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# Wheat drought-tolerance to enhance food security in Tunisia, birthplace of the Arab Spring

Walid Sadok[a,*], Rémy Schoppach[a], Michel E. Ghanem[b], Claudio Zucca[c], Thomas R. Sinclair[d]

[a] Department of Agronomy and Plant Genetics, University of Minnesota, St. Paul, MN, USA
[b] International Center for Agricultural Research in the Dry Areas (ICARDA), North-Africa Platform, Rabat, Morocco
[c] Integrated Water and Land Management and Ecosystems Program, International Center for Agricultural Research in the Dry Areas (ICARDA), Amman, Jordan
[d] Crop Science Department, North Carolina State University, Raleigh, NC, USA

A R T I C L E I N F O

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A B S T R A C T

The beginning of the 'Arab Spring' in 2011, a regional revolution which started in the Tunisian city of Sidi Bouzid in late 2010, occurred in part as a result of drought-triggered high wheat prices, which in the past led to 'bread riots' across several Middle East and North Africa (MENA) nations. Here we present, for the first time, an analysis of possible amelioration of wheat yield loss and greater stability in bread supply resulting from the incorporation of putative drought-tolerant traits into wheat cultivars grown in Tunisia. To this end, we used a simulation crop modeling approach using SSM-Wheat to evaluate yield loss or gain resulting from three types of water-saving traits that have been recently identified in wheat. These consisted in partial stomatal closure at high soil water content, overall decrease in transpiration rate (TR), and partial stomatal closure under elevated vapor pressure deficit (VPD). To capture large gradients in seasonal precipitation across wheat growing areas over a small country such as Tunisia, a grid pattern of 29 × 29 km was established as a basis for the geospatial simulation. Surprisingly, the simulation reflected opposite strategies in terms of water use (water-saving vs aggressive water use). The highest yield gain (30%) resulting from water-saving modification was found to occur in the food-insecure region of Sidi Bouzid. Traits enabling aggressive water use were found to be generally favorable across Tunisia, with one trait leading to up to 80% and 40% increases in yield and its stability in the food-challenged south of the country. However, major yield penalties were found to occur if water-saving traits were to be deployed in the 'wrong' region. Those findings could be used as a blueprint to navigate complex trait × environment interactions and to better inform local breeding and management programs to improve wheat yield and it stability in Tunisia and the MENA region in general.

## 1. Introduction

Wheat is a major part of human diet worldwide, representing the main import of calories for humanity. Over the last decades, wheat production shortages resulting from recurrent and increasingly severe droughts amplified by anthropogenic climate change have increasingly become a worldwide source of food security concerns (Lobell et al., 2011). This situation is far more dire in developing countries where wheat is the main staple food, particularly in the Middle-East and North Africa Region (MENA) where food security is critical to the social, economic and political stability of the entire region and neighboring states in Sub-Saharan Africa and southern Europe.

As the country where the so-called *Arab Spring* started, Tunisia embodies particularly well those challenges. Tunisia is a densely populated (11 million inhabitants), small Mediterranean country (164,000 $km^2$) located on the northern tip of Africa, where wheat (predominantly durum, *Triticum durum* Desf.) is cultivated across a very large annual precipitation gradient ranging from less than 200 mm in the south to over 1000 mm in the northwestern region (Fig. 1). Historically, Tunisia was considered the 'Granary of Rome' during the Roman Era, and had a similar role with France when it was a French protectorate (Latiri et al., 2010). While wheat is widely cultivated in the country, Tunisia is now a food-deficit nation with a 121% increase in wheat imports between 1984 and 2016 (Khaldi and Saaidia, 2017), with large inter-annual fluctuations due to rainfall variation (World Food Programme (WFP, 2011). Between 2012 and 2016, the 5-year average of total wheat production in Tunisia was 12.6 Million quintals (Mq), the vast majority of which (10.26 Mq) resulted from durum wheat with a total acreage of approx. 725 Mha (Khaldi and Saaidia, 2017). Local wheat yields are inconsistent on an interannual basis, with

* Corresponding author.
*E-mail address:* msadok@umn.edu (W. Sadok).

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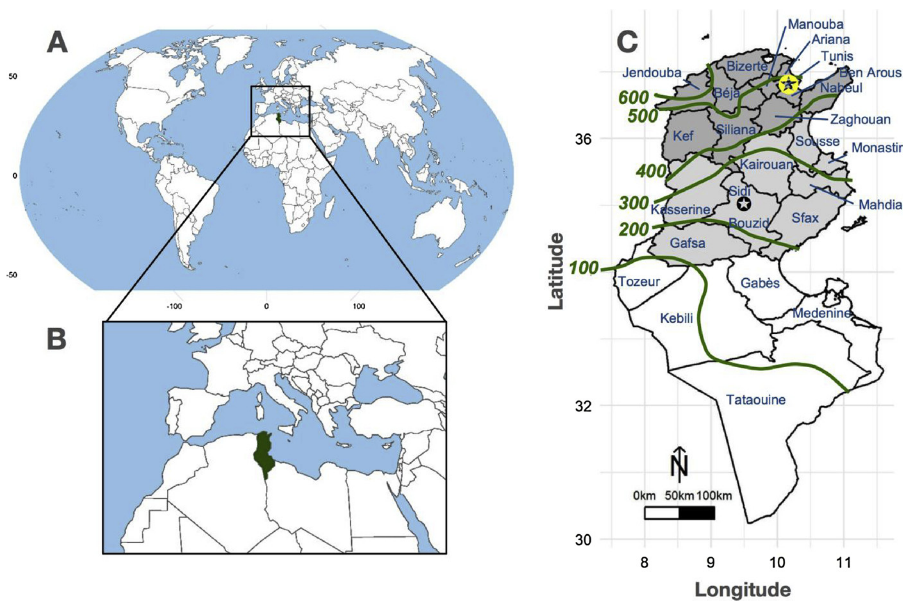


**Fig. 1.** Tunisia location (A and B) and map (C) illustrating its 24 governorates, three main regional subdivisions[1] and average yearly (1909–1996) precipitation (mm) isohyets (Benzarti, 2003). In panel C, the stars in the yellow and black backgrounds indicate the locations of the capital city (Tunis) and the city of Sidi Bouzid, respectively.

