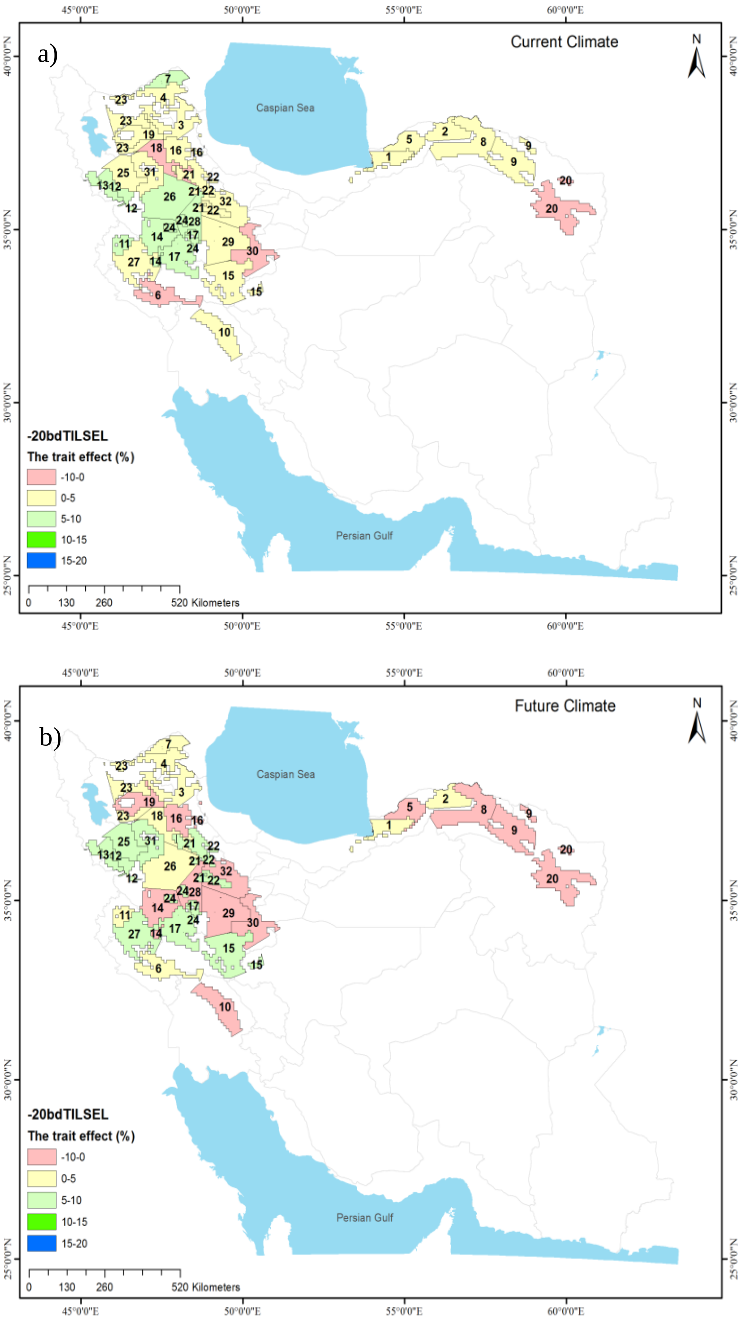

Figure 8. Yield increase, as a percentage of current cultivars, in a modified cultivar with 20% shorter biological days from first tiller to first node (-20bdTILSEL) in rainfed conditions of Iran under current (a) and future (b) climates. Climatic characteristics and codes of the RWSs are presented in Table 1.

Decreasing phyllochron (-10Phyl)

The range of variation of phyllochron for wheat genotypes had been reported between 70–120 ˚C (Mossad *et al.* 1995; Borras-Gelonch *et al.* 2011). Under the current climate, increasing leaf area development resulted in yield gains exceeding 5% in seven RWSs (Figure 10). The RWSs located in the west of Iran gained from this trait under the current climate, while their impact on the other RWSs located in the east, northeast, and northwest was not significant under both current and future climates. This trait had no significant positive effect on Yw under future climate, with only 6 RWSs exhibiting yield improvements greater than 5% (Figure 10).

