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Full Length Research Paper

Role of leaf rolling on agronomic performances of durum wheat subjected to water stress

**Amal Ben-Amar^{1*}, Anne-Aliénor Véry², Hervé Sentenac², Abdelaziz Bouizgaren³,
Said Mahboub¹, Nasser Elhaq Nsarellah⁴ and Keltoum El Bouhmadi¹**

¹Laboratory of Ecology and Environment, Ben M'Sik Faculty of Sciences, Hassan II University of Casablanca, Morocco.

²Biochimie et Physiologie Moléculaire des Plantes, UMR Univ Montpellier, CNRS, INRA, Sup Agro, Montpellier, France.

³UR Amélioration des Plantes et Qualité, Institut National de la Recherche Agronomique, INRA- Marrakech, Morocco.

⁴UR Amélioration des Plantes, Institut National de la Recherche Agronomique, INRA- Settat, Morocco.

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In arid and semi-arid climates characterized by low rainfall with a great annual and inter-annual irregularity, drought can occur at any time inducing large losses in crop yield. Leaf rolling is one of the adaptive morphological responses to the water deficit observed in a number of species including cereals. It reduces the leaf area exposed to sunlight and transpiration. The aim of the present work was to characterize the agronomical impact of water stress on a set of 16 Moroccan durum wheat varieties and to examine the possible correlations between leaf rolling and agronomic performances of these varieties. Experiments were conducted during three cropping seasons on a soil with a clay-loam texture at Tamellalet, in Marrakech region. The water stress was applied for one week to the studied varieties at tillering, and the degree of leaf rolling was determined at the end of the stress period. Strong differences between the varieties in the degree of leaf rolling upon water stress and in the ability to counteract drought were observed. Varieties displaying high leaf rolling showed less reduction in the yield components (number of ears per plant, number of grains per ear and weight of grains). The strong correlation observed between the degree of leaf rolling and maintaining of agronomic performance suggests that leaf rolling can be a criterion for water stress tolerance in durum wheat. This trait could thus be used as a morphological marker of tolerance to water stress.

Key words: Durum wheat, water stress, leaf rolling, agronomic traits, grain yield, drought tolerance, Morocco.

INTRODUCTION

Durum wheat (*Triticum turgidum* L. subsp. durum) accounts for about 10% of the global wheat production (Kantety et al., 2005). Its cultivation is concentrated in latitudes corresponding mostly to the North America, the Middle East, Australia and especially the Mediterranean

Basin. The aforementioned represent around 60% of its total growing area. In the southern Mediterranean countries, it occupies a key place in agricultural production. In Morocco for instance, out of a total of 8.7 million hectares cultivated annually, 5.3 million hectares

*Corresponding author. E-mail: benamar2003@gmail.com.

are devoted to cereals, and durum wheat cultivation (1.1 to 1.3 million ha) ranks third after bread wheat and barley (Belaid et al., 2003; MAPM, 2014).

Durum wheat is mainly grown under rainfed conditions (e.g., cultivated in "Bour" at 81% in Morocco) (MAPMDREF, 2016). Its cultivation under arid and semi-arid conditions is thus expected to face water deficit or drought (Chennafi et al., 2006), and its annual production is therefore highly dependent on unpredictable seasonal rainfalls and temperatures (Anderson, 2010; Royo et al., 2010). In the Mediterranean region, losses in durum wheat yield due to water deficit vary from 10 to 80% depending on the year (Nachit et al., 1998).

In durum wheat as in other crops, the comparison between optimal yields and mean yields observed in the field generally reveals considerable differences, especially in traditional farming systems. These differences are explained by the influence of agronomic, genetic and climatic factors (Ricroch et al., 2011). Water stress can be quantified as the ratio between the amount of water required for optimal growth of the plant and that available in its environment (Laberche, 2004). In wheat, the moisture deficit in the soil affects the three main components of yield, namely the number of ears, the number of grains per ear and the weight of 1000 grains (Assem et al., 2006). The effect on these components, and therefore on yield, depends on the stage at which the deficit occurs (Mongensen et al., 1985; Debaeke et al., 1996). For instance, drought, at the beginning of cultivation cycle is known to affect emergence and tillering and, at end of the cycle, to affect the filling of the grains (Fisher, 1973; Watts and El Mourid, 1988; Kobata, 1992).

Maintenance of the major physiological functions (photosynthesis, transpiration, growth) under water shortage represents an important challenge (Passioura, 1996; Tardieu, 2003, 2005; Amigues et al., 2006). In addition to the maintenance of growth of leaves and reproductive organs, delayed leaf senescence, by keeping the photosynthetic capacity, helps to feed the reproductive organs. This strategy can allow high yields but also increases the risk of total yield loss. It is favorable in conditions of moderate water deficit but may prove to have detrimental consequences in the case of more severe water deficit (Amigues et al., 2006). Tolerance to water deficit may therefore be considered rather as the ability of a genotype to produce an acceptable yield under conditions of water deficit according to the scenario of the constraint (degree, developmental stage, duration) (Yokota et al., 2006; Hamon, 2007; Tardieu and Tuberosa, 2010).

In cereals, leaf rolling is a characteristic response to water deficit (O'Toole and Cruz, 1980; Kadioglu et al., 2012). It is believed to occur when the evaporative demand is no longer balanced by water uptake by the roots. This movement of the limb is indeed caused by the loss of turgor of bulliform cells, which are large epidermal

cells of the upper epidermis (Begg et al., 1980; Willmer, 1983; Jane and Chiang, 1991). The degree of leaf rolling is often used as a marker of intensity of drought stress in cereal cultures (Riboldi et al., 2016), but leaf rolling can also be considered as a mechanism of avoidance of dehydration (Belhassen et al., 1995; Amokrane et al., 2002). It contributes, by decreasing the leaf surface exposed to sunlight, to the reduction of transpiration and to increase water use efficiency in water stressed conditions (O'Toole and Cruz, 1979; Monneveux and Belhassen, 1996). Furthermore, it allows the plant, by limiting the direct illumination of leaf surface, to avoid overheating of leaf tissues, harmful to cellular metabolism and is considered to play a significant role in the resistance to high temperatures and end-of-cycle water deficit (Ortiz et al., 1991). In rice, leaf rolling was reported to improve photosynthetic efficiency and to delay leaf senescence (Richards et al., 2002; Richards et al., 2004; Zhang et al., 2009). The available photosynthetic surface of rolled leaf is however reduced, which has a negative impact on plant growth (Li et al., 2016a).

The objective of this study was to characterize 16 durum wheat varieties for their leaf rolling ability under drought stress and their agronomic performance in order to investigate the relationship between leaf rolling and tolerance or sensitivity to water stress applied at tillering .

MATERIALS AND METHODS

Plant material and experimental site

The study concerns 16 varieties of durum wheat (*Triticum turgidum* L. var. *durum*) provided by the National Institute of Agronomic Research of Settat (Morocco): Kyperounda ("2777"), Amjad, Anouar, Irden, Isly, Jawhar, Korifla, Marjana, Marouane, Massa, Oum Rabia, Sebou, Tomouh, Vitron, Waha and Yasmine. These varieties displayed diverse ranges of agronomic adaptation, a number of them being adapted to semi- arid areas (Taghouti et al., 2010; Nsarellah et al., 2011; Zarkti et al., 2012). The field experimentation was conducted at Tamellalet, CMV 408, Marrakech region (31°81'N, 7°50'W), during three consecutive cropping seasons: 2013-2014, 2014-2015 and 2015-2016. The Supplementary Table 1 represents more information on durum wheat varieties studied.

Climatic conditions

The monthly precipitations recorded over the three crop years, quite variable from one year to another, are given in Supplementary Table 2. The rainfall received from sowing to maturity was 186 mm, 171 mm, and 95 mm for the first, the second and the third years, respectively. The end-of-cycle period of culture at the field trial site coincided with low rainfall associated with high temperatures. Irrigation water was added to overcome the water deficit during the whole cultivation cycle, to meet the needs of the crop, fully or only partially when water stress was applied.

Field trial stress application

After the preparation of the soil (tillage, then leveling of the plot and

Table 1. Water to be delivered by precipitation and irrigation to control and stressed parcels.

Month		Dec	Jan	Feb	March	April	May	Total	Water deficit of the week
Mean ET ₀ in the Haouz (mm)*		60	60	65	93	112	152	542	
wheat Kc**		0.35	0.4	0.6	0.8	1.1	1.1	4.35	
ETM (mm)=ET ₀ *Kc: the quantity in mm / 30 days		21	24	39	74	123	167	448	
m ³ equivalent for 16 m ²		0.336	0.384	0.624	1.184	1.968	2.672	7.168	
Water to be received:									
	1st year	0.336	0.384	0.624	1.184	1.968	2.672	4.496	
Control parcel (m ³)	2nd year	0	0.384	0.624	1.184	1.968	2.672	6.832	
	3rd year	0	0.384	0.624	1.184	1.968	2.672	6.832	
	1st year	0.336	0.288	0.624	1.184	1.968	2.672	4.4	(24/31)*7=5,4mm
Stressed parcels 1 (m ³)	2nd year	0	0.384	0.468	1.184	1.968	2.672	6.676	(39/28)*7=9,75mm
	3rd year	0	0.384	0.468	1.184	1.968	2.672	6.676	(39/28)*7=9,75mm
	1st year	0.336	0.288	0.624	1.184	1.968		4.4	(24/31)*7=5,4mm
Stressed parcels 2 (m ³)	2nd year	0	0.384	0.468	1.184	1.968	2.672	6.676	(39/28)*7=9,75mm
	3rd year	0	0.384	0.468	1.184	1.968	2.672	6.676	(39/28)*7=9,75mm

*ET₀: Evapotranspiration of reference crop, from IAV of Agadir publication towards ORMVA technicians of the Haouz (2001); **Kc : crop coefficient.

limitation of the three subplots of 16 m² each) with a clay-loam soil, it was proceeded to the mineral fertilization consisting of a triple super phosphate feed (TSP-46%) as a baseline fertilizer applied before sowing (with a dose of 130 g / 16 m²) and ammonitrate 33% as a cover fertilizer (with a dose of 220 g / N). 16 m²) applied to tillering. The application of fertilizers was done on the fly.

A fungal treatment (product offered by the INRA of Settat) was applied on March 20th for the second and the third year, then during the first year this product was applied late at the stage of the run. Fertilization during the first, second and third years of study took place on 30/11/2013, 29/12/2014 and 30/12/2015, respectively. Before the sem-grains durum wheat, the three subplots were first irrigated to saturation of the soil. After 24 h, the water was brought in daily to reach the lost ETM (Table 1).

Seeding was carried out the first year on 01/12/2013 and the two other years in early January (01/01/2014 for the second year and 01/01/2015 for the third year). The test was carried out under two irrigation treatments. The first treatment (T1) consisted of normal irrigation (control) providing volumes of water just to compensate for the

ETM. The second treatment (T2) consisted of a week of water stress, applied 46 days after the semi, during tillering: the first year of irrigation was stopped on 16/01/2014, and 16 / 02/2014 for the second year and 16/02/2015 for the third year. The total water amounts received by the two irrigation treatments are given in Table 2.

The trial was set up on a plot of 48 m² (Supplementary Figure 1) divided into 3 subplots of 16 m². One subplot was used for the control treatment (T1). The water stress treatment (T2) was applied to the two other subplots. Each subplot received the 16 varieties studied. Each variety was sown on one line with 30 seeds on the line (Supplementary Figure 1). The arrangement of these varieties at each subplot was organized according to a completely randomized experimental setup. Sowing was done in December in the first year and in January in the following two years. The period of stress application coincided with the second week of January in first year, and the second week of February in second and third years. The water deficit on the two plots under water stress during the week was as follows:

First year

*1st plot: 24 mm/31 days * 7days = 5.4 mm which represents the water deficit of the stress week.

* 2nd plot: 24 mm/31 days * 7 days = 5.4 mm which represents the water deficit of the stress week.

Second year

* 1st plot: 39 mm/28 days * 7 = 9.75 mm which represents the water deficit of the stress week?

* 2nd plot: 39/28 * 7 = 9.75 mm which represents the water deficit of the stress week.

Third year

* 1st plot: 39 mm/28 days * 7 = 9.75 mm which represents the water deficit of the stress week?

* 2nd plot: 39 mm/28 days * 7 = 9.75 mm which represents the water deficit of the stress week?

The total water amounts received with the two irrigation treatments are given in Table 1.

Table 2. Data on the different vegetative stages of durum wheat.