national averages never exceeding 25 and 21 q $ha^{-1}$ for durum and bread wheat, respectively (Khaldi and Saaidia, 2017). Such values are well below the yield potential estimated nationally at an average of 50 q $ha^{-1}$ (ONAGRI, 2018)

Over the last decade, Tunisia has experienced five major drought events reducing yields by up to 50% (World Food Programme (WFP, 2011; USDA-FAS, 2005, 2007, 2009, 2011, 2013, 2016), which resulted in spikes in wheat imports. Such large decreases in yield indicate that the limited set of cultivars available in the country is not equipped with traits to enable stable and economically-viable yields when subjected to drought. In fact, along with social factors, local drought, along with a surge in imported wheat prices as a result of drought in 2010 were contributors to triggering the Tunisian *Jasmine revolution* in the food-insecure central region of Sidi Bouzid between December 2010 and January 2011 (World Food Programme (WFP, 2011; FAO, 2013). Similarly, there is evidence that the Syrian revolution that started in March of the same year was driven in part by the 2006-10 drought (De Châtel, 2014).

Most MENA countries, including Tunisia, can experience a Mediterranean-type drought where crops typically grow on stored soil moisture. This condition has led to suggestions that crop genetics and management strategies need to emphasize plant 'water-saving' traits in such climates (Passioura, 2012; Sinclair et al., 2017). Under this paradigm, one of the most effective strategies to enhance productivity is through early-season water-saving to enable enhanced soil moisture availability to sustain the critical period of seed-fill. On Australian wheat, Richards and Passioura (1981) exploited such an idea to design cultivars with decreased metaxylem vessel size in the seminal roots as a way to decrease root hydraulic conductance to enable water-saving. Their effort led to a breeding program that resulted in yield increases of up to 11% in rainfed south-Australian environments (Richards and Passioura, 1989).

An alternative framework to identifying water-saving genotypes is by characterizing more directly water use by examining the relationship between whole-plant transpiration rate (TR) to increasing vapor pressure deficit (VPD) before the onset of drought (Sinclair et al., 2005) or TR response to progressive soil drying (Sinclair and Muchow, 2001). While the immediate consequence of these traits would be a partial inhibition of crop $CO_2$ assimilation, the long-term benefit would seemingly be increased water availability for sustained physiological activity during late-season seed growth. In this framework, genotypes reducing TR during times of the day where VPD exceeds a certain threshold ($VPD_{Th}$) or exhibiting an early stomata closure under drought would enable yield increases through water-saving. Consistently with this, various simulation modeling efforts on crops such as soybean (Sinclair et al., 2010), maize (Messina et al., 2015) and Lentil (Guiguitant et al., 2017) have shown that limiting TR to a constant rate over a $VPD_{Th}$ ranging from 1 to 2 kPa yielded major yield gains under terminal drought environments. Similarly, early stomata closure in response to soil drying has been shown to lead to increasing yields in maize (Sinclair and Muchow, 2001) and soybean (Sinclair et al., 2010).

On wheat, Schoppach et al. (2017a) found that a group of 23 cultivars that were released in south-Australia exhibited without exception the water-saving TR limitation. More recently, Tamang et al. (2019), identified a substantial diversity in TR response curves to VPD in a worldwide wheat panel. The latter study, which covered a set of 54 lines identified a substantial, 3-fold variation among the slopes characterizing linear TR responses to VPD, which pointed to the previously untested possibility that the lowest slopes could be associated with water-saving. Furthermore, the study also suggested that the highest slopes could be associated with higher yields under relatively well-watered environments. Regarding TR response to soil drying in wheat, Schoppach and Sadok (2012) identified a significant variability among a group of 7 drought-tolerant lines. However, in contrast to precious evidence form simulation modeling on other crops, several drought-tolerant genotypes in that group exhibited a delayed decrease in TR in response to soil drying.

Despite the recent progress in characterizing the diversity of these responses in wheat, there has been no effort to examine, using crop simulation modeling, the potential yield gains or penalties that would be associated with variation in $VPD_{Th}$, slopes of linear TR responses to VPD or TR response to soil drying. Such simulations would be particularly useful in the case of Tunisia, which as for most MENA countries, is subject to large gradients in seasonal precipitation across wheat growing areas. Because i) such gradients are normally not captured in regional or continent-wide yield assessment studies, and ii) internal disparities in food availability are important drivers of socio-economic and political instability in all MENA countries, the overarching goal of this study is to characterize yield gains and penalties resulting from the above traits, at fairly high geospatial resolution. This study was done specifically for Tunisia to assess the changes in wheat yield that might result from altering the expression of three plant traits suggested for stabilizing wheat yield under dryland conditions.

## 2. Materials and methods

### 2.1. Description of the Tunisian environment

Tunisia is a Mediterranean country located in North Africa, situated in the transition zone between the arid Saharan climate and the Mediterranean sub-humid climate, at the eastern end of the Atlas Mountains. Tunisia is composed of 24 administrative divisions, called governorates, which occupy three main pedo-climatic subdivisions (Fig. 1). The northern region is composed of 11 governorates with annual precipitation that ranges from > 1500 mm in the sub-humid north to 400 mm in the semi-arid south of this region (Benzarti, 2003). Further south is the central region (8 governorates) that is typically a steppe area with mainly a semi-arid climate receiving 200–400 mm of precipitation per year. The southern-most region is made up of 5 governorates and is mainly arid (< 200 mm per year) with a large number of oasises (Benzarti, 2003). Local precipitation patterns are under strong topographic and coastal influence due to over 1300 km of Mediterranean coastline on the northern and eastern sides of the country (Berndtsson, 1989).

Rainfed wheat (durum) is the most widely cultivated cereal in Tunisia and the crop is mainly grown in the northern and central regions. Wheat yield potential decreases along the north-south precipitation gradient (Latiri et al., 2010). However, wheat is also grown in areas with precipitation less than 150 mm in the southernmost governorates of the country from Gabes to Tataouine (Perrot, 1909; Émile, 1950; Abaza, 2012).