Increasing radiation use efficiency (+20IRUE)

The amount of radiation use efficiency in wheat had been reported as high as 3 g MJ^{-1} (Hussain *et al.* 2004). The impact of this trait on yield under the current climate was stronger than in the future climate. Specifically, yield increases exceeding 5% were observed in 9 RWSs located in western Iran under the current climate, whereas under the future climate, such gains were observed in only 7 RWSs (Figure 11).

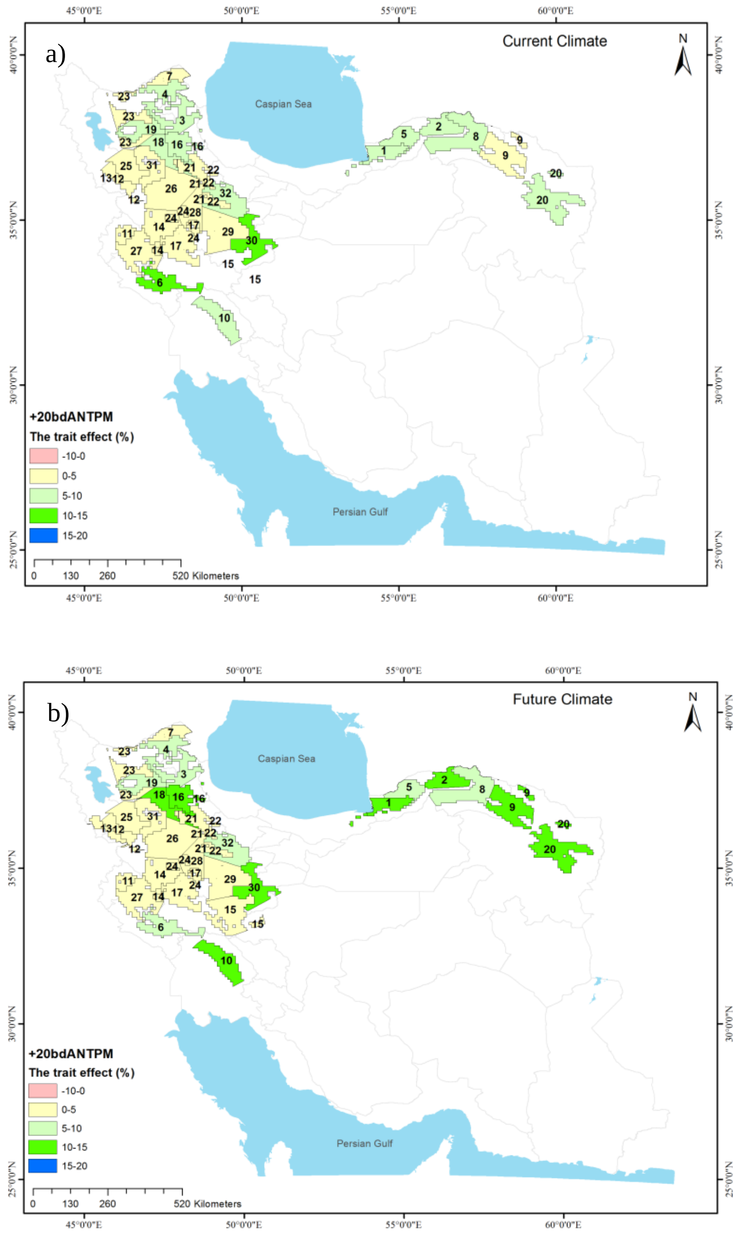

Figure 9. Yield increase, as a percentage of current cultivars, in a modified cultivar with 20% longer biological days from anthesis to physiological maturity (+20bdANTPM) in rainfed conditions of Iran under current (a) and future (b) climates. Climatic characteristics and codes of the RWSs are presented in Table 1.