Year	Semi date	Early emergence	Early tillering	Early run	Beginning of heading	Maturity
1	01/12/2013	12/12/2013	21/12/2013	04/02/2014	24/02/2014	02/04/2014
2	01/01/2014	10/01/2014	19/01/2014	04/03/2014	24/04/2014	31/05/2014
3	01/01/2015	12/01/2015	22/01/2015	07/03/2015	28/04/2015	03/06/2015

Leaf rolling determination

In our experiment, the degree of winding of durum wheat varieties studied was evaluated according to the indices used at INRA to estimate the winding and the type of adaptation of each of the varieties having manifested a winding under the supervision of Dr N. Nasser Elhaq (Research director at INRA Settatt Genetic improvement and plant genetic resources unit Specialized: Genetic improvement of cereals). There are other methods for estimating leaf roll in cereals, for example in rice, Leaf Roll Index (LRI) has been calculated at flag leaf level with the following formula: $LRI = (Lw - Ln) / Lw$ (Li et al., 2016). Lw was the largest flag leaf width in extending leaf blade, Ln was the natural distance from flag leaf margins at the same Lw measurement area.

One week after the water stress application, the flag leaf rolled from noon to 4 pm (at the daytime of peak temperature), and beyond 4 pm, unrolled. The degree of leaf rolling was evaluated from noon to 2 pm on the 7th day of water stress, based on the indices established by the INRA of Settatt (N. Nsarellah (Research director at INRA Settatt Genetic Improvement and Plant Genetic Resources Unit and Specialized: Genetic improvement of cereals) 8 different rolling degrees from absence of rolling to a leaf rolled all over its length displaying a thorn shape (Table 4 and Supplementary Figure 2). The flag leaf is the most sensitive leaf to water stress, when the soil starts to dehydrate; this leaf rolls on itself and just 30 min after hydration of the soil the leaf begins to unfold. Its presence is obligatory for growth and normal production in wheat, because it feeds the ear (Table 4).

Agronomic parameter measurements

- (i) The number of tillers per plant was counted in each plant.
- (ii) The height of the plant at maturity was measured from the visible base to the average top of the ears.
- (iii) The number of ears per plant was counted in each plant.
- (iv) The number of grains per ear was counted in each ear in the different varieties.
- (v) The weight of 1000 grains (WTG) was determined per variety using a balance, with 1000 grains counted.
- (vi) The grain yield (in g) per plant was calculated by multiplying the number of ears per plant by the number of grains per ear and by 10^{-3} times the weight of 1000 grains.

Statistical analyses

Statistical analysis of the data was performed using the Statistical Product and Service Solutions, SPSS software version 20.0, an IBM product since 2009 (Hejase and Hejase, 2013: 58; <https://www-01.ibm.com/support/docview.wss?uid=swg24031901>). For each irrigation treatment, we performed variance analysis to determine the effect of the year, the variety and the irrigation treatment and that of their interaction. When the effect of the variety was significant, we performed the Newman and Keuls test to identify groups of homogeneous varieties. The Newman and Keuls test is a multiple comparison procedure that allows sample means

significantly different from each other to be identified. This procedure is often used as a post-hoc test whenever an analysis of variance (ANOVA) revealed a significant difference between three or more sample means.

RESULTS

Yield variability of the different durum wheat varieties in control and water stress conditions

The grain yield of all sixteen varieties of durum wheat was determined at the end of each three cropping seasons by examining the number of ears per plant, the number of grains per ear and the weight of 1000 grains (Figure 1; Supplementary Table 5) in twenty plants randomly chosen per variety.

Under normal irrigation conditions (T1 treatment), the mean grain yield over the three crop years varied between varieties by a factor of 2.3 (from 11.5 g per plant in Anouar to 26.5 g per plant in 2777). Only moderate conservation of the grain yield varietal distribution was observed between years ($0.43 < R < 0.65$; Figure 1A). However, the range of grain yield variation between varieties was very similar on each of the three crop years (factor of 2.45 to 2.9; Figure 1A). The variety showing the highest yield was consistently 2777, while that showing the lowest one varied (Jawhar, Tomouh or Waha).

In plants subjected to the one-week water stress at tillering (T2 treatment), the grain yield decreased in all varieties (Supplementary Table 5). The extent of decrease depended on the variety. This led to a strong extension in the range of grain yield variation between varieties as compared to the control treatment. In the water stressed plants, the mean grain yield over the different campaigns ranged within a factor of 25 between varieties (from 0.9 g/plant in Marjana to 22.5 g/plant in 2777). Thus, the range of grain yield variation between varieties in water stressed plants increased by a factor of 5 to 11 as compared to that in the control plants on the three crop years (Figure 1B). A stronger conservation of yield between years ($0.57 < R < 0.89$; Figure 1B) than for plants grown under full irrigation was observed. It should be noted that four varieties susceptible to rust, 2777, Isly, Marjana and Yasmine, did not produce any grain in the first year in the water stressed parcels due to fungal infection. Only results of the two last years concerning grain yield under water stress were taken into account in the analyses for these varieties.

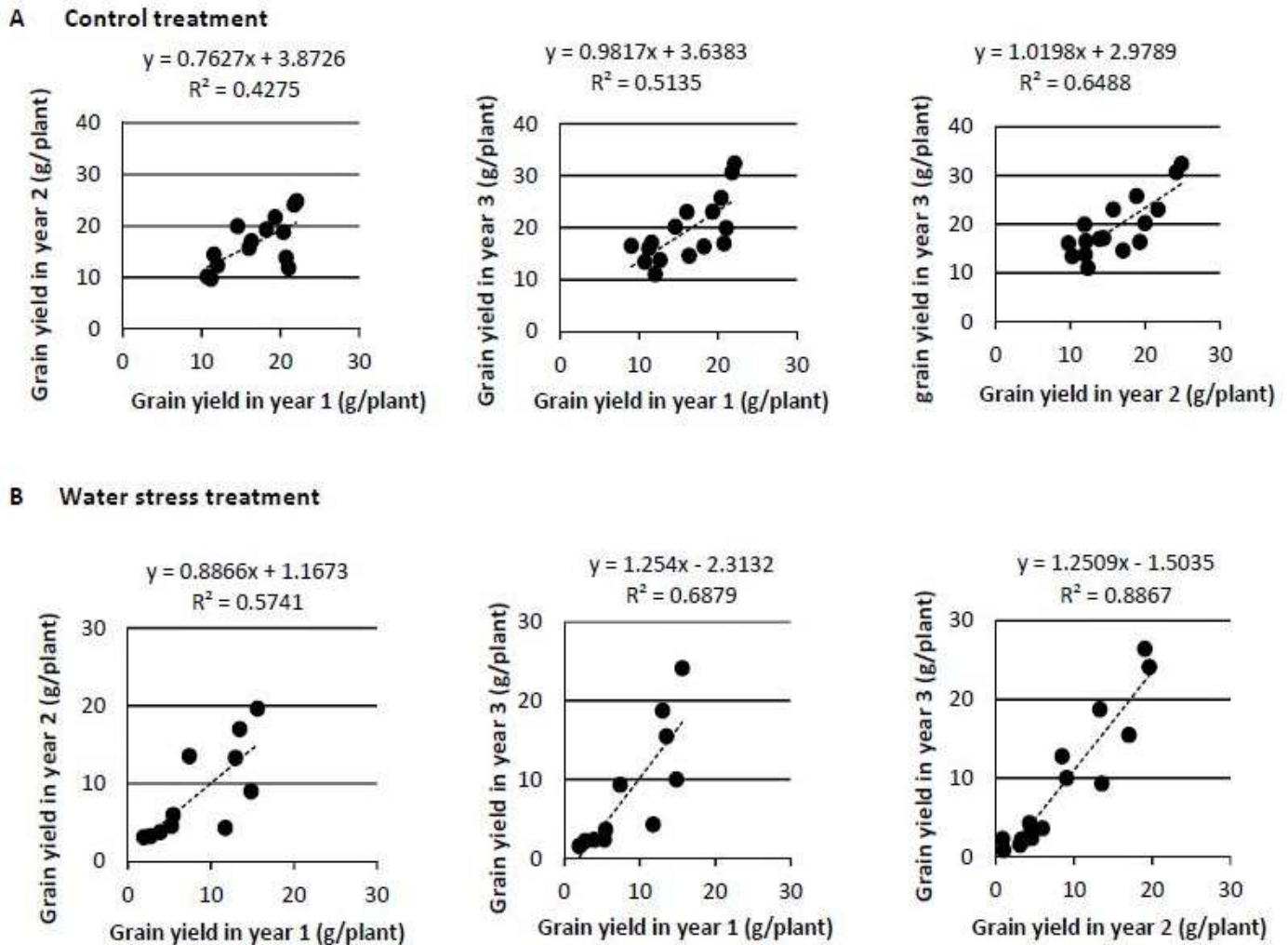


Figure 1. Grains yield of the 16 durum wheat varieties under control conditions (A) or subjected to water stress treatment (B). The grains yield was determined for each variety in plants grown in control conditions (A) or subjected to water stress treatment (B), using mean values of the number of ears per plant, the number of grains per ear and the grains weight, determined for each variety and treatment on 20 plants randomly chosen. Comparison between year 1 and year 2 (left), year 1 and year 3 (middle) and year 2 and year 3 (right).

Similar conclusions as those relative to the grain yield could be drawn when analysing the different yield components (the number of ears per plant, the number of grains per ear and the weight of 1000 grains), and the number of tillers and height of plants at maturity (Table 3). The variance analysis of examined agronomic parameters and yield indicated both highly significant inter-varietal and inter-annual variations (Tables 3 and 6). The variability between varieties was higher in water stressed parcels than in control ones for all the agronomic parameters. In water stressed parcels, the variability between varieties was also higher than the variability between years, except for the weight of grains. The variability between years was the highest in control conditions, except for the number of grains per ear and the weight of grains (Table 3). The parameters showing

the highest variability between varieties were the height of plants at maturity and the number of grains per ear in both control and water stress conditions (Table 3). Two varieties, Irden and 2777, showed the best performance both in control conditions and when subjected to water stress (Supplementary Table 3): Irden for the mean number of ears over the three years (9.9 in control conditions, and 11% less in water stress), and 2777 for the mean values of other yield parameters (10.7 tillers in control conditions and 9% less under water stress, 61 grains per ear in control conditions, and 5% less under water stress, 46 g per 1000 grains, and 8% less under water stress). 2777 also showed the tallest plants at maturity (103 cm as mean height in control conditions and 5% less under water stress).

The varieties showing the worst performances varied

Table 3. Variance analysis (ANOVA) of agronomic parameters in control (T1) and water stressed (T2) cultures.

Parameter*	Source: Between years			Between varieties			Combined effect (year x variety)		
	df	F-value	P ($\alpha=5\%$)	df	F-value	P ($\alpha=5\%$)	df	F-value	P ($\alpha=5\%$)
Well-watered parcel (T1)									
Number of tillers per plant	2	266.253	<0.001	15	44.801	<0.001	30	24.607	<0.001
Height of plants at maturity	2	327.845	<0.001	15	225.093	<0.001	30	43.327	<0.001
Number of ears per plant	2	238.373	<0.001	15	53.143	<0.001	30	23.447	<0.001
Number of grains per ear	2	37.956	<0.001	15	281.234	<0.001	30	41.456	<0.001
Weight of 1000 grains	2	13.805	<0.001	15	6.822	<0.001	29	3.506	<0.001
Water stressed parcels (T2)									
Number of tillers per plant	2	91.856	<0.001	15	369.216	<0.001	30	42.718	<0.001
Height of plants at maturity	2	85.694	<0.001	15	853.708	<0.001	30	38.241	<0.001
Number of ears per plant	2	53.544	<0.001	15	322.496	<0.001	30	35.759	<0.001
Number of grains per ear	2	669.269	<0.001	15	1103.024	<0.001	30	264.808	<0.001
Weight of 1000 grains	2	262.050	<0.001	15	192.341	<0.001	29	87.451	<0.001

*df = degree of freedom, F-value = Fischer ratio, P = probability.

on the other hand according to the agronomic parameter in control conditions, but Marjana was the worst for all parameters when plants were subjected to water stress (Supplementary Tables 3 to 7): the lowest mean number of tillers over the three years, in control conditions (8.15) was displayed by Waha, and under water stress (53% less) by Marjana, the lowest mean number of ears in control conditions (7.1) and under water stress (52% less) were both found in Marjana, the lowest mean number of grains per ear, in control conditions (40.5) was displayed by Anouar, and under water stress (53% less) by Marjana, and the lowest mean weight of 1000 grains, in control conditions (36 g) occurred in Jawhar, and under water stress (58% less) in Marjana. In addition, the smallest plants at maturity, in control conditions (71 cm mean height) were displayed by Tomouh, and under water stress (48% less) by Marjana.