### 2.2. Model description

Crop development, growth and yield were simulated using the Simple Simulation Model, adapted for wheat (SSM-Wheat). This model was originally developed by Amir and Sinclair (1991a, b) and Sinclair and Amir (1992) and fully described by Soltani and Sinclair (2012) and Soltani et al. (2013). The SSM model has already been applied to geospatial analyses in the southern U.S. wheat growing region (Lollato et al., 2017) and its adaptation for wheat grown in the Middle-East is fully described in Schoppach et al. (2017b). Briefly, this model is based on stable parameters measured independently for each simulated genotype so the model does not involve calibration as required by most crop models (see Section 2.4.2 for genotype-specific parameters reflecting water-use traits). In the model, plant leaf-area development is calculated as a function of temperature accumulation expressed as cumulative temperature units (°C). To obtain leaf area index (LAI), plant leaf area was multiplied by plant density, which in these simulations was held constant 300 plants $m^{-2}$. This density is typical to the MENA region in general (Soltani and Hoogenboom, 2007; Schoppach et al., 2017b) and is within the range of densities (250–350 plants $m^{-2}$) previously reported for Tunisia (Mailhol et al., 2004; Rezgui et al., 2000, respectively). Daily crop growth is a function of quantity of radiation intercepted calculated from LAI, multiplied by photosynthetically active radiation use efficiency (RUE), which was set to 2.2 g $MJ^{-1}$ (Soltani et al., 2013) in these simulations. The development of soil water deficit as simulated by decreases in fractions of transpirable soil water (FTSW) results in decreased daily growth. Grain yield is simulated by assuming a constant linear increase in harvest index (HI) through the seed filling period (0.014 g $g^{-1}d^{-1}$, Moot et al., 1996). Therefore, any impacts on crop mass accumulation will have a direct influence on seed growth rate (Schoppach et al., 2017b).

#### 2.2.1. Adaptation to an hourly timestep

SSM-Wheat originally operated on a daily time step where TR was calculated based on daily dry mass production multiplied by the weighted daily VPD and divided by a constant 'intrinsic' transpiration efficiency coefficient (TEC) set to 5.8 Pa for wheat (Schoppach et al., 2017b). To take into account the genetic variability of the response of TR to VPD through the daily cycle, the model was modified to function on an hourly time step. This conversion protocol from daily to hourly weather data input was successfully used previously in SSM models for sorghum (Sinclair et al., 2005), soybean (Sinclair et al., 2010), maize (Messina et al., 2015) and lentil (Guiguitant et al., 2017).

#### 2.2.2. Weather generation

Weather variability in Tunisia can be quite substantial from one year to the next, resulting in large year-to-year yield variability. This made it necessary to simulate 33 years of daily weather in order to capture the typical range of conditions in a given location (Sinclair et al., 2014). Owing to the lack of availability of weather data spanning the entire country over the considered period, it was necessary to generate weather data. To this end, we used the same method for generation of weather data as in Schoppach et al. (2017b). The generated weather data covered the 33-year period from 1979 to 2008 in each one of the 183 locations where yield was simulated (see next section).

### 2.3. Soil data, root development and water extraction

In the SSM-Wheat model used here, the soil is treated as a large bucket that expands with increasing depth of water extraction. Using the Harmonized World Soil Database (HWSD, 2012; Wieder et al., 2014), the fraction of sand (%), silt (%), clay (%), rock fragments (%), and bulk density was obtained for each grid location. These primary data were used to define curve number for runoff, volumetric soil water content at saturation and at drained upper limit, extractable soil water and drainage factor. Averages ( ± S.D.) and ranges (min-max) for the soil parameters included in the study region are as follows: rock fragments (%): 0.083 ± 0.068 (0.028 - 0.308); bulk density: 1.389 ± 0.088 (1.218–1.623); curve number: 77.469 ± 4.765 (65.000–95.000); volumetric soil water content at saturation: 0.442 ± 0.031 (0.351 - 0.524); volumetric soil water content at drained upper limit: 0.242 ± 0.030 (0.160 - 0.335); extractable soil water: 0.130 ± 0.006 (0.100 - 0.132); drainage factor: 0.301 ± 0.060 (0.200 - 0.500).

Maximal soil depth was assumed to not exceed 1.2 m across the 183 simulated locations. This value is within the range (1–1.5 m) of reported in studies characterizing soil depth in wheat-producing regions in Tunisia (Belhouchette et al., 2008, 2012). The maximum increase per biological day in depth for water extraction was set at 3 cm. At plant emergence, the extraction zone was set at 0.2 m depth and was not allowed to exceed 1.2 m at the end of root elongation. Water was considered accessible to the plant if it did not drain deeper than the root system extraction zone. Water input to the soil was only by rainfall, and loss by plant uptake, soil evaporation, run-off, and drainage below the root extraction depth.

### 2.4. Crop yield simulations and data analysis

Simulations were initiated for every location and year on 31 August. Since the date was at the end of the dry season for this region, it was assumed that there was no stored transpirable soil water on this date. From this starting date to the emergence date, soil water status at each location was updated daily based on rainfall, soil evaporation, run-off and drainage. No irrigation was implemented in these simulations. In addition, no nitrogen limitation was simulated in this study so that the yield results reflected only the environmental limitation of water availability.