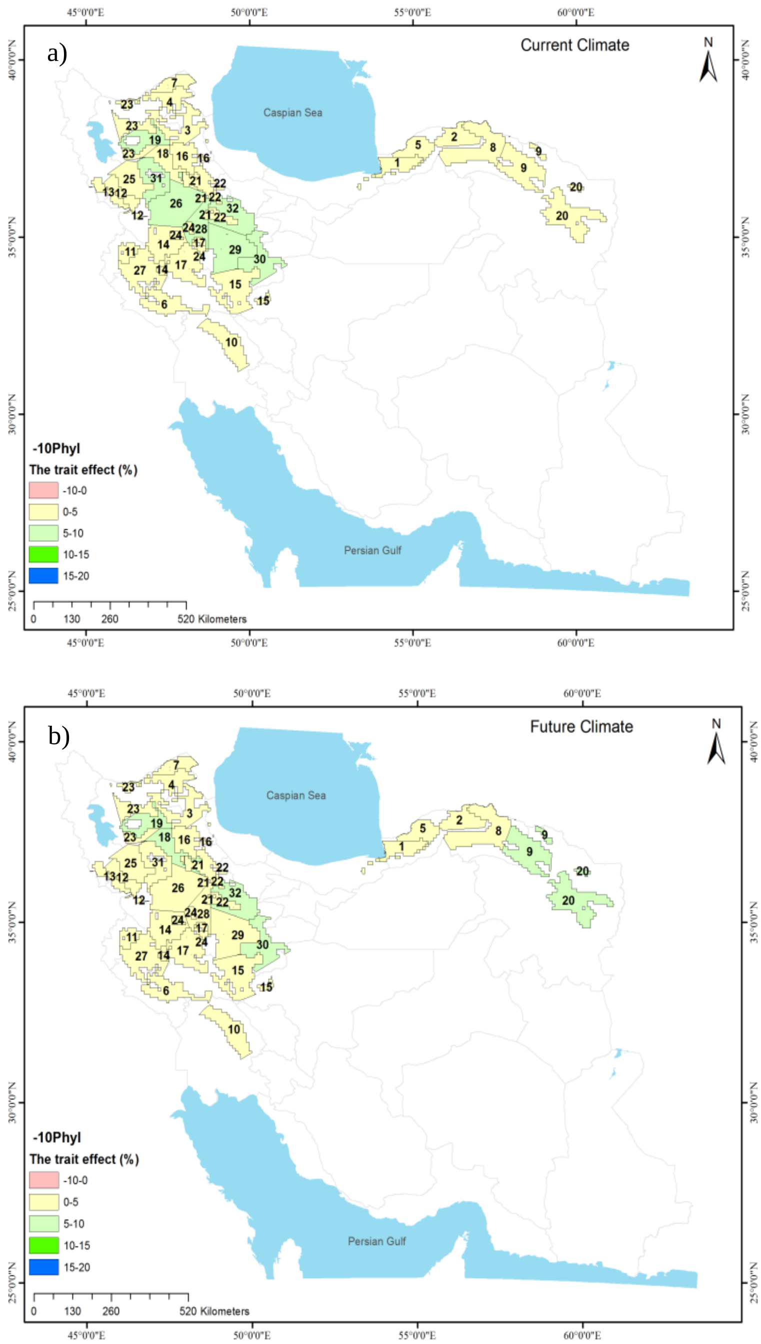

Figure 10. Yield increase, as a percentage of current cultivars, in a modified cultivar with 10% shorter phyllochron (-10Phyl) in rainfed conditions of Iran under current (a) and future (b) climates. Climatic characteristics and codes of the RWSs are presented in Table 1.

Effect of the key traits across Iran

Increasing grain filling duration was identified as a key trait for improving yield under both current and future climate conditions in the RWSs located in the eastern regions and around the Caspian Sea (Figure 12). However, in the western and northwestern regions, the importance of this trait appeared to be climate-dependent. For instance, increasing grain filling duration was the key trait at RWSs No. 14 and 19 under the current climate. In contrast, under the future climate, decreasing phyllochron at