From agronomic performances measured in the control and water stressed parcels, the performance decrease due to water stress (or conversely preservation under water stress) was also examined for all selected agronomic parameters (Supplementary Figure 3). An important variability in the sensitivity to water stress was observed within the panel of wheat varieties (mean grain yield decrease under water stress from 21 to 93%). Slight differences were noticed for the different agronomic parameters: the weight of grains showed the largest range of variability in stress sensitivity between species (mean decrease under water stress varying by a factor of 8.3), and the number of ears per plant showed the lowest range of variability (mean decrease under water stress varying by a factor of 5). Analysis of inter-annual variation indicated that the preservation of agronomic performances under water stress was more strongly reproducible (slope of inter-annual correlation between

1.02 and 1.07, 0.79 <R <0.89 for grain yield; Supplementary Figure 3) than the agronomic performances in control conditions or under water stress (Figure 1 and Table 5). Thus, the sixteen varieties of durum wheat of our study displayed a large range of variability in their agronomic performance, especially when subjected to the one-week water stress. Low inter-annual variability was noticed when the decrease in performance due to water stress was considered.

Effect of water stress on leaf rolling in the different durum wheat varieties

Plants of the water-stressed parcels displayed flag leaf rolling at the end of the water stress treatment during the hottest hours of the day, in contrast to those of the well-watered control parcel where no leaf rolling was observed at that time. A large variability among the 16 durum wheat varieties in the degree of leaf rolling was noticed (Figure 2). Indeed, observed rolling in the different varieties ranged from concerning at most the very tip (mean score of the variety between 0 and 1, e.g., in Marjana and Waha) to reaching at least two third of the leaf (mean score between 6 and 7, e.g., in Irden and 2777). Thus, the rolling behavior in the different varieties almost ranged from absence of rolling (score 0) to maximal degree (score 7), all the rolling degrees being represented. The same range of variation among varieties was observed in each of the three crop years (Table 4 and Figure 2A-C).

Most of the studied varieties showed little inter-annual variations in their degree of leaf rolling following the water stress treatment (Figure 2D). Amjad, Irden, Oum Rabia, Tomouh and Vitron, for instance, maintained the same

Table 4. Leaf rolling index.

Rolling class	Rolling index	Description
No rolling	0	Absence of rolling
	1	The tip of the leaf rolls up
Weak rolling	2	A quarter of the leaf rolls up
	3	One third of the leaf rolls up
Medium rolling	4	Half of the leaf rolls up
	5	More than half of the leaf rolls up
High rolling	6	Two third of the leaf rolls up
	7	Thorn shape of leaf fully rolled

Table 5. Grain yield in control conditions and in case of water stress in durum wheat varieties studied.

	Yield control			Yield stress		
	Y1	Y2	Y3	Y1	Y2	Y3
2777	30,356895	29,44682	38,4478545	32,7505232	25,779264	34,422328
Amjad	26,3008424	27,4332175	28,203751	27,3126036	23,12386	21,7600535
Sebou	27,553653	20,3063395	20,164889	22,6749605	20,785234	13,083834
Vitron	25,085586	29,74033	29,377455	28,0677903	17,6184465	22,811722
Irden	31,4400595	35,810755	40,350417	35,8670772	25,688186	30,3891495
Yassmine	23,4497815	23,5332675	27,719531	24,90086	12,0627955	16,783031
korifla	21,022584	24,1561476	20,478958	21,8858965	11,210721	19,1771
Marouane	29,3426855	16,788875	20,00176	22,0444402	19,7521525	5,06861
Isly	18,526273	22,43526	22,145231	21,035588	4,81052	3,420162
Massa	25,253107	22,898212	19,868142	22,6731537	7,244058	4,75215
Oum rabia	20,4252375	19,6140565	17,356197	19,1318303	6,2803195	4,4084845
Anouar	15,0064275	15,260097	15,421576	15,2293668	3,999351	3,718512
Tomouh	14,248202	14,188638	16,63162	15,02282	6,076832	3,436372
Waha	17,152797	16,2869025	14,3515595	15,9304197	2,5892985	3,2894645
Marjana	13,9232915	14,193675	13,645991	13,9209858	1,273194	1,2759825
Jahwar	13,5480875	16,685339	19,742334	16,6585868	2,282578	0,9451155

degree of rolling over the three years of study. In varieties where the rolling behavior varied with the crop year, the observed score was generally shifted by less than 1 (that is to adjacent indices in plus or minus directions in the classification scale) from the previous year's value. For instance, the variety Massa, a weak-rolling variety, was given a mean rolling score of 3 (one third of the leaf rolled) during the first two years, while in the third year its rolled leaf area decreased a bit and its mean rolling score became close to 2 (one fourth of the leaf rolled). Only 3 out of the 16 varieties showed inter-annual variations of rolling score higher than 1 unit (Figure 2A-D). These three varieties, Sebou, Isly and Jawhar, corresponded to high, medium and weak-rolling ones, respectively. Sebou and Isly displayed a higher rolling score by 1.5-2 during the first year as compared to the two other years, and Jawhar, a higher rolling score by 2.5 in the third year as compared to the first ones.

A ranking of the 16 varieties according to their mean rolling score over the three years is shown in Figure 2E. Two varieties, Marjana and Waha, could be sorted in the "no rolling" class (mean score <1; Table 3). Four varieties, Jawhar, Tomouh, Anouar, Massa, corresponded to the weak rolling class (1<mean score<3). Four varieties, Oum Rabia, Marouane, Isly, Yassmine, showed medium rolling (3<mean score<5), and the six last ones, Korifla, Sebou, Amjad, Vitron, 2777 and Irden, displayed high rolling (mean score >5).

Correlations between leaf rolling under water stress and preservation of agronomic performance

Possible correlation between the grain yield and the extent of leaf rolling under water stress in the different wheat varieties was examined (Figure 3). A highly

Table 6. Variance analysis (ANOVA) of yield in control (T1) and water stressed (T2) cultures.

Parameter*	Source: between years			Between varieties			Combined effect (year x variety)		
	df	F-value	P ($\alpha=5\%$)	df	F-value	P ($\alpha=5\%$)	df	F-value	P ($\alpha=5\%$)
Control yield	2	194,01	<0.001	15	234,44	<0.001	30	32,68	<0.001
Yield stress	2	148,12	<0.001	15	1399,19	<0.001	30	201,42	<0.001

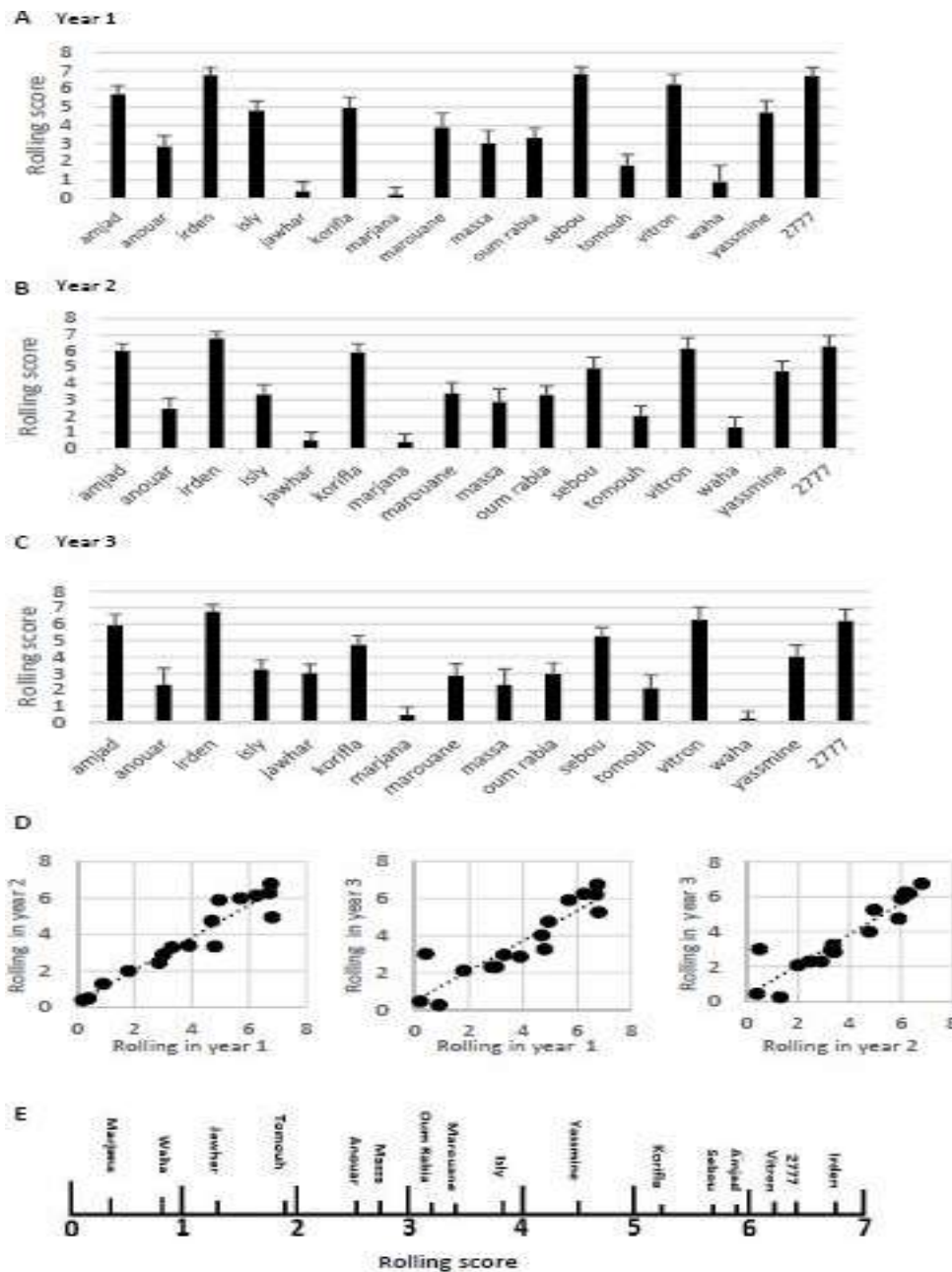


Figure 2. Leaf rolling index of 16 varieties of durum wheat subjected to water stress, over three crop years. Variation of flag leaf rolling among 16 varieties of durum wheat subjected to water stress in the first (A), second (B) and third (C) crop year. The rolling index was determined on 20 plants per variety randomly chosen. Data are means \pm SE. In panel D, variation among year of the leaf rolling index of the 16 varieties (D). Comparison between year 1 and year 2 (left), year 1 and year 3 (middle), year 2 and year 3 (right). In panel E, ranking of the 16 varieties of durum wheat according to their mean leaf rolling index over the 3 years.