#### 2.4.1. Simulations for optimal sowing dates

Simulations were done initially to determine the optimum sowing date at each grid location based on maximum yield calculated using the 'standard' traits model. Nine sowing dates ranging from October 1 to December 31 every 15 days were simulated in each location for the 33

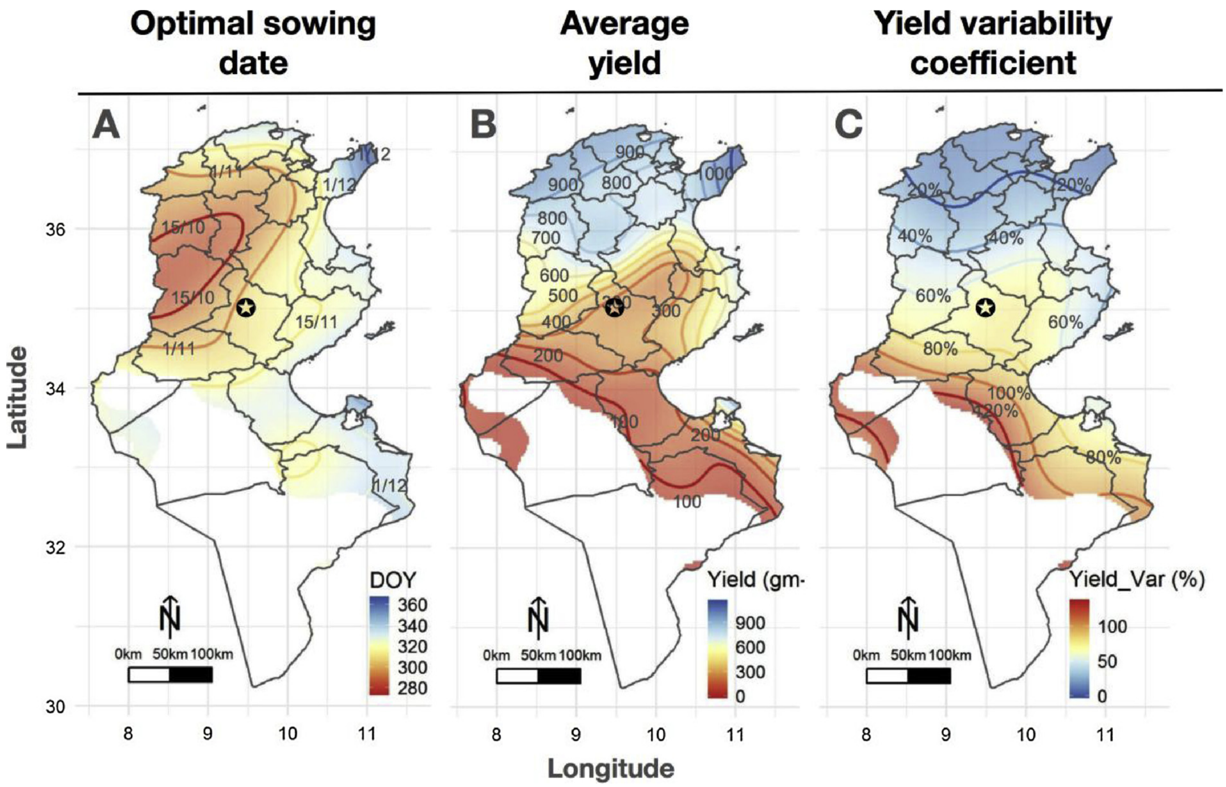


**Fig. 2.** Location-dependent optimal sowing dates (A), yield potential (B) and yield variability coefficients (C) for wheat grown in Tunisia. Optimal sowing dates ranged from 15/10 (red) to 31/12 in.(dark blue). Yield outputs ranged from 100 g $m^{-2}$ (red) to 1100 g $m^{-2}$ (blue), with variability coefficients that ranged from 20% (blue) to 120% (red), dependently on the region. In each map, contour lines delineate regions with the same values for the considered variables. The internal subdivisions represent the 24 governorates of the country. In each map, the star indicates the location of the city of Sidi Bouzid. The blank area represents a region that is not suitable for growing wheat (see Materials and methods for details).

years of available weather data. For every year and location, the best sowing date was the one that led to maximum final grain yield. A single optimal sowing date for each location was then calculated by averaging the best sowing dates from each year (Fig. 2). In the analysis, we excluded regions where wheat yields did not exceed 0.3 t $ha^{-1}$ over 50% of the years, as these options were not considered to be economically viable.

### 2.4.2. Water trait simulations

Three plant traits were simulated as possible approaches to increase crop yield. An initial set of simulations were done for a 'standard' wheat cultivar. The first variable trait studied was the threshold in fraction of transpirable soil water ($FTSW_{Th}$) at which partial stomata closure was initiated to cause a decrease in transpiration rate (TR). For the standard cultivar, a value of $FTSW_{Th} = 0.5$ was used (Fig. 3) (Schoppach and Sadok, 2012). Early initiation of the decrease in TR with soil drying to obtain water saving was done by setting $FTSW_{Th} = 0.7$ (Kashiwagi et al., 2015). An aggressive use of water was achieved by delaying the decrease in TR to $FTSW_{Th} = 0.3$ (Kashiwagi et al., 2015).

The second water-trait simulated was a change in TR by changing the transpiration efficiency coefficient by ± 25% from that of the standard situation (Tamang et al., 2019). These changes can be illustrated in the resultant shift in TR over the entire range of VPD (inset on Fig.4).

The third water-trait was to achieve water savings by introduction of a breakpoint in the TR vs. VPD response so that there was a threshold VPD ($VPD_{Th}$) above which TR was constant (inset on Fig. 5). Therefore, at any time during the daily cycle when VPD exceeded $VPD_{Th}$ there was water savings that could be potentially available of use by the crop later in the growing season. The two simulated thresholds were 1.0 (Sinclair et al., 2005; Sadok and Sinclair, 2009; Guiguitant et al., 2017) and 2.0 kPa (Schoppach et al., 2017b).

### 2.4.3. Data analysis

All the statistical analyses were done using Microsoft Excel 2016 macros. The maps were generated using R scripts (R Core Team, 2017) using a kriging method to extrapolate data between simulated points (Schoppach et al., 2017b). In each location and year, the effects of drought tolerance traits were evaluated through 3 main metrics; (i) the yield ratio between the average yield of the standard genotype and the yield resulting from the same genotype expressing each one of the evaluated water traits, (ii) the probability of getting a yield advantage from the considered water trait over the 33 simulated years and (iii) the average decrease in yield variability coefficient due to the introduction of the water trait of interest. For each location, the yield variability coefficient was calculated as the standard deviation of the yield divided by the average yield multiplied by 100. The decrease in yield variability was defined as the value of the coefficient without the trait minus the value of the coefficient with the trait. Negative values therefore indicate that the considered trait reduced the year-to-year yield variability.