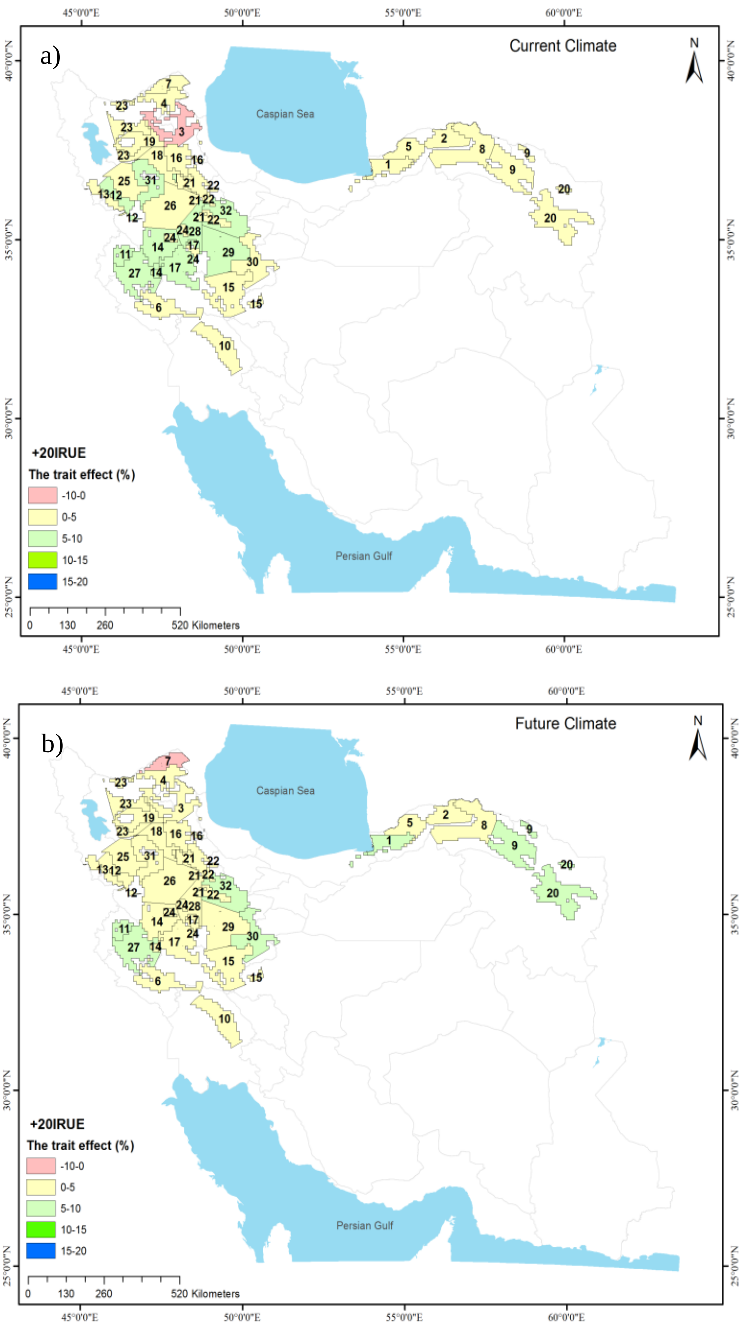

Figure 11. Yield increase, as a percentage of current cultivars, in a modified cultivar with 20% higher radiation use efficiency (+20IRUE) in rainfed conditions of Iran under current (a) and future (b) climates. Climatic characteristics and codes of the RWSs are presented in Table 1.

RWS No. 19 and reducing the overall growth stage duration at RWS No. 14 were identified as the key traits to improve the yield (Figure 12). Under the current climate, increasing grain filling duration was identified as the key trait for yield improvement in 13 RWSs, followed by decreasing growth stage duration in 11 RWSs, increasing leaf area development in 7 RWSs, and increasing radiation use efficiency in 1 RWS. Under the future climate, increasing grain filling duration was the key trait in 16 RWSs, while decreasing growth stage duration, increasing radiation use efficiency, and increasing leaf area development were identified as key traits in 12, 1, and 3 RWSs, respectively (Figure 12). In 23 out of the 32 RWSs, the key trait for improving Yw remained consistent under both current and future climates. However, in 9 RWSs, all located in the western or northwestern regions of Iran, the key trait shifted in response to climate change (Figure 12).