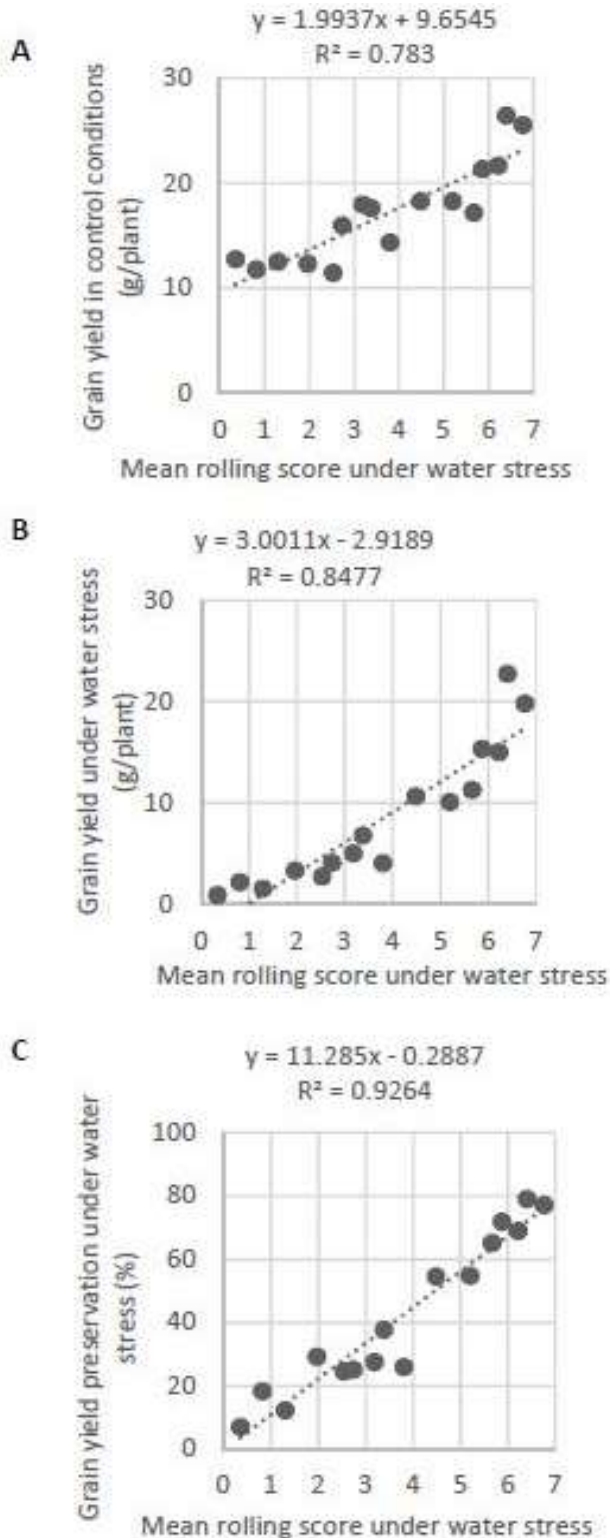


Figure 3. Correlation analysis between the grain yield of the 16 durum wheat varieties and the rolling index under water stress. The grain yield was determined each year for each variety in control (A) or water stress (B) conditions as in Fig. 1 and was averaged over the three campaigns. In panel C, correlation between the mean rolling index under water stress over the three campaigns and the grain yield preservation under water stress.

significant positive correlation ($R = 0.93$) was noted between the mean level of preservation of grain yield under water stress and the average leaf rolling score over the three campaigns (Figure 3C). The grain yield under water stress showed weaker correlation with the leaf rolling score ($R = 0.85$; Figure 3B) than the grain yield preservation under water stress. A positive correlation was also noted between the grain yield in well-irrigated plants and the leaf rolling score, but the strength of this correlation was the weakest ($R = 0.78$; Figure 3A).

The mean levels of preservation over the three campaigns of each of the grain yield parameters were found to be positively correlated with the mean leaf rolling score under water stress (Figure 4C-E). The preservation of the number of grains per ear and the number of ears per plant, as well as that of other agronomic parameters like the number of tillers and the height of plant at maturity showed strong correlations with the mean rolling score ($0.89 < R < 0.93$; Figure 4A-D). Only the preservation of the weight of grains showed weaker correlation with leaf rolling ($R = 0.74$; Figure 4E). A separate analysis of the three cropping campaigns confirmed the weaker correlation with leaf rolling for the preservation of grain weight in the two last years (Supplementary Figure 4). On the other hand, the lowest correlation with leaf rolling in the first year was found for the number of ears (Supplementary Figure 4).

DISCUSSION

The experimentation was conducted on a set of durum wheat varieties maintained at the National Gene Bank of Morocco (INRA, Settat). This set gathered varieties originating from different world areas, although essentially Mediterranean ones (and mostly Morocco), and were issued from breeding programs at work at different periods (<http://wheatatlas.org/varieties>) over the 20th century (oldest variety: Kyperounda "2777" released in 1956 in Cyprus; most recent varieties: Irden and Marouane released in 2003 by INRA Morocco). Most of the selected varieties have been released in the late 1980s and the 1990s, as a result of programs in which the objective of productivity increase and yield stabilization between years was associated with a reduction of the plant cycle duration and plant size (Nsarellah et al., 2011; Taghouti et al., 2017). These objectives led to varieties with strongly homogenized plant development and, owing to the reduction in plant cycle and biomass, tended to improve the tolerance to drought. A disparity in drought adaptation however remained in the durum wheat cultivars released during that period (Nsarellah et al., 2011), a specific objective of tolerance to abiotic stresses having been introduced as one of the most recent steps in breeding programs with released varieties more systematically tolerant to drought only since the beginning of the 21st century (Nsarellah

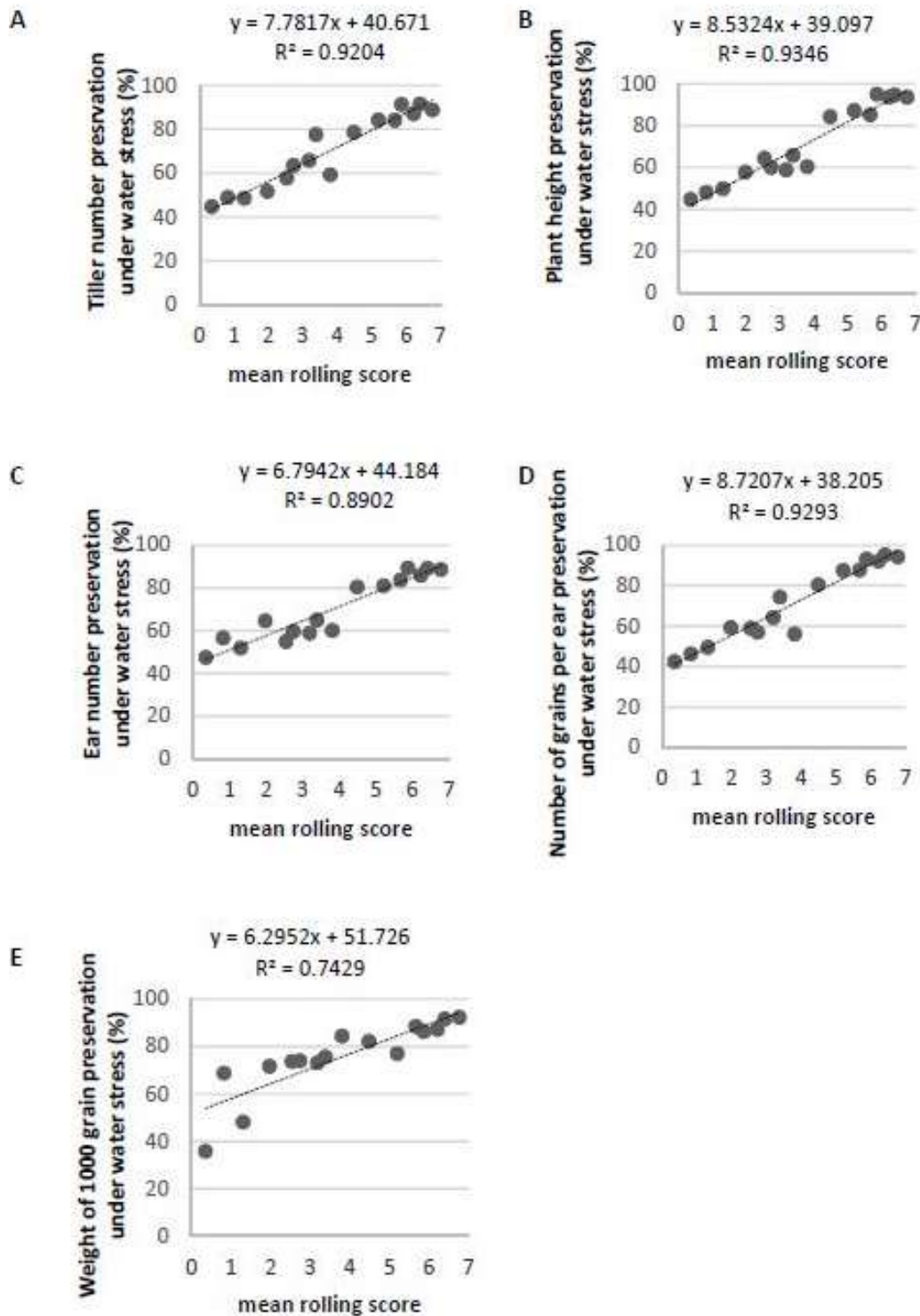


Figure 4. Correlation between the mean leaf rolling index and the maintaining of agronomical performances upon water stress within the panel of the 16 durum wheat varieties. The rolling indices correspond to those of Fig. 2D averaged over the three experimental campaigns. The preservation under water stress of the number of tillers (A), the plant height at maturity (B), the number of ears (C), grains per ear (D), and weight of 1000 grains (E), was determined by comparison with plants grown in parallel on the well-watered control parcel. In each experimental campaign, values of the different agronomical parameters were determined on twenty plants randomly chosen in each variety and each irrigation regime, and were averaged. Shown data correspond to the average over the three campaigns of mean values of preservation of performance under water stress determined each year.

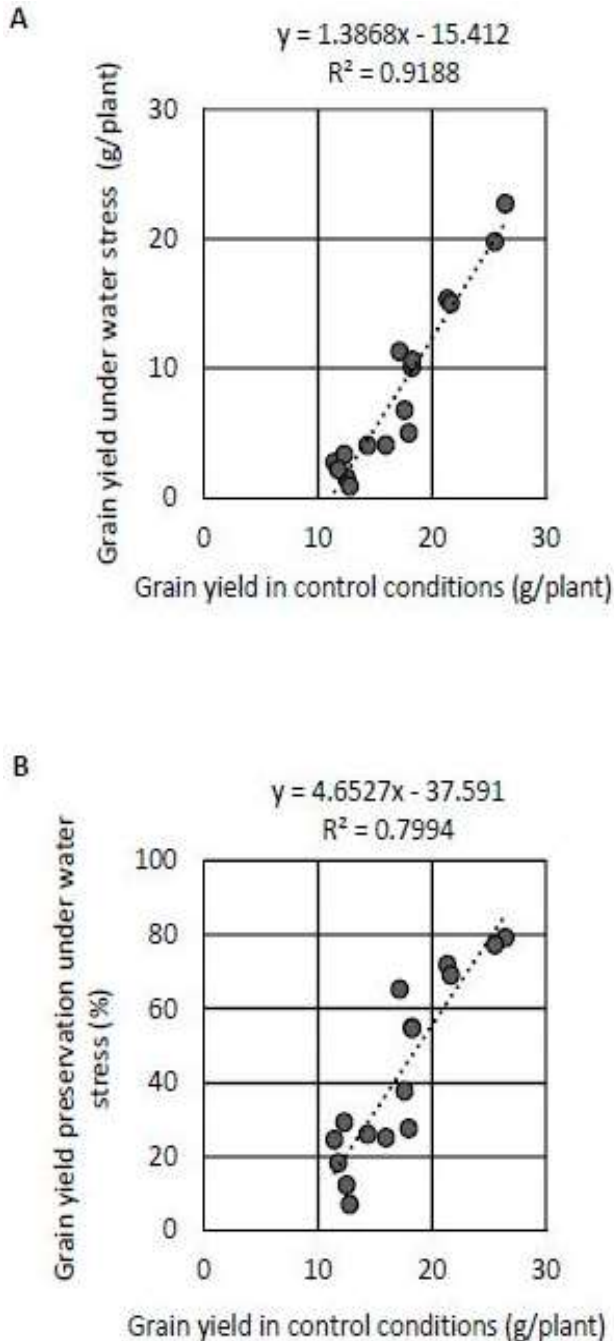


Figure 5. Analysis of correlation between the grain yield of the 16 durum wheat varieties in control and water stress conditions. Grain yield in control conditions was correlated to grain yield in water stress conditions in (A) and to grain yield preservation under water stress conditions in (B). Grain yield was determined as in Figure 3.

et al., 2011). The selected panel of 16 varieties of the present study displayed in our trial a large range of sensitivity to water stress with mean grain yield preservation over the three campaigns varying by a factor

of 12 between varieties (Figure 1 and Supplementary Figure 3). The grain yield under water stress in our panel of varieties appeared strongly correlated to that in control conditions (Figure 5; $R = 0.92$). This is in line with the assumption that selection for high yield over the years tend to associate characters of general dependability, the yield improvement being then based on the ability of the plant to overcome varying small or bigger stresses (Duvick, 2005; Tardieu, 2012).