## 3. Results

### 3.1. Wheat yield potential in Tunisia as a function of climatic subdivisions

Not surprisingly, simulated wheat yields were much greater than commonly experienced in the various regions of Tunisia since only the weather conditions were considered while none of the other major limitations to wheat productivity in country (namely nitrogen supply, weed control, pest control, harvest losses) were considered. Nevertheless, the gradient of wheat production across Tunisia was accurately generated with the greatest yields in the north (average: 840 g

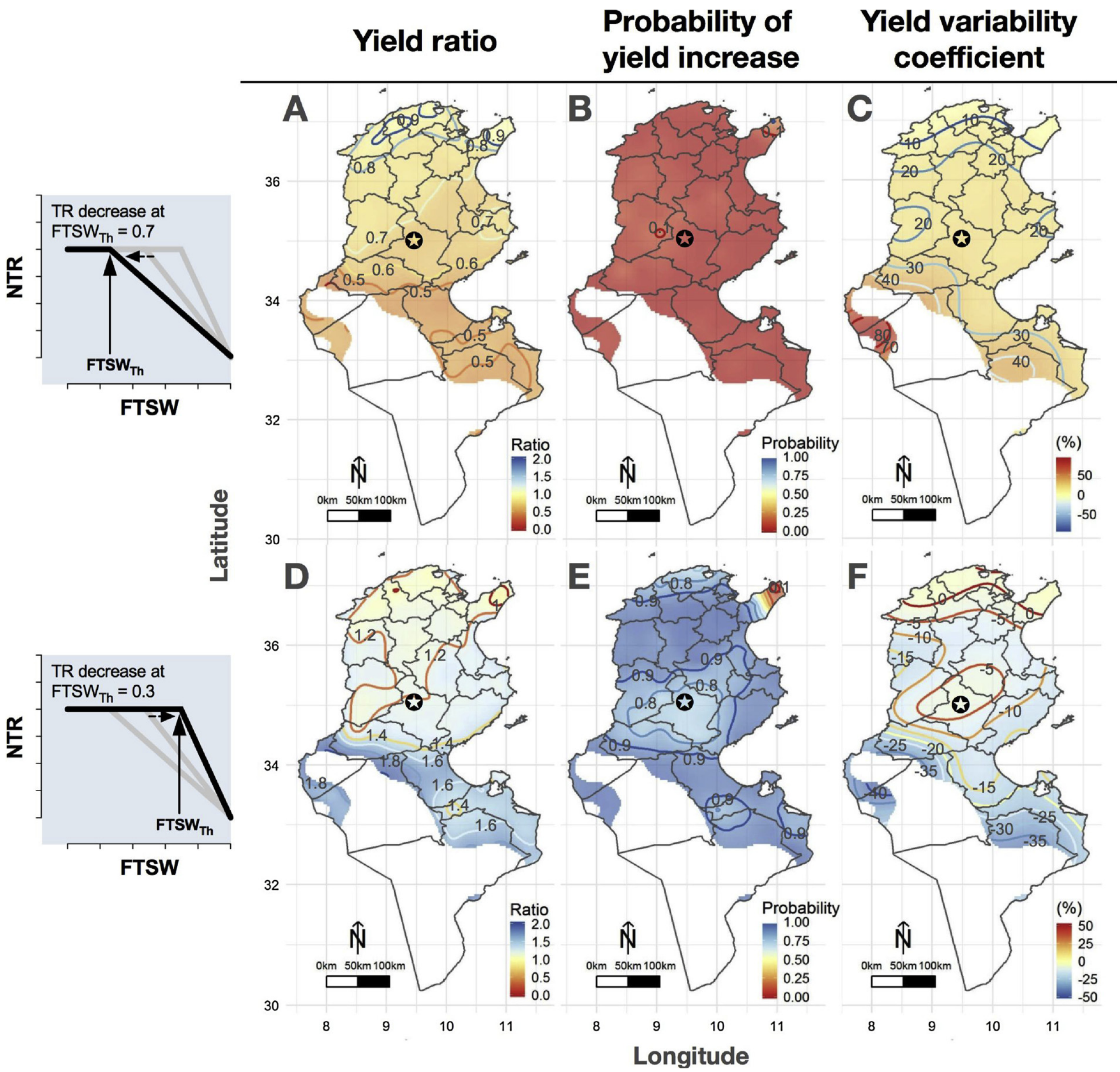


**Fig. 3.** Yield ratios, probabilities for yield increase and yield variability coefficients resulting from deploying wheat genotypes exhibiting an early (A–C) or delayed (D–F) decrease in normalized transpiration rate (NTR) response to decreasing fraction transpirable soil water (FTSW). Insets on the left-hand side show the modalities of NTR response curves to FTSW for a standard genotype (grey line) and for a hypothetical genotype with a higher (top) or lower (bottom) FTSW threshold ($FTSW_{Th}$) for NTR decrease. Panels A and D present the ratio between the yield of the standard wheat and those with altered $FTSW_{Th.}$ Panels B and E present probabilities of yield increase from changing $FTSW_{Th}$. Panels C and F present the variability coefficients where positive and negative values indicate increases or decreases in yield variability, respectively. The internal subdivisions represent the 24 governorates of the country and the star symbol locates the city Sidi Bouzid. The blank area represents desert regions not suited for growing wheat.

$m^{-2}$), decreasing to lower yields in the central and southern regions (average of 432 g $m^{-2}$ and 105 g $m^{-2}$, respectively). The north-south yield gradient revealed by the simulation is consistent with government-reported rainfed yields in the north which are typically double those of the central region (250 g $m^{-2}$ vs 120 g $m^{-2}$; Latiri et al., 2010; Ben Zekri MGhirbi, 2017). While much higher, the yield outputs simulated for the north are consistent with findings from well-managed, rainfed experimental plots in the northern part of the country (ONAGRI, 2018) with yields over 750 g $m^{-2}$ in an area where the our simulation estimates yields at approx. 800 g $m^{-2}$.