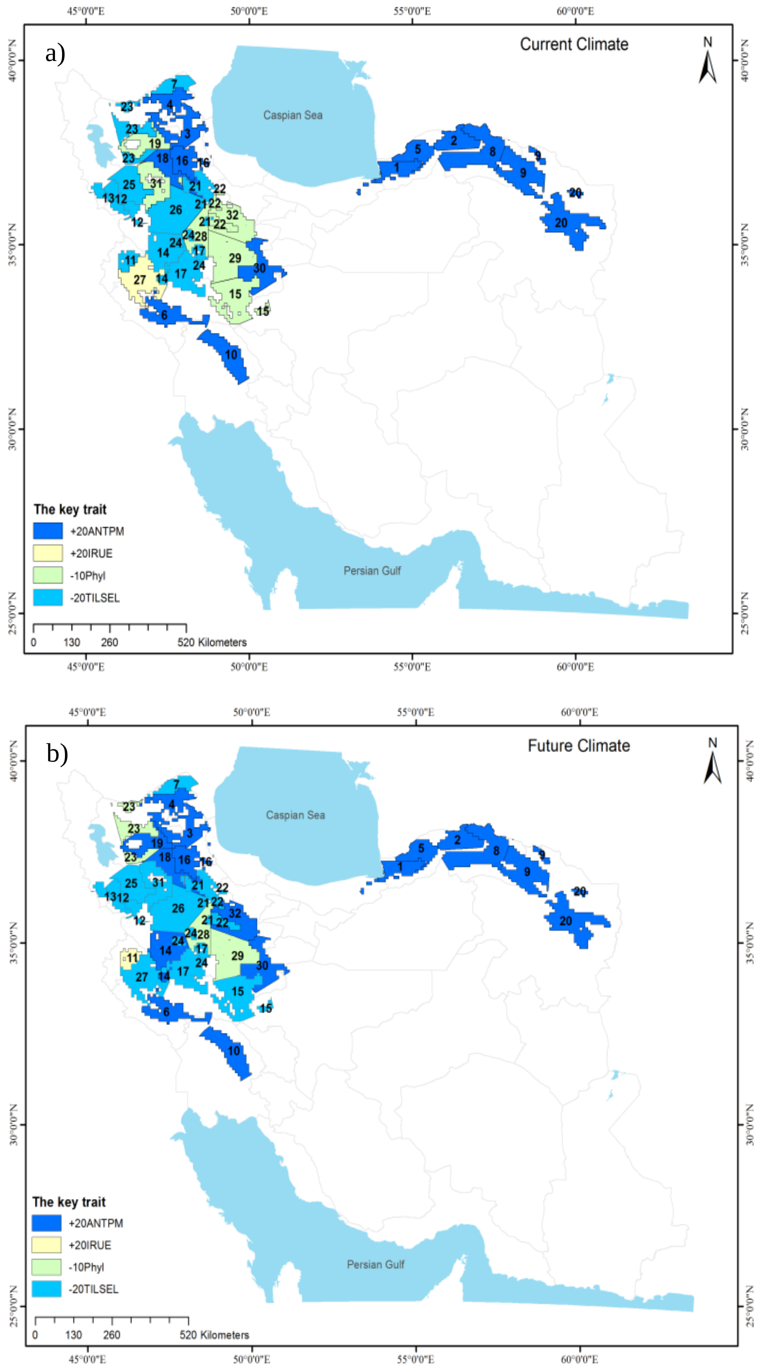

Figure 12. The key trait offering the highest yield advantage for rainfed wheat at each RWS across Iran under (a) current and (b) future climates. Climatic characteristics and codes of the RWSs are presented in Table 1.

Discussion

The RWSs situated in the western and northwestern regions of Iran exhibited the lowest Yw, especially under current climate conditions (Figure 5). These areas were located in the Zagros Mountain range, where the majority of precipitation occurs during winter months, a period typically characterized by freezing temperatures that are too cold for wheat growth. Although enough precipitation was recorded during the winter months when wheat was present in the field in the RWSs of western and northwestern Iran (Table 1), two major factors, cold winter temperatures that limit crop growth and terminal drought stress occurring later in the growth season, were the main reasons for low yield in these regions under the current climate. For example, although RWS No. 13 in Baneh, located in western Iran, received 616 mm of precipitation during the growing season (Table 1), only 17 mm occurred during the grain filling period. Consequently, the final yield was merely 207.5 g m^{-2} (Figures 5 and 6). Similar patterns were also observed in the RWSs located in eastern Iran. The CV of the simulated grain yield for the current cultivars ranged from 22% to 51%, depending on the RWS. Yield variability increased under future climate change (Figure 6); however, the investigated traits with positive effects caused the CV of yield to remain at the current level or decrease slightly (data not shown).