The application of the one-week water stress widely affected the agronomic performances of the durum wheat varieties studied (Supplementary Table 3). All studied parameters (number of tillers, plant height, number of ears, number of grains, weight of grains) were affected, although slight variations in the level of sensitivity between the different parameters were noticed (e.g., decrease under water stress between 4.5 and 10% for the different parameters in the tolerant variety 2777, between 51 and 64% in the sensitive variety Marjana). The parameters that were the most affected (e.g., number of ears in 2777, number of grain per ear in Isly, and weight of grains in Marjana) depended on varieties. The water stress was applied at tillering. Grain yield is set up all over the plant cycle. At tillering is set up the number of tillers. Moreover, from the middle of tillering when the apex makes its floral transition and elaborates sketches of spikelets, the fertility of the ears starts being developed. Thus, a stress at tillering is expected to be able to affect different parameters of yield in relation to ear number and features. All the varieties from our panel were early or semi-early varieties, except 2777 which was classified as semi-late variety. A significant difference in the stage of embryonic ear development upon drought stress application in 2777 as compared to the other varieties may explain at least in part the low sensitivity of this variety to the applied water stress. In the other varieties, the quite similar cycles make it unlikely that differences in the developmental stage upon drought stress application would explain the strong differences observed between varieties in terms of subsequent agronomic performances. The observed strong differences between varieties in the sensitivity to the applied drought stress may denote differences in efficiency in water absorption of the water available for the crop or in its use (Royo et al., 2014). The response of the studied varieties to the imposed water stress appeared strongly linked to the ability of these varieties to manifest leaf rolling under water stress conditions (Figures 3 and 4). Leaf rolling in cereals is known as an adaptive response to water deficit in leaf tissues (O'Toole and Cruz, 1980; Kadioglu et al., 2012). Leaf rolling is believed to occur when the evaporative demand is no longer balanced by water uptake by the roots and the extent of rolling is often used as a marker of intensity of drought stress in cereal cultures (Riboldi et al., 2016). When leaf tissue

hydration is restored, the leaf unrolls. Upon rolling, by decreasing the leaf surface exposed to sunlight, the water loss by transpiration is reduced (O'Toole and Cruz, 1979). This also allows the plant, by limiting the direct illumination of leaf surface, to limit the heating of leaf tissues, harmful to cellular metabolism. In rice, it was as such, reported to improve photosynthetic efficiency and to delay leaf senescence (Richards et al., 2002; Richards et al., 2004; Zhang et al., 2009). It however reduces the available photosynthetic surface, which negatively affects the plant growth (Li et al., 2016 b).

Leaf shape (angle, width/area), which influences light capture and gas exchange capacity, belongs to the agronomic traits highly considered for potential in grain yield improvement (Yuan, 1997; Wang and Li, 2005; Moon et al., 2011). Leaf rolling, which controls the photosynthetic surface and the water status of the leaf, is one of the traits commonly considered in modern programs of cereal selection (Turner, 1982; Richards et al., 2002; Hu et al., 2009). In rice, a number of QTL of leaf rolling have been mapped (Price et al., 1997, Singh and Mackill 2008, Zhang et al., 2016). Little assessment of the impact of leaf rolling on productivity under water stress conditions is yet available in other cereals (wheat, sorghum, etc.) (Peleg et al., 2009; Bogale et al., 2011). However, for example, five leaf-rolling QTLs co-localizing with QTLs associated with productivity in a population of durum wheat crossed with emmer wheat were recently reported (Peleg et al., 2009).

In the studied panel of durum wheat varieties, leaf rolling positively correlated with the maintaining of growth (height at maturity) and with that of the grain yield parameters (Figures 3 and 4). Only the preservation of grain weight showed lower correlation with leaf rolling index (Figure 4, Supplementary Figure 4), which is in agreement with the period of application of the drought stress which induced the leaf rolling at early stage of plant and ear development. The strong positive correlation observed between the leaf rolling index and the maintaining of grain yield in plants subjected to water stress, may be explained by better preservation of the water in leaf tissues when rolling is stronger, thanks to the reduction of the surface of heated tissue and transpiration. This would help maintaining photosynthetic activity and metabolism during the critical period of water stress, allowing to preserve agronomic performance. Epidermal bull-shaped cells (so-called bulliform cells) are involved in the regulation of leaf rolling (Itoh et al., 2005; Li et al., 2010; Zou et al., 2011; Xiang et al., 2012). According to Willmer (1983), these cells serve as water storage. The loss of turgor pressure in these cells due to the lack of water causes a winding of the leaves. During drought, loss of moisture due to vacuoles causes bulliform cells to roll the leaves of many grass species as the two edges of the leaf fold together (Hsiao et al. 1984, Mouliia 1994, Price et al 1997). Once enough water is available, these cells expand and the leaves unfold

again. Folded leaves provide less sun exposure and, as a result, they receive less heat, which reduces transpiration and helps retain the remaining water in the plant. In addition, they also play a role in the development of developing leaves (Moore and Clarke, 1998). Thus, bulliform cells can be considered as a primary target in molecular selection, to modulate leaf rolling and unwinding in response to alternating wet and dry periods.

During water deficit, it may be possible that the water, coming from bulliform cells, contributes to the maintenance of the mesophyll cell functioning, thus allowing them to store photosynthetic assimilates (Bois et al., 1987). This could explain that varieties displaying strong rolling maintain at best agronomic performance. On the other hand, in varieties with low or no rolling under stress conditions, a decrease in transpiration via stomatal closure would cause tissue heating and slow down photosynthesis. In this case, both the water stress, the reduction of the photosynthetic capacity of the plant during this period of tillers developments and formation of the ears will penalize the yield. Based on the present results, leaf rolling is concluded to be one of the morphological parameters that can be used as powerful indicator of strong productive performance in semi-arid conditions, for pertinent selection of adapted wheat varieties.

Conclusion

Leaf rolling belongs to the traits commonly considered in modern programs of cereal selection for drought tolerance. Very few, and contradictory, results however exist on its impact on yield. Here, a water stress was applied at tillering and resulted in a decrease in height and number of stems and a reduction in the yield components in the sixteen varieties of durum wheat studied, thus affecting the final grain yield. These negative impacts of the water stress were much reduced in the varieties with strong rolling behavior. This provides evidence that leaf rolling can mitigate the effects of water deficit.

The agronomic parameters studied in our sixteen varieties of durum wheat revealed a significant variability according to the rolling group. The high-rolling varieties (Amjad, Vitron, 2777, and Irden) showed the best performances in terms of yield (number of ears per plant, number of grains per ear, and weight of grains) in both water stress and control conditions. This suggests that these varieties with high leaf rolling behavior are likely to display a general tolerance to environmental conditions. These varieties are thus promising for cultivation in arid and semi-arid zones. In these areas, high temperatures may also be a limiting factor in durum wheat production, which justifies the choice of both high-rolling and short-cycle varieties that escape drought and high temperatures at the end of the cycle (Karrou, 2003).

Future physiological and genetical investigations will allow to better understand the mechanisms underpinning leaf rolling and their contribution to drought resistance.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

ACKNOWLEDGEMENTS

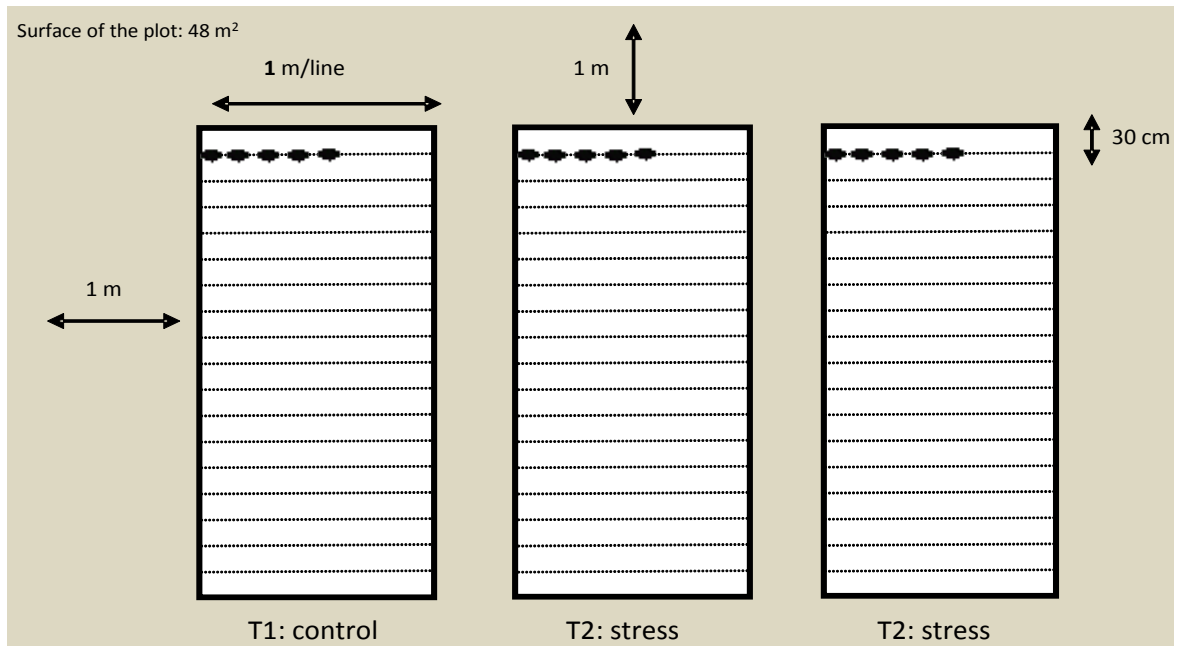
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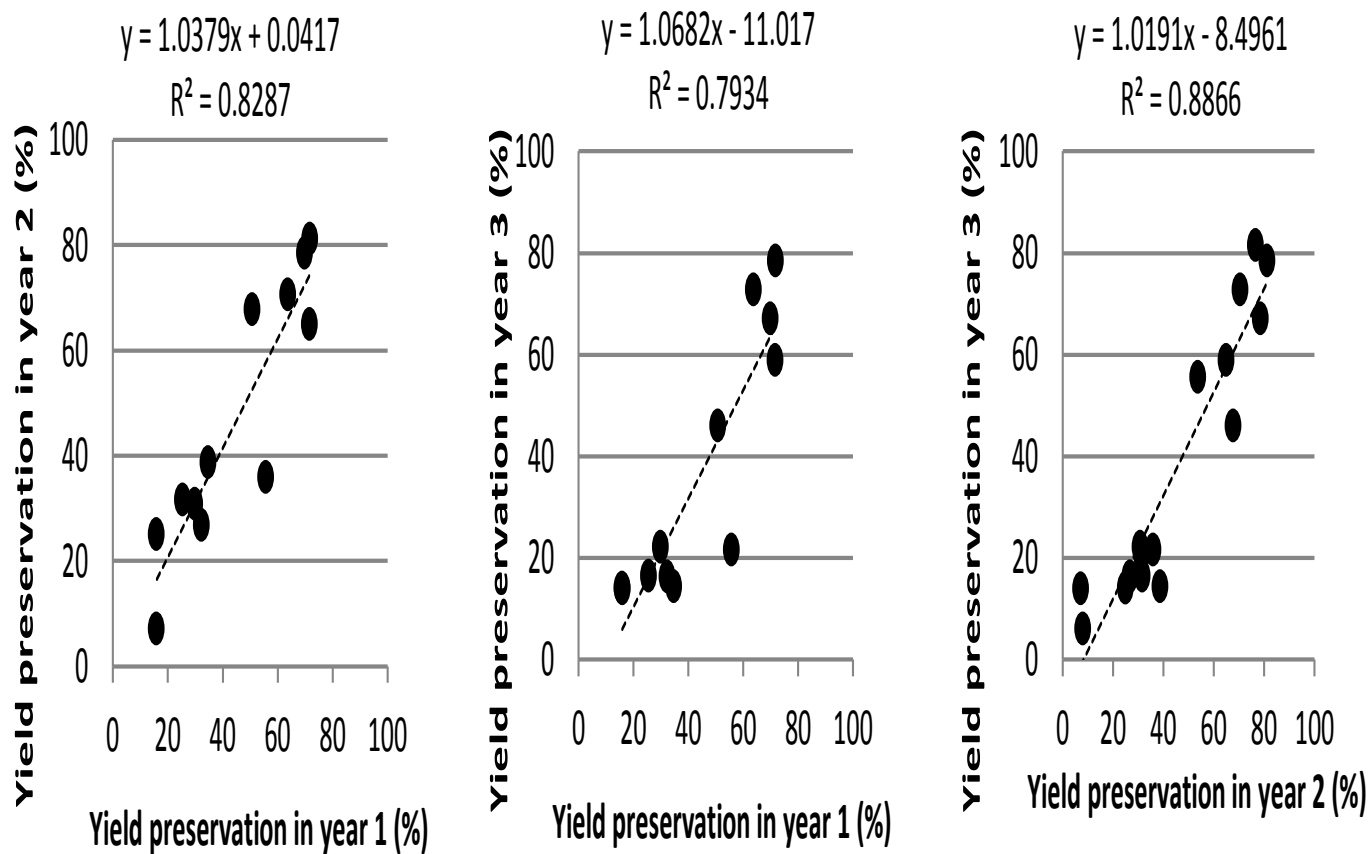
SUPPLEMENTARY FIGURES AND TABLES



Supplementary Figure 1. Scheme of the experimental plot. Sixteen varieties of durum wheat (Kyperounda ("2777"), Amjad, Anouar, Irden, Isly, Jawhar, Korifla, Marjana, Marouane, Massa, Oum Rabia, Sebou, Tomouh, Vitron, Waha and Yasmine) were sown on three identical parcels of 5.5 m² at Tamellalet (Marrakech region, CMV 408, Morocco), each parcel receiving all varieties. Each variety occupied one line, with random position in the parcel. Seeds were sown every 3.45 cm with 30 seeds per line, the lines being spaced by 30 cm. One parcel was watered all over the culture (T1 treatment: control) to fully compensate the mean evapotranspiration of the culture (ETM). In the two other parcels, plants were subjected to 1 week of water stress at tillering stage (T2 treatment: stress) with ETM compensated at only 75%, and besides this stress were watered like in the control parcel.