In terms of yield fluctuation, simulated annual yields varied consistent with the extreme variation reported for the country (World Food Programme (WFP, 2011; USDA-FAS, 2005, 2007, 2009, 2011, 2013, 2016), as they showed yield variability in the northern environment (up to 20–40%) and much greater variation in the central and southern regions, with values as high as 60% and 120%, respectively. These fluctuations are consistent with government data reporting large interannual yield fluctuation in the central/southern region within the last decade (e.g., 100 to 300 g $m^{-2}$, Ben Zekri MGhirbi, 2017). These results reflect the high inter-annual variation in precipitation regimes that are associated with increasing aridity.

### 3.2. *Wheat yield potential in Tunisia as a function of drought tolerance traits*

Simulations based on variation in the FTSW threshold at which partial stomatal closure was initiated with soil drying revealed major yield gains attainable with high probability (0.9) resulting from aggressive water use ($FTSW_{Th}$ = 0.3) in all regions (Fig. 3). Those gains were found to increase dramatically along a north-south gradient. In the more productive north, yield benefits of 20% were found as a result of this trait, which were doubled in the central part (40% yield gains) of

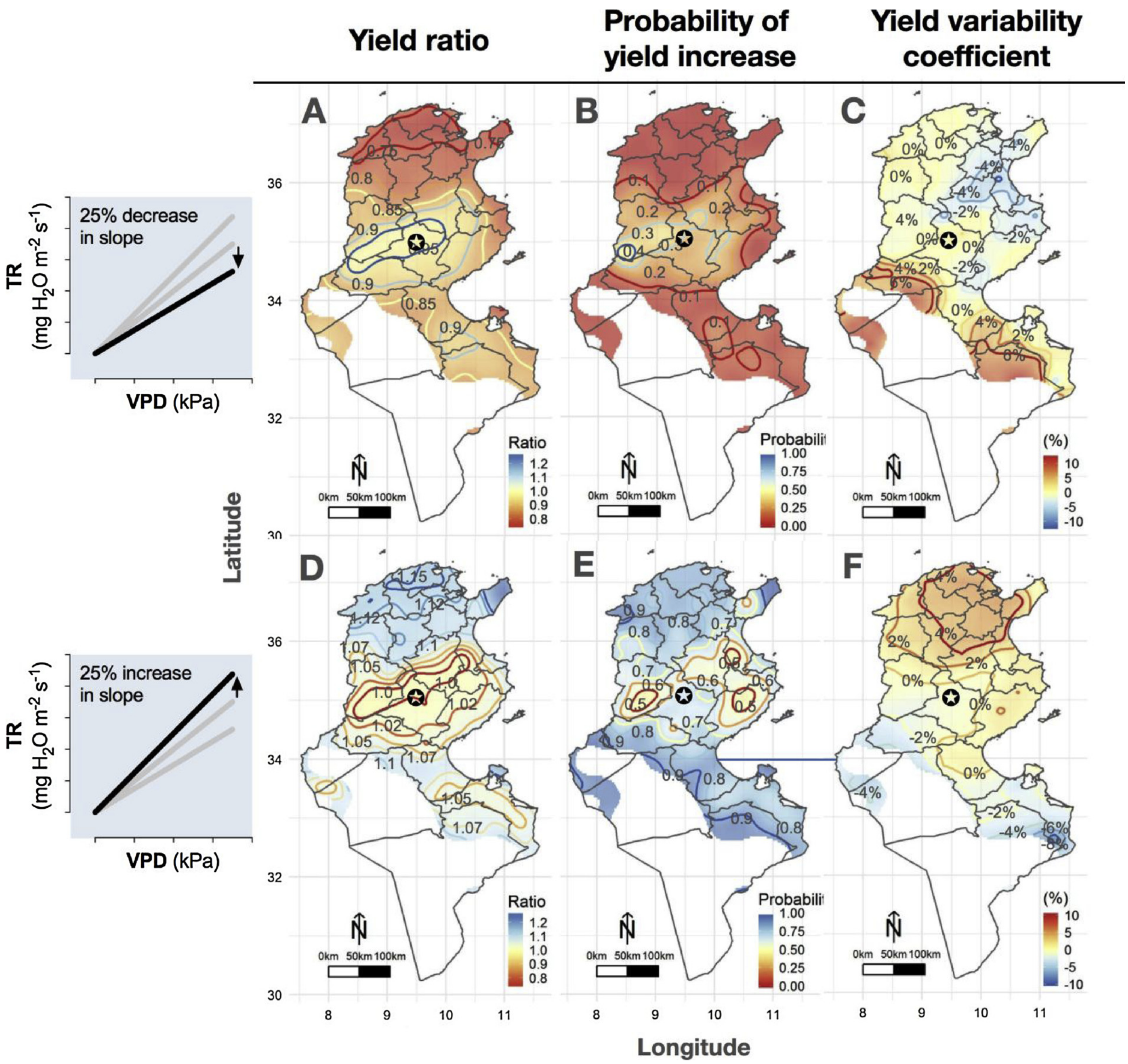


**Fig. 4.** Yield ratios, probabilities for yield increase and yield variability coefficients resulting from deploying wheat genotypes exhibiting an altered transpiration efficiency coefficient shown as a 25% decrease (A–C) or 25% increase (D–F) in the slope of transpiration rate (TR) versus vapor pressure deficit (VPD). The components of the figure are as described in the caption for Fig. 1.

the country (Fig. 3). Those benefits were even further amplified in the arid-to-semi-arid south, nearly doubling yields (80% increase) in the governorates of Gafsa, Gabes and Tozeur (Fig. 3). Importantly, all these yield gains were associated with substantial decreases in yield variability, from 5 to 10 in the north, 15% in the center and up to 40% in the south (Fig. 3). On the other hand, large yield penalties resulting from water-saving $FTSW_{Th}$ ( = 0.7), were observed. These increased along a north-south gradient, reaching losses as high as 20% in the north, 40% in the center and 50% in the south. Such penalties were also associated with higher yield variability in the 10–40% range across the country, peaking to 80% in the south (Fig. 3).