Under the future climate, rising temperatures contributed to more favorable growing conditions for wheat in the RWSs located in the west, east, and northwest of Iran, resulting in higher yields compared to the current climate. The elevated temperatures resulted in an acceleration of the crop development, which helped the crop to, at least partly, escape from terminal drought. In addition, improvements in water use efficiency and radiation use efficiency, attributable to the fertilization effect of elevated atmospheric CO_2 concentrations, were other possible reasons for this increased yield under future climate (Sultana *et al.* 2009).

In regions affected by terminal drought stress, genotypes with early flowering have had higher yield since the plant can escape from drought stress during the grain filling period (Farooq *et al.* 2014). However, shortened growth duration can limit biomass accumulation due to reduced interception of solar radiation (Araus *et al.* 2002). Conversely, extending maturation and thereby improving resource capture can increase yield, especially under the future climate with warmer temperatures (Semenov *et al.* 2014). Temperature is a key factor influencing crop phenology. When ambient temperature is below the optimal value, phenological development would accelerate (or the duration of growth stages would decrease) by increasing temperature (Chmielewski *et al.* 2004). Thus, it may not be necessary to decrease the vegetative period through breeding, as this reduction is likely to occur naturally in most RWSs due to rising temperatures under future climate conditions

(Figure 5). In addition, integrating a shortened vegetative period into wheat breeding programs should be approached with caution, as it showed negative effects on yield in some RWSs under both current and future climates, with more pronounced yield reduction under future conditions (Figure 8). The optimum vegetative growth period for rainfed chickpea has been analyzed in India, which demonstrated that its variation was not associated with the latitude of the locations, but was instead correlated with rainfall (Vadez *et al.* 2013). Their findings demonstrated that the relation between the yield of rainfed chickpea and the duration from sowing to flowering was well described by a third-order polynomial function. It means that there is an optimum value for this phenological phase, beyond or below which yield tends to decline. On the other hand, a decrease in the number of days for assimilate accumulation may reduce the production of mass, as a shortened vegetative phase limits the time for resource capture and storage (Araus *et al.* 2002).

It has been reported that there is a strong correlation between yield and transpiration during the grain filling stage (Araus *et al.* 2002; Zaman-Allah *et al.* 2011; Soltani and Sinclair 2012a). Various strategies have been proposed to enhance transpiration during the grain filling period. One approach is to use less water from the soil during the vegetative growth period, thereby reserving moisture for later use during the grain filling period (Sinclair *et al.* 2010; Zaman-Allah *et al.* 2011; Soltani and Sinclair 2012b; Vadez *et al.* 2013; Semenov *et al.* 2014). Another strategy is to increase plant access to more water in the soil through modification of traits such as increased root depth (Sinclair *et al.* 2010; Soltani and Sinclair 2012a; Semenov *et al.* 2014), provided that water is available at deeper soil layers. However, additional water availability at deeper depths is not always guaranteed (Vadez 2014). A further strategy is to extend the grain filling period, which may allow the crop to utilize potential late-season rainfall during this critical phase. In regions with moderate drought stress during the grain filling period, such as the RWSs located near the Caspian Sea, a longer grain filling period may enable the crop to benefit from potential late-season rainfall. In such environments, an extended grain filling period is considered a key trait for improving yield.