Supplementary Figure 2. Representative picture of the different leaf rolling classes. Flag leaf rolling level was assessed at the end of the water stress period, between 12 and 14 p.m.

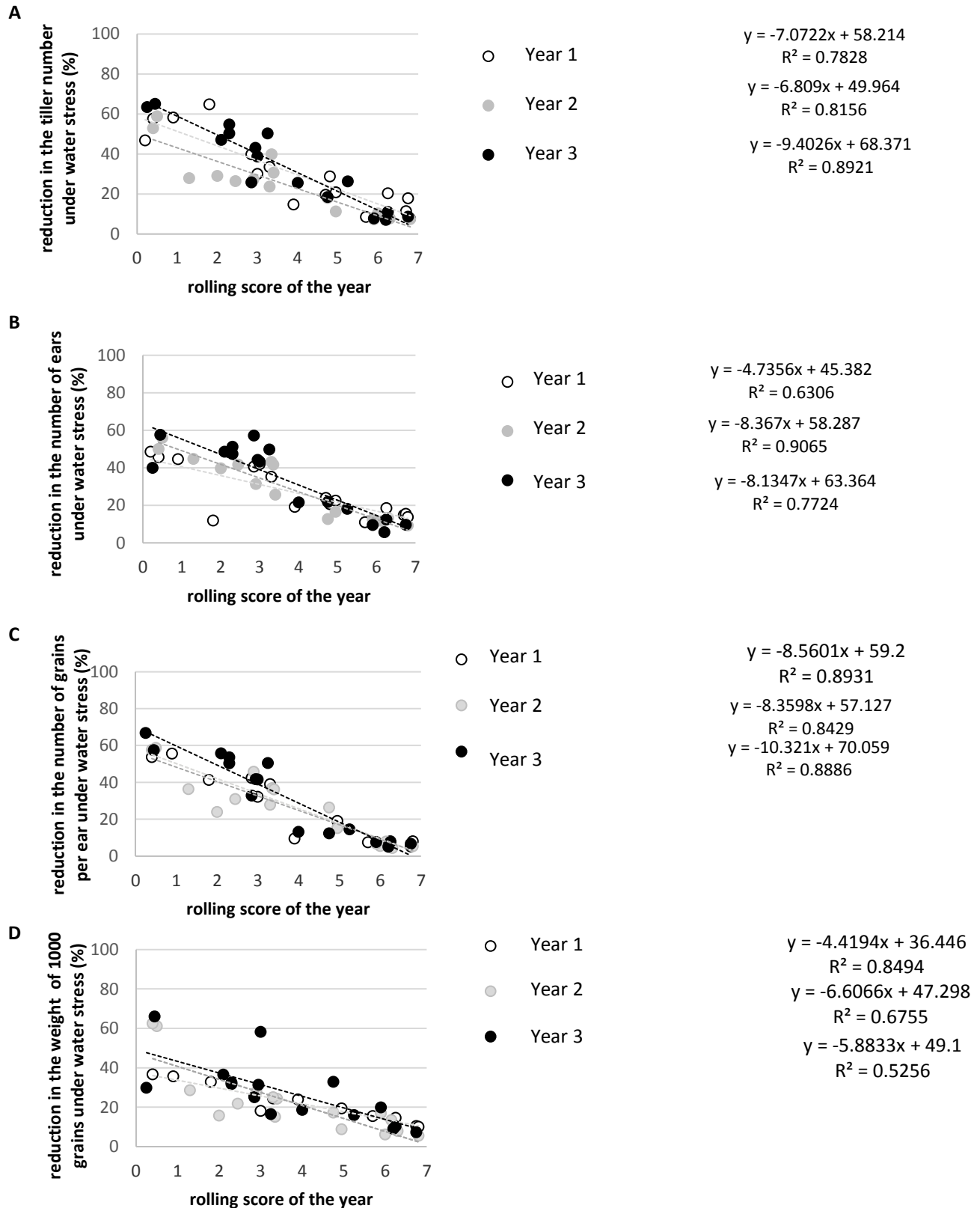


Supplementary Figure 3. Grain yield preservation of the 16 durum wheat varieties under water stress. The percentage of grain yield preservation under water stress was determined for each variety as $100 - (\text{yield in control conditions} - \text{yield in water stress}) / \text{yield in control conditions}$. Comparison between year 1 and year 2 (left), year 1 and year 3 (middle), and year 2 and year 3 (right). Grain yield data used for grain yield preservation calculation are those shown in Figure 1, determined using mean values of the number of ears per plant, the number of grains per ear and the grain weight, measured for each variety and treatment on 20 plants randomly chosen.

Supplementary Table 1. Climatic data recorded at the experimental station during the three crop years 2013-2014 to 2015-2016.

Crop year	2013-2014			2014-2015			2015-2016		
	Precipitation (mm)	T max (°C)	T min (°C)	Precipitation (mm)	T max (°C)	T min (°C)	Precipitation (mm)	T max (°C)	T min (°C)
December	20.8	19.1	4.8						
January	66.2*	17.5	4.7	20.5	16.9	3.6	8.6	21.8	5.0
February	17.0	17.5	4.8	10.5	15.7	4.1	31.8	19.5	4.5
March	37.0	22.0	7.7	80.6	22.9	8.6	42.2	20.5	5.5
April	30.7	27.5	11.7	7.4	25.4	11.9	5.6	24.3	8.8
May	1.8	31.6	16.5	18.5	32.0	15	6.8	28.6	12.6
June	12.6	33	15.0	33.5	33.0	17.7	0	34.4	15.6

*Main precipitations as storm after water stress application to the experimental culture.



Supplementary Figure 4. Correlation between the leaf rolling score specific to each year and the maintaining of agronomical performances upon water stress within the panel of the 16 durum wheat varieties. The rolling indices correspond to those of Figure 2A-C. The water stress-induced reduction in the number of stems (A), ears (B), grains (C), and weight of 1000 grains (D), was determined by comparison with plants grown in parallel on the well-watered control parcel. Data on twenty plants randomly chosen in each variety and each irrigation regime were averaged.

Supplementary Table 2. Mean variation over three years in the tiller number per plant in wheat varieties grown under control conditions (T1) or subjected to water stress (T2).

Variety	Year 1			Year 2			Year 3			Mean		
	T1	T2	% reduction	T1	T2	% reduction	T1	T2	% reduction	T1	T2	% reduction
2777	9.20 ^{cd} ±0.951	8.15 ^f ±0.99	11.40 ^{ab}	10.90 ^{cd} ±0.91	10.05 ⁱ ±0.95	7.60 ^a	12.05 ^h ±0.76	11.20 ^h ±0.83	6.80 ^a	10.7 ^a ±1.41	9.80 ^f ±1.51	8.55 ^a ±2.30
Amjad	9.95 ^{def} ±0.826	9.10 ^g ±0.97	8.55 ^a	9.25 ^{def} ±0.85	8.30 ^g ±0.92	9.80 ^a	11.55 ^{gh} ±0.94	10.55 ^{gh} ±1.14	8.30 ^a	10.25 ^a ±1.22	9.31 ^{ef} ±1.16	8.78 ^a ±0.98
Anouar	7.15 ^a ±1.089	4.30 ^b ±0.81	39.9 ^d	7.20 ^a ±0.89	5.30 ^{cd} ±0.57	25.35 ^c	10.40 ^{de} ±1.57	4.70 ^c ±0.66	53.60 ^e	8.23 ^a ±1.85	4.76 ^{abcd} ±0.50	39.16 ^{bcd} ±14.20
Irden	10.05 ^{ef} ±0.945	8.25 ^f ±0.86	17.90 ^a	10.10 ^{ef} ±0.64	9.35 ^h ±0.67	7.25 ^a	12.05 ^h ±0.89	11.00 ^h ±1.16	8.50 ^a	10.71 ^a ±1.13	9.53 ^f ±1.40	10.91 ^{ab} ±5.72
Isly	7.80 ^{ab} ±1.005	5.55 ^c ±0.61	27.35 ^c	10.15 ^{ab} ±0.99	6.10 ^e ±0.72	39.00 ^d	11.05 ^{ef} ±1.15	5.50 ^d ±0.61	49.70 ^{de}	9.66 ^a ±1.66	5.71 ^{abcde} ±0.32	38.68 ^{bcd} ±10.70
Jawhar	10.15 ^{ef} ±1.23	4.30 ^b ±0.74	57.00 ^f	8.15 ^{ef} ±0.75	3.35 ^a ±0.59	58.50 ^e	9.80 ^{cd} ±1.01	6.00 ^d ±0.97	38.00 ^c	9.36 ^a ±1.06	4.55 ^{abc} ±1.32	51.16 ^a ±11.24
Korifla	8.15 ^b ±1.23	6.45 ^d ±0.52	19.15 ^b	8.25 ^b ±0.72	7.65 ^f ±0.81	6.85 ^a	10.55 ^{def} ±1.09	8.60 ^f ±0.88	17.95 ^b	8.95 ^a ±1.38	7.56 ^{bcd} ±1.10	14.65 ^{ab} ±7.26
Marjana	7.90 ^{ab} ±1.021	4.20 ^b ±0.77	46.30 ^e	8.70 ^{ab} ±0.87	4.10 ^b ±0.55	52.50 ^e	9.15 ^{bc} ±0.87	3.20 ^a ±0.52	64.70 ^f	8.58 ^a ±0.65	3.83 ^{ab} ±0.55	54.5 ^a ±9.26
Marouane	10.85 ^f ±1.09	9.25 ^f ±1.02	14.30 ^{ab}	6.35 ^f ±0.99	4.40 ^b ±0.50	29.05 ^c	8.90 ^b ±0.78	6.60 ^e ±0.99	25.55 ^b	10.2 ^a ±2.21	6.73 ^{bcd} ±2.40	22.96 ^{abcd} ±8.19
Massa	9.00 ^c ±0.98	6.30 ^d ±0.74	29.35 ^c	10.25 ^c ±0.97	7.45 ^f ±1.09	26.85 ^c	11.05 ^{ef} ±1.32	5.50 ^d ±0.76	49.55 ^{de}	9.68 ^a ±1.00	6.41 ^{abcd} ±0.95	35.25 ^{abode} ±12.51
Oum.rabia	8.95 ^c ±1.06	5.95 ^{cd} ±0.89	32.85 ^{cd}	9.30 ^c ±1.13	7.10 ^f ±0.55	22.50 ^{bc}	11.95 ^{gh} ±1.19	6.80 ^e ±1.10	42.20 ^{cd}	9.95 ^a ±1.65	6.61 ^{bcd} ±0.56	32.51 ^{abode} ±9.70
Sebou	7.20 ^a ±1.06	6.10 ^{cd} ±0.86	14.55 ^{ab}	8.40 ^a ±1.23	7.45 ^f ±0.83	9.95 ^a	9.50 ^{bc} ±1.05	7.00 ^e ±0.97	25.05 ^b	7.96 ^a ±1.15	6.85 ^{bcd} ±0.66	16.51 ^{ab} ±7.76
Tomouh	10.10 ^{ef} ±1.45	3.55 ^a ±0.61	64.35 ^f	8.10 ^{ef} ±0.72	5.75 ^{de} ±0.72	27.95 ^c	7.75 ^a ±0.85	4.10 ^b ±0.72	46.40 ^{de}	9.31 ^a ±1.25	4.46 ^{abc} ±1.15	46.23 ^{cde} ±17.95
Vitron	8.10 ^b ±1.17	6.45 ^d ±0.69	18.90 ^b	9.40 ^b ±0.82	8.55 ^g ±0.76	8.60 ^a	11.35 ^{gh} ±0.81	10.10 ^g ±0.85	10.80 ^a	9.18 ^a ±1.66	8.36 ^{def} ±1.86	12.76 ^{ab} ±6.08
Waha	9.10 ^{cd} ±1.12	3.80 ^{ab} ±0.77	57.90 ^f	7.15 ^{cd} ±0.81	5.15 ^e ±0.67	27.00 ^c	8.20 ^a ±0.83	3.00 ^a ±0.45	63.00 ^f	8.8 ^a ±0.95	3.98 ^a ±1.11	49.3 ^{de} ±19.11
Yasmine	9.20 ^{cd} ±1.11	7.40 ^e ±0.51	18.35 ^b	8.90 ^{cd} ±1.07	7.30 ^f ±0.73	16.90 ^{ab}	11.95 ^{gh} ±1.05	8.90 ^b ±0.91	24.90 ^b	10.11 ^a ±1.71	7.86 ^{def} ±0.89	20.05 ^{abc} ±3.95

*Same letter indicates no difference between varieties with significance level $\alpha=5\%$.