Water-saving by reducing the slope of TR response to VPD surprisingly resulted in yield penalties across the entire country. Those penalties were quite substantial, ranging from 10% to 25%, with little probability for yield increase or prospects for better yield stability (Fig. 4). Increasing the slope, which resulted in a more aggressive use of water actually resulted in small yield increases in nearly all regions of Tunisia. The greatest benefit occurred in the north where yield increases ranged from 10 to 15% with high probability (0.7-0.9), and with marginal increase in yield variability (2–4%). These outputs were obtained because increased TR allowed rapid use of water by the crop so that a greater proportion of the soil water was used to support transpiration and crop growth, rather than lost in soil evaporation.

Water-saving due to imposition of limited TR at elevated VPD resulted in greatest yield benefits as compared to the previous two approaches to water saving (Fig. 5). Imposing a maximal rate to transpiration generated marginal yield gains with a 2 kPa threshold and substantial yield gains with a 1 kPa threshold, particularly in the food-insecure central and southern regions of Tunisia. In the central governorate of Sidi Bouzid, yield gains ranged between 15 and 30% with a high probability (0.8–0.9). Comparable yields were found for the remaining central governorates, particularly in the non-coastal areas (Fig. 5).

In addition, water-saving resulting from imposing a limitation on TR at the lowest $VPD_{Th}$ (1 kPa) reduced yield variability up to 10% in these areas. Comparable yield gains (15–20%) resulting from this trait were identified in the southern, coastal areas of the governorates of Gabès and Medenine, but with only a marginal effect on yield variability (0–2% increase). In contrast to those benefits, introduction of the limited-transpiration trait with the 1.0 kPa $VPD_{Th}$ resulted in yield

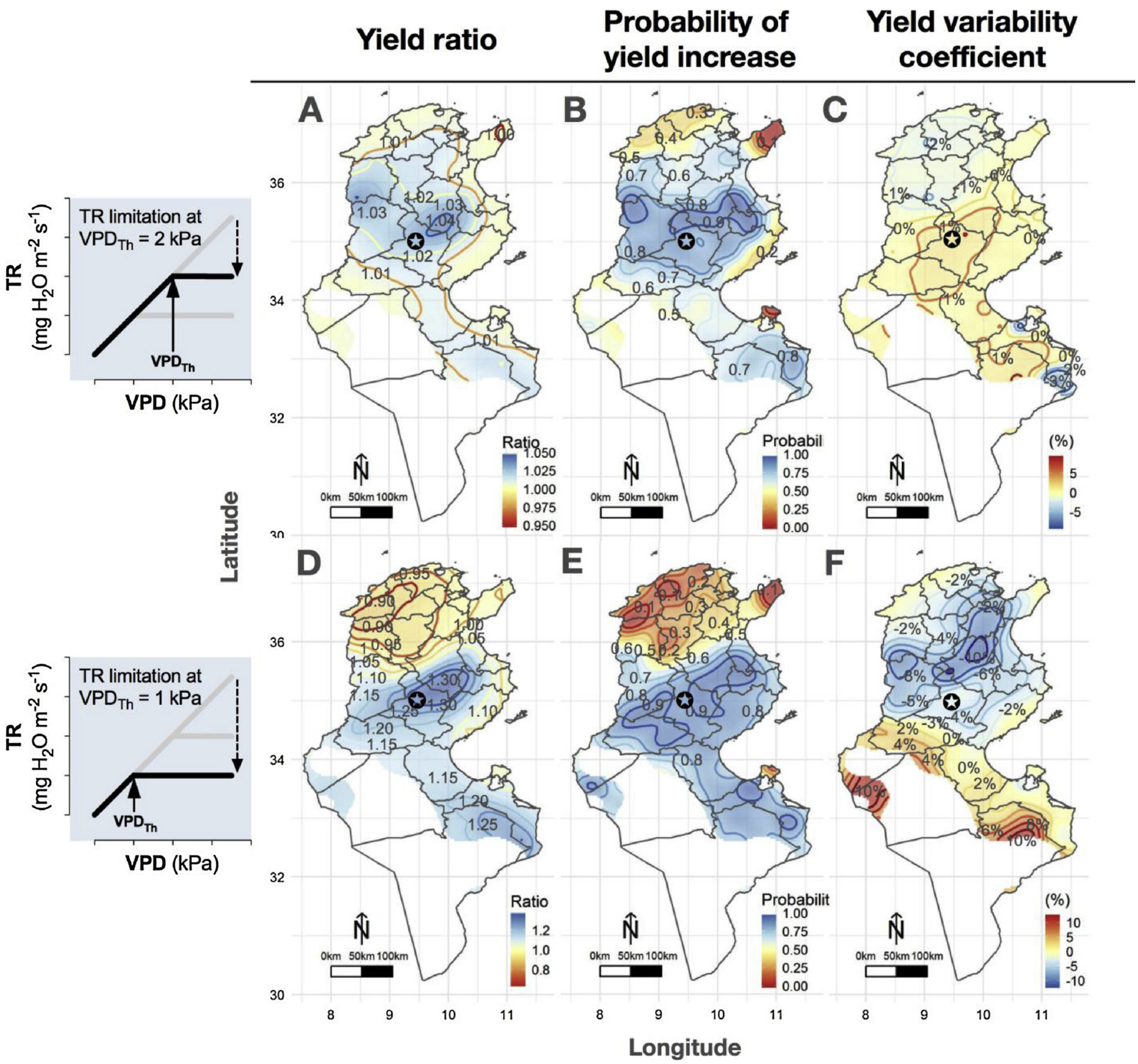


**Fig. 5.** Yield ratios, probabilities for yield increase and yield variability coefficients resulting from deploying wheat genotypes exhibiting a limitation on transpiration rate (TR) response to increasing vapor pressure deficit (VPD) at VPD thresholds ($VPD_{Th}$) of 2 kPa (A–C), or 1.5 kPa (D–F). The components of the figure are as described in the caption for Fig. 1.

penalties of 5 to 10% in the northern, most productive region. Such yield penalties arose as a result of the crop being unable to take full advantage of available soil moisture to maximize gas exchange and growth as a result of the low $VPD_{Th}$.