Faster leaf area development can increase radiation capturing and dry matter production. It would also shade the soil surface, thereby reducing evaporation of water from the soil surface and improving water availability for the crop. It has been reported that cereal genotypes with more leaf area production during vegetative growth were able to produce more yield under terminal drought conditions (Richards and Townley-Smith 1987; Turner and Nicolas 1998). This enhanced early-season leaf area expansion, occurring when water is generally sufficient, resulted in more dry matter production as the higher leaf area could capture more radiation for photosynthesis (Abidi *et al.* 2024). In a study conducted under irrigated conditions in Gorgan, Iran, a 30% reduction in wheat yield was associated with a 20% decrease in the canopy closure rate (Soltani and Galeshi 2002). Nevertheless, under rainfed conditions where water availability is limited, faster leaf area development resulted in either a yield loss or a yield increase, depending on the drought pattern that occurred during the growing season (Connor *et al.* 2011). Rapid leaf area development could result in rapid water uptake, especially in regions with severe terminal droughts, thereby reducing soil water during grain filling (Ludlow and Muchow 1990). The negative effect of decreasing phyllochron on yield in some years was neutralized in the simulations by its positive impact in Iran, especially under the future climate.

While enhancing radiation use efficiency is generally considered a desirable trait in crop improvement (Parry *et al.* 2011), the findings of this study suggest that radiation use efficiency was not an important target trait for consideration in breeding programs of rainfed wheat to prepare climate-ready genotypes in Iran. Increasing radiation use efficiency resulted in greater crop biomass accumulation, which in turn elevated the transpiration rate during the early growing season. As a consequence, water was used more rapidly, leading to earlier depletion of soil moisture reserves before grain filling, a critical stage when drought stress commonly occurs in rainfed agricultural systems in Iran. For example, in RWS Meshkinshahr (RWS No. 3), increasing radiation use efficiency led to approximately a 14% reduction in total evapotranspiration during the grain-filling period, which consequently resulted in a lower yield compared to the current cultivar under the current climate conditions (Figure 11).

Using data-driven methods (e.g., Random Forest, XGBoost) is also common for exploring hypothetical trait responses. Mechanistic modeling and data-driven approaches represent two fundamentally different philosophies for assessing plant traits. Mechanistic models are built on established principles of plant physiology to simulate growth processes over time, offering high interpretability and the unique ability to extrapolate to novel environments, such as future climate scenarios, but they can be complex to build and parameterize (Soltani and Sinclair 2012c). In contrast, data-driven methods like Random Forest and XGBoost excel at finding complex, non-linear patterns within large historical datasets, often achieving superior predictive accuracy for conditions covered by the training data; however, they operate as "black boxes" with poor explanatory power and fail dramatically when applied outside the scope of their training data. The choice thus hinges on the core objective: mechanistic models can be used for causal understanding and exploring the unknown, while data-driven approaches can be used for fast, accurate prediction within a well-defined and data-rich domain.

Conclusion

Under both current and future climate conditions, two crop traits were identified as key for improving the water-limited potential yield of rainfed wheat in Iran: (i) increasing grain filling period, (ii) decreasing growth stage duration. The yield improvement associated with these traits was primarily attributed to better alignment of phenological development with periods of higher moisture availability throughout the growing season. Increasing grain filling duration was generally an effective trait across the country under both current and future climates. Its impact was particularly pronounced in regions adjacent to the Caspian Sea, where higher spring precipitation (April to June) prevails. In contrast, decreasing growth stage duration showed a more site- and climate-specific effect, indicating a significant genotype × environment (G×E) interaction. These G×E interactions pose a substantial challenge in breeding programs aimed at developing cultivars for future climate conditions. In some RWSs, this trait had a negative impact on yield under both current and future climates, with a more pronounced detrimental effect under future climate conditions. The beneficial effect of this trait was observed in RWSs located in the Zagros Mountain range in western and northwestern Iran, where terminal drought stress tends to be more severe for the rainfed wheat. Overall, this study demonstrates that in the rainfed wheat systems under both current and future climates, the crop traits most effective for enhancing yield vary across regions, depending on the drought patterns and thermal regimes throughout the growing season. Given that climate change is expected to alter these environmental conditions, the development or introduction of cultivars specifically adapted to future regional climates will be essential. Consequently, an effective breeding program for rainfed wheat should begin with a comprehensive assessment of regional moisture and temperature patterns. The key traits identified through this evaluation should then be systematically incorporated into breeding strategies to inform parent selection and facilitate the development of cultivars with improved yield potential under water-limited conditions.

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Conflict of Interest

The authors declare no conflict of interest with any organization concerning the subject of the article.

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