Supplementary Table 3. Mean variation over three years in the plant height at maturity in wheat varieties grown under control conditions (T1) or subjected to water stress (T2).

Variety	Year 1			Year 2			Year 3			Mean		
	T1	T2	% reduction	T1	T2	%reduction	T1	T2	%reduction	T1	T2	%reduction
2777	100.45 ^b ±1.53	97.35 ^a ±3.57	3.15 ^a	105.90 ^j ±1.77	97.40 ^k ±4.46	8.00 ^a	102.50 ⁱ ±6.76	97.75 ^k ±5.98	4.60 ^{ab}	102.95 ^c ±2.75	97.5 ^d ±0.21	5.2 ^a ±2.55
Amjad	90.45 ^a ±1.79	86.05 ⁱ ±4.07	5.00 ^a	92.35 ^a ±1.56	86.20 ⁱ ±4.07	6.65 ^a	96.75 ^{gh} ±4.49	93.30 ^j ±4.96	3.55 ^a	93.18 ^{abc} ±3.231	88.51 ^{bcd} ±4.14	5.06 ^a ±1.55
Anouar	60.70 ^a ±1.21	45.30 ^d ±8.25	25.20 ^c	87.20 ^l ±1.19	58.45 ^e ±4.05	33.00 ^d	84.85 ^{cde} ±10.36	46.00 ^e ±5.68	44.75 ^e	77.58 ^{ab} ±14.66	49.91 ^a ±7.39	34.31 ^{bc} ±9.84
Irden	100.60 ^h ±1.14	94.50 ^g ±4.23	5.90 ^a	100.65 ⁱ ±1.22	93.35 ^j ±4.06	7.30 ^a	93.95 ^g ±6.96	88.25 ⁱ ±8.46	6.30 ^{ab}	98.4 ^{bc} ±3.85	92.03 ^{cd} ±3.32	6.5 ^a ±0.72
Isly	80.50 ^e ±1.43	56.05 ^e ±6.83	30.20 ^d	87.20 ^l ±1.50	63.60 ^f ±6.31	27.20 ^c	91.10 ^{ef} ±7.01	36.85 ^{bc} ±5.02	59.35 ^{gh}	86.26 ^{abc} ±5.36	52.16 ^a ±13.79	38.91 ^d ±17.75
Jawhar	70.90 ^c ±3.81	31.65 ^a ±2.53	54.85 ^f	75.00 ^c ±2.24	36.45 ^a ±3.88	51.30 ^g	69.80 ^a ±8.09	39.00 ^{cd} ±4.41	43.60 ^e	71.9 ^a ±2.74	35.7 ^a ±3.73	49.91 ^d ±5.75
Korifla	79.80 ^e ±1.05	61.95 ^f ±7.14	22.45 ^c	82.00 ^e ±1.21	76.90 ^h ±3.47	6.20 ^a	89.35 ^{def} ±5.33	80.50 ^h ±7.11	9.90 ^{bc}	83.716 ^{abc} ±5.00	73.11 ^{bc} ±9.83	12.85 ^{ab} ±8.51
Marjana	76.45 ^d ±1.57	35.65 ^b ±5.31	53.25 ^f	80.05 ^d ±1.93	41.25 ^b ±5.84	48.30 ^g	89.15 ^{def} ±5.85	32.70 ^b ±7.14	62.90 ^h	81.88 ^{abc} ±6.54	36.53 ^a ±4.34	54.81 ^d ±7.42
Marouane	85.20 ^f ±1.10	66.90 ^a ±9.08	21.25 ^c	67.55 ^a ±1.57	40.10 ^b ±4.67	40.50 ^e	87.20 ^{cde} ±4.43	50.70 ^d ±4.24	41.60 ^e	79.98 ^{ab} ±10.81	52.56 ^a ±13.49	34.45 ^{bc} ±11.44
Massa	77.60 ^d ±1.14	52.80 ^e ±5.39	31.75 ^d	83.20 ^e ±2.19	55.40 ^d ±8.45	33.45 ^d	90.55 ^{def} ±5.92	42.55 ^{de} ±3.20	52.80 ^f	83.78 ^{abc} ±6.49	50.25 ^a ±6.79	39.33 ^d ±11.69
Oum.rabia	70.90 ^c ±1.02	45.80 ^d ±5.36	35.05 ^{de}	100.25 ⁱ ±1.77	68.55 ^g ±3.91	31.80 ^d	94.70 ^g ±5.05	41.85 ^{de} ±6.90	55.70 ^g	88.61 ^{abc} ±15.59	52.06 ^a ±14.41	40.85 ^b ±12.96
Sebou	79.85 ^e ±1.38	73.50 ^h ±5.25	7.90 ^a	81.30 ^{de} ±1.26	68.85 ^g ±5.09	15.00 ^b	100.00 ^{hi} ±0	79.95 ^h ±7.62	20.15 ^d	87.05 ^{abc} ±11.23	74.1 ^{bc} ±5.57	14.35 ^{ab} ±6.15
Tomouh	66.75 ^b ±6.31	40.60 ^c ±3.76	38.40 ^e	70.85 ^b ±1.87	48.00 ^c ±5.87	32.25 ^d	75.05 ^b ±12.01	34.05 ^b ±6.48	53.30 ^f	70.88 ^a ±4.15	40.88 ^a ±6.97	41.31 ^d ±10.82
Vitron	90.50 ^g ±2.03	82.85 ⁱ ±6.07	8.35 ^a	94.15 ^h ±1.72	88.15 ⁱ ±2.73	6.20 ^a	89.90 ^{def} ±5.11	85.65 ⁱ ±6.18	4.70 ^{ab}	91.51 ^{abc} ±2.30	85.55 ^{bcd} ±2.65	6.41 ^a ±1.83

Supplementary Table 3. Contd.

W ^{eh} _a	66.45 ^b ±6.42	40.90 ^c ±4.98	37.90 ^e	83.25 ^e ±7.99	45.20 ^c ±3.47	45.15 ^f	82.35 ^c ±6.48	25.40 ^a ±5.23	68.95 ⁱ	77.35 ^{ab} ±9.45	37.16 ^a ±10.41	50.66 ^d ±16.24
Y ^a _{ssmine}	81.50 ^a ±1.76	68.05 ^g ±5.92	16.30 ^b	87.50 ^f ±1.10	71.70 ^g ±3.90	17.90 ^b	84.30 ^{cd} ±8.00	73.35 ^g ±7.86	13.00 ^c	84.43 ^{abc} ±3.00	71.03 ^b ±2.71	15.73 ^{ab} ±2.49

*Same letter indicates no difference between varieties with significance level $\alpha=5\%$.

Supplementary Table 4. Mean variation over three years in the number of ears per plant in wheat varieties grown under control conditions (T1) or subjected to water stress (T2).

Variety	Year 1			Year 2			Year 3			Mean		
	T1	T2	% reduction	T1	T2	% reduction	T1	T2	% reduction	T1	T2	% reduction
2777	8.45 ^{ef} ±0.99	7.20 ^{gh} ±0.89	14.45 ^{ab}	9.10 ^{de} ±0.85	7.90 ^f ±1.02	13.00 ^a	11.40 ^f ±0.59	10.75 ⁱ ±0.63	5.50 ^a	9.65 ^a ±1.55	8.61 ^e ±1.88	10.98 ^a ±4.80
Amjad	7.75 ^{ode} ±0.85	6.90 ^{efg} ±1.11	10.90 ^a	8.30 ^{cd} ±0.65	7.35 ^e ±0.87	11.10 ^a	10.60 ^e ±0.82	9.60 ^h ±0.82	9.20 ^a	8.88 ^a ±1.51	7.95 ^e ±1.67	10.40 ^a ±1.04
Anouar	6.65 ^{ab} ±0.58	3.95 ^a ±0.60	40.10 ^{cd}	7.20 ^b ±1.39	4.20 ^b ±0.41	39.25 ^c	8.80 ^c ±0.69	4.30 ^{bc} ±0.92	50.60 ^{ef}	7.55 ^a ±1.11	4.15 ^{ab} ±0.18	43.31 ^d ±6.32
Irden	9.10 ^f ±1.41	7.70 ^h ±1.12	14.65 ^{ab}	9.25 ^e ±0.71	8.40 ^f ±0.75	8.80 ^a	11.40 ^f ±0.68	10.30 ⁱ ±0.86	9.35 ^a	9.91 ^a ±1.28	8.80 ^e ±1.34	10.93 ^a ±3.23
Isly	6.30 ^a ±0.73	5.00 ^{bc} ±0.56	19.60 ^{ab}	10.20 ^f ±1.00	5.95 ^d ±0.75	41.05 ^c	10.15 ^e ±0.58	5.10 ^d ±0.71	49.70 ^e	8.88 ^a ±2.23	5.35 ^{abcd} ±0.52	36.78 ^{bcd} ±15.49
Jawhar	8.65 ^{ef} ±1.22	4.70 ^{bc} ±0.47	44.85 ^d	7.60 ^{bc} ±1.04	3.35 ^a ±0.58	55.10 ^d	8.10 ^b ±0.85	4.60 ^{cd} ±0.68	42.45 ^{de}	8.11 ^a ±0.52	4.21 ^{ab} ±0.75	47.46 ^d ±6.71
Korifla	7.35 ^{bcd} ±1.03	5.70 ^d ±0.57	20.95 ^{ab}	8.40 ^{de} ±0.68	7.35 ^e ±0.58	11.90 ^a	8.95 ^{cd} ±0.51	7.00 ^a ±0.72	21.40 ^c	8.23 ^a ±0.81	6.68 ^{bcd} ±0.86	18.08 ^{abc} ±5.35
Marjana	7.10 ^{bc} ±1.02	3.65 ^a ±0.74	47.20 ^d	6.20 ^a ±1.05	3.10 ^a ±0.64	48.00 ^{cd}	8.00 ^b ±0.64	3.40 ^a ±0.50	57.15 ^f	7.10 ^a ±0.9	3.38 ^a ±0.27	50.78 ^d ±5.52
Marouane	9.15 ^f ±1.18	7.40 ^{gh} ±1.14	18.25 ^{ab}	6.25 ^a ±0.91	4.65 ^b ±0.74	23.95 ^b	9.10 ^{cd} ±0.85	3.90 ^{ab} ±0.30	57.05 ^f	8.16 ^a ±1.66	5.31 ^{abcd} ±1.84	33.08 ^{abcd} ±20.95
Massa	8.35 ^{ef} ±0.87	4.85 ^{bc} ±0.58	41.60 ^{cd}	9.25 ^e ±0.96	6.35 ^d ±0.48	30.60 ^b	9.50 ^d ±0.76	5.00 ^d ±0.64	46.90 ^e	9.03 ^a ±0.60	5.40 ^{abcd} ±0.82	39.70 ^{cd} ±8.31
Oum.rabia	8.10 ^{de} ±0.71	5.25 ^{cd} ±0.63	35.05 ^c	9.05 ^{de} ±1.23	5.15 ^c ±0.87	42.25 ^c	8.95 ^{cd} ±0.82	5.00 ^d ±0.85	43.50 ^{de}	8.70 ^a ±0.52	5.13 ^{abcd} ±0.12	40.26 ^{cd} ±4.56
Sebou	8.05 ^{de} ±0.68	6.95 ^{efg} ±0.82	13.25 ^{ab}	7.25 ^b ±1.20	6.05 ^d ±0.60	15.00 ^a	9.10 ^{cd} ±0.64	7.45 ^e ±0.99	17.80 ^{bc}	8.13 ^a ±0.92	6.81 ^{bcd} ±0.70	15.35 ^{ab} ±2.29
Tomouh	6.35 ^a ±0.48	5.60 ^d ±0.68	11.50 ^a	7.05 ^b ±0.94	4.25 ^b ±0.55	38.75 ^c	8.75 ^c ±1.01	4.50 ^{cd} ±0.51	48.05 ^e	7.38 ^a ±1.23	4.78 ^{abc} ±0.71	32.76 ^{abcd} ±18.99
Vitron	8.10 ^{de} ±1.33	6.60 ^{ef} ±0.82	17.00 ^{ab}	9.05 ^{de} ±0.60	8.00 ^f ±0.56	11.20 ^a	10.05 ^e ±0.75	8.80 ^g ±0.89	12.20 ^{ab}	9.06 ^a ±0.97	7.80 ^{de} ±1.11	13.46 ^{ab} ±3.10
Waha	8.20 ^{de} ±1.00	4.55 ^b ±0.68	43.80 ^{cd}	7.50 ^b ±0.88	4.15 ^b ±0.93	43.10 ^c	6.00 ^a ±0.56	3.60 ^a ±0.50	39.50 ^d	7.23 ^a ±1.12	4.10 ^{ab} ±0.47	42.13 ^{cd} ±2.30
Yassmine	8.35 ^{ef} ±0.87	6.35 ^e ±0.58	22.90 ^b	8.30 ^{cd} ±0.57	7.25 ^e ±0.71	12.30 ^a .90	10.20 ^e ±0.76	8.00 ^f ±0.85	20.90 ^c	8.95 ^a ±1.08	7.20 ^{cd} ±0.82	18.70 ^{abc} ±5.63

*Same letter indicates no difference between varieties with significance level $\alpha=5\%$.