## 4. Discussion

### *4.1. Opposite outcomes of water-saving or aggressive water use illuminate critical context-dependencies driving drought tolerance under a Mediterranean environment*

A first major finding of this analysis, was that water-saving traits yielded contrasting outcomes dependently on the trait and location. Water-saving by initiating stomatal closure at higher soil moisture (*i.e.*, high $FTSW_{Th}$, Fig. 3) or by reducing the slope of TR response to VPD -a trait examined here for the first time (Fig. 4), universally resulted in yield penalties across the entire country. Particularly in the case of high $FTSW_{Th}$, our findings on Tunisia contradict previous simulation results on maize (Sinclair and Muchow, 2001) and soybean (Sinclair et al., 2010) which found that under Midwestern U.S. conditions, such trait would be beneficial. Our simulation indicates that under Tunisian conditions, these traits, although allowing for water-saving, were not beneficial in terms of productivity as they did not allow for taking advantage of available soil moisture to sustain gas exchange and growth. In other words, this behavior, in the specific context of Tunisia was ultimately ‘wasteful’ as it was too conservative to enable yield gains.

A widely different outcome was found in the case of water-saving due to imposition of limited TR at elevated VPD, particularly at a $VPD_{Th}$ of 1 kPa, which resulted in substantial yield gains in the center and south and to relatively marginal yield penalties in the north. In the case of this trait, the yield gains were enabled by the ability of the genotypes to save water needed for seed fill, but while allowing for maximal gas exchange favorable times of the day (*i.e*, VPD $<$ 1 kPa). Yield losses, however, were mainly due to the fact that limited TR resulted in unnecessary limitations on carbon assimilation, as enough moisture was available to trade transpirational water loss for $CO_2$ uptake. These findings are consistent with previous simulations carried out on sorghum (Sinclair et al., 2005), soybean (Sinclair et al., 2010), maize (Messina et al., 2015), lentil (Guiguitant et al., 2017), and point to this trait being universally useful, independently from the crop.

A third major outcome of this investigation was that in contrast to the current thought, traits resulting in aggressive water consumption, were found to be generally beneficial, as they enabled the rapid use of soil moisture to sustain gas exchange and growth, a resource that could be otherwise lost to evaporation. Increasing the slope of TR response to VPD was found to be particularly beneficial in the well-watered north with a relatively neutral effect on the rest of the country. This finding is consistent with recent evidence we assembled on wheat showing that cultivars equipped with linear and high slopes of TR responses to VPD tend to be expressed by cultivars released for well-watered environments (Tamang et al., 2019). Decreasing $FTSW_{Th}$, was found to generate yield gains across the entire country, proportionally to increasing aridity (Fig. 3) a finding that is consistent with Schoppach and Sadok (2012) who found that drought tolerant, south-Australian wheat cultivars expressed $FTSW_{Th}$ that were higher than those of the check cultivar.

Taken together, these findings converge to indicate that various water use strategies, could lead to similar or opposite outputs dependently on their associated tradeoffs and the location's specific environment, providing strong support to the idea that context-dependencies are key drivers of yield performance under drought (Hammer et al., 2006; Tardieu, 2012). From a practical standpoint, they also highlight the critical importance of accounting for trait × environment interactions in assigning specific cultivars to specific regions (see next section).

### *4.2. Recommendations to increase wheat food security in Tunisia by breeding for specific cultivars tailored to local context-dependencies*

In Tunisia, where major yield losses resulting from drought are incurred every 2–3 years, most of the durum wheat production is based on a limited set of 5 cultivars released in 80′s-90′s, none of which is actually drought-tolerant (ONAGRI, 2018). Furthermore, these varieties are typically released to farmers across regions with highly contrasting water availability regimes.

Here, using geospatially-explicit mechanistic crop model, and using Tunisia as a case study for the MENA region, simulations were done to provide a biologically-informed approach to identify specific locations-trait association to enhance wheat food security. These associations were identified such that they highlighted potential to enhance − or penalize − yields, and to influence year-to-year yield stability or both, across the Tunisian agricultural landscape. Importantly, the simulations offered evidence for substantially increasing wheat yields in the food-insecure, central and southern parts of the country, including highly volatile areas such as Sidi Bouzid, a region where the Tunisian revolution started, and which is currently undergoing a major shift in its agricultural landscape in order to boost wheat production. The findings of this simulation analysis are therefore potentially critical to help local decision-makers, agronomists, breeders and farmers develop locally-adapted cultivars to maximize local food security.

In this case, recommendations for crop improvement need to be targeted specifically in the case of Tunisia to the three main climatic subdivisions of the country. In the north, deploying wheat genotypes with aggressive water use either in response to increasing evaporative demand or soil drying, would be recommended. In sharp contrast, in the central part of the country, genotypes exhibiting a water-saving behavior as a result of limited TR at a low $VPD_{Th}$ or an aggressive water use under drought were found to favorable. In this subdivision, the food-insecure region of Sidi Bouzid was found to be focal point of substantial potential yield gains arising from both traits. In this governorate, cropland area allocated to wheat is on the rise, with 22% increase in sown areas between 2017 and 2018 (WMC Portail, 2018), highlighting a potential for significantly increasing wheat production as a result of these trait modifications. For this region, the recommendation would be therefore to breed for the integration of both traits in the local germplasm.

Finally, for the similarly challenged southern region, while both water-saving (as a result of limited TR at a low $VPD_{Th}$) and aggressive water use (by decreasing $FTSW_{Th}$) led to yield gains, the recommendation would be to deploy genotypes expressing the latter trait. This is because the yield gains associated with water-saving were not only smaller but were associated with increases in yield variability (Fig. 5), while the opposite strategy generated higher yield gains and substantial increases in stability (Fig. 3). Therefore, the best breeding strategy would be to integrate this trait in local breeding programs.

In conclusion, these simulations re-emphasize the critical importance of designing and implementing breeding programs only after exploring with simulations temporal and geospatial perspectives on the yield responses – both positive and negative – on any contemplated alteration in plant traits (Sinclair et al., 2010; Cooper et al., 2014; Messina et al., 2015). Finally, while this simulation focuses on water-use traits, future efforts to enhance wheat food security in Tunisia should also tackle other key factors such as limited nitrogen availability, deficient weed control and infrastructural constraints that conspire with water limitation to hamper productivity increases (Aubry et al., 1994; Latiri et al., 2010; Khaldi and Saaidia, 2017).

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