Supplementary Table 5. Mean variation over three years in the number of grains per ear in wheat varieties grown under control conditions (T1) or subjected to water stress (T2).

Variety	Year 1			Year 2			Year 3			Mean		
	T1	T2	%reduction	T1	T2	%reduction	T1	T2	%reduction	T1	T2	%reduction
2777	62.10 ⁱ ±1.20	n.a.	n.a.	65.00 ^f ±2.40	62.20 ^j ±2.01	4.30 ^a	56.95 ^{fg} ±2.23	54.10 ^j ±2.19	4.85 ^a	61.35 ^f ±4.07	58.15 ^{abc} ±5.72	4.57 ^a ±0.39
Amjad	60.60 ⁱ ±1.04	56.15 ⁱ ±4.24	7.40 ^a	60.70 ^{de} ±1.17	57.40 ^{hi} ±1.90	5.40 ^a	54.00 ^{ef} ±2.61	49.90 ⁱ ±3.69	7.55 ^{abc}	58.43 ^{def} ±3.83	54.48 ^c ±4.01	6.78 ^a ±1.20
Anouar	42.70 ^c ±1.30	24.60 ^c ±	42.15 ^d	41.20 ^{ab} ±1.43	28.50 ^d ±4.87	30.75 ^{cd}	38.05 ^a ±3.56	18.90 ^{bc} ±1.11	49.80 ^{fg}	40.65 ^a ±2.37	24.00 ^{abc} ±4.82	40.90 ^a ±9.58
Irden	60.95 ⁱ ±1.31	57.80 ⁱ ±3.84	5.20 ^a	61.45 ^e ±1.31	58.20 ^j ±2.64	5.30 ^a	58.55 ^g ±3.60	54.70 ⁱ ±4.90	6.45 ^{ab}	60.31 ^{ef} ±1.55	56.90 ^c ±1.91	5.65 ^a ±0.69
Isly	49.35 ^e ±2.05	n.a.	n.a.	39.95 ^a ±1.79	25.25 ^c ±6.23	36.60 ^d	42.80 ^{bc} ±9.63	21.20 ^c ±3.28	47.90 ^f	44.03 ^{abc} ±4.81	23.22 ^{ab} ±2.86	40.31 ^a ±3.71

Supplementary Table 5. Contd.

Jawhar	35.70 ^a ±0.92	16.55 ^b ±1.14	53.65 ^e	40.80 ^{ab} ±1.54	16.90 ^a ±1.94	58.40 ^f	51.50 ^e ±3.17	30.10 ^e ±2.10	41.15 ^e	42.66 ^{ab} ±8.06	21.18 ^{abc} ±7.72	51.06 ^a ±8.91
Korifla	50.50 ^f ±1.19	40.90 ^g ±3.59	18.90 ^b	58.85 ^d ±1.38	54.90 ^h ±3.56	6.80 ^a	50.90 ^e ±2.82	44.65 ^g ±2.97	12.25 ^{bc}	53.41 ^{bcd} ±4.70	46.81 ^{abc} ±7.24	12.65 ^a ±6.05
Marjana	45.40 ^d ±1.27	n.a.	n.a.	49.30 ^c ±6.13	20.95 ^b ±2.52	56.40 ^f	39.45 ^{ab} ±5.48	16.80 ^{ab} ±2.30	56.60 ^h	44.71 ^{abc} ±4.96	18.87 ^a ±2.93	56.5 ^a ±0.14
Marouane	57.85 ^h ±1.59	52.40 ^{±1.23}	9.30 ^a	50.90 ^c ±5.38	32.50 ^b ±2.50	35.25 ^d	52.70 ^e ±2.53	35.40 ^f ±5.11	32.55 ^d	53.81 ^{bcd} ±3.60	40.10 ^{abc} ±10.75	25.70 ^a ±14.26
Massa	54.15 ^g ±1.56	36.80 ^f	31.80 ^c	50.55 ^c ±1.46	27.45 ^{cd} ±4.65	45.65 ^e	40.85 ^{ab} ±3.13	19.00 ^{bc} ±3.14	53.00 ^{gh}	48.51 ^{abcde} ±6.87	27.75 ^{abc} ±8.90	43.48 ^a ±10.76
Oum.rabia	51.25 ^f ±1.25	31.30 ^e	38.85 ^d	51.50 ^c ±1.46	37.20 ^f ±4.06	27.65 ^c	41.30 ^{ab} ±2.47	24.10 ^d ±3.25	41.50 ^e	48.01 ^{abcd} ±5.81	30.86 ^{abc} ±6.56	36.00 ^a ±7.35
Sebou	57.45 ^h ±2.96	53.00 ^{±3.19}	7.65 ^a	50.10 ^c ±1.44	42.55 ^g ±3.63	15.05 ^b	52.80 ^e ±4.69	45.20 ^g ±3.34	13.90 ^c	53.45 ^{bcd} ±3.71	46.91 ^{abc} ±5.43	12.20 ^a ±3.98
Tomouh	45.15 ^d ±1.95	26.55 ^d ±2.50	41.05 ^d	42.80 ^b ±4.85	32.60 ^e ±2.13	23.15 ^c	45.15 ^{cd} ±3.95	20.00 ^c ±2.02	55.30 ^{gh}	44.36 ^{abc} ±1.35	26.38 ^{abc} ±6.30	39.83 ^a ±16.10
Vitron	51.60 ^f ±1.81	47.50 ^h ±4.05	8.00 ^a	59.20 ^d ±1.54	54.55 ^h ±3.15	7.85 ^a	58.65 ^g ±3.92	54.25 ^f ±2.84	7.35 ^{abc}	56.48 ^{cdef} ±4.23	52.10 ^{bc} ±3.98	7.73 ^a ±0.34
Waha	38.90 ^b ±1.41	17.30 ^b ±1.55	55.45 ^e	40.45 ^a ±1.50	25.80 ^{cd} ±7.25	35.95 ^d	47.45 ^d ±3.64	15.80 ^a ±1.70	66.50 ⁱ	42.26 ^{ab} ±4.55	19.63 ^{abc} ±5.39	52.63 ^a ±15.46
Yassmine	54.10 ^g	n.a.	n.a.	50.90 ^c ±1.55	37.55 ^f ±4.54	26.00 ^c	54.75 ^{ef} ±6.34	47.55 ^f ±4.53	12.55 ^{bc}	53.25 ^{bcd} ±2.06	42.55 ^{abc} ±5.0	19.27 ^a ±9.51

*Mean on years 2 and 3 only

n.a.: no grain in T2 plants due to fungal infection

Same letter indicates no difference between varieties with significance level $\alpha=5\%$.

Supplementary Table 6. Mean variation over three years in the weight of 1000 grains in wheat varieties grown under control conditions (T1) or subjected to water.

Variety	Year 1			Year 2			Year 3			Mean		
	T1	T2	% reduction	T1	T2	% reduction	T1	T2	% reduction	T1	T2	% de reduction
2777	42.00 ^{bc} ±3.28	n.a.	n.a.	42.00 ^{ef} ±1.71	38.67 ^f ±1.59	8.00 ^{ab}	50.00 ^c ±1.86	45.33 ^f ±3.54	9.00 ^{ab}	44.66 ^a ±6.08	42 ^{ab} ±4.7093	8.5 ^a ±0.70
Amjad	41.33 ^{bc} ±9.05	34.67 ^g ±2.05	14.00 ^a	43.00 ^f ±3.53	40.33 ^f ±2.15	6.00 ^a	40.33 ^{ab} ±11.38	32.00 ^d ±2.94	18.33 ^{abc}	41.55 ^a ±2.30	35.66 ^{ab} ±2.64	12.77 ^a ±4.59
Anouar	37.66 ^b ±6.59	28.00 ^{de} ±2.31	24.33 ^{abc}	34.67 ^{ab} ±2.12	27.33 ^{bc} ±1.81	21.67 ^{bcd}	40.00 ^{ab} ±4.15	27.33 ^{bc} ±3.57	31.67 ^{cd}	37.44 ^a ±3.78	27.55 ^{ab} ±4.50	25.89 ^a ±7.01
Irden	39.00 ^{bc} ±0.28	35.00 ^g ±3.53	10.33 ^a	42.33 ^{ef} ±3.48	40.00 ^f ±2.60	5.66 ^a	46.00 ^{bc} ±6.06	42.67 ^f ±3.28	6.67 ^a	42.44 ^a ±3.78	39.22 ^b ±3.46	7.55 ^a ±0.91
Isly	37.33 ^b ±9.81	n.a.	n.a.	35.67 ^{abc} ±0.60	30.00 ^{bcd} ±1.39	15.00 ^{abcd}	39.33 ^{ab} ±3.06	33.00 ^d ±2.52	16.33 ^{abc}	37.44 ^a ±4.5	36.5 ^{ab} ±4.0	15.66 ^a ±0.94
Jawhar	29.00 ^a ±0.06	18.33 ^b ±0.84	36.67 ^c	38.67 ^{bcd} ±2.24	15.00 ^a ±2.90	61.33 ^e	39.67 ^{ab} ±0.94	16.67 ^a ±3.64	58.00 ^e	35.78 ^a ±5.03	16.66 ^{ab} ±2.64	52 ^a ±7.87
Korifla	39.33 ^{bc} ±1.90	31.67 ^g ±4.87	19.00 ^{abc}	40.33 ^{cdef} ±1.53	33.67 ^{de} ±1.41	17.00 ^{abcd}	44.67 ^{abc} ±1.14	29.67 ^{bcd} ±1.40	33.00 ^{cd}	41.44 ^a ±6.50	31.67 ^{ab} ±11.67	23 ^a ±15.74
Marjana	39.33 ^{bc} ±3.76	n.a.	n.a.	39.33 ^{bcd} ±5.15	14.67 ^a ±0.03	62.00 ^e	43.33 ^{ab} ±3.36	15.00 ^a ±2.53	66.00 ^e	40.66 ^a ±1.73	14.83 ^a ±0.23	64 ^a ±2.82
Marouane	39.67 ^{bc} ±6.12	30.00 ^{ef} ±3.15	23.67 ^{abc}	37.67 ^{bcd} ±2.01	28.67 ^{bc} ±3.82	24.00 ^{cd}	41.33 ^{ab} ±0.77	31.33 ^{cd} ±1.59	25.00 ^{bcd}	39.55 ^a ±7.37	30 ^{ab} ±7.21	24.22 ^a ±6.98
Massa	36.00 ^{ab} ±0.88	29.33 ^{ef} ±1.11	18.00 ^{ab}	36.33 ^{abcd} ±2.65	26.33 ^b ±3.32	28.00 ^d	37.33 ^{ab} ±3.32	25.33 ^b ±1.64	32.00 ^{cd}	36.55 ^a ±3.60	26.99 ^{ab} ±5.03	26 ^a ±7.39
Oum.rabia	44.00 ^{bc} ±0.88	33.33 ^g ±3.88	24.33 ^{abc}	41.33 ^{def} ±0.97	31.33 ^{de} ±2.12	25.00 ^{cd}	44.00 ^{abc} ±2.94	30.33 ^{cd} ±3.63	31.00 ^{cd}	43.11 ^a ±4.04	31.66 ^{ab} ±2.08	26.77 ^a ±5.63
Sebou	44.66 ^{bc} ±2.24	40.33 ^h ±1.07	9.67 ^a	38.00 ^{bcd} ±3.10	34.67 ^e ±1.41	8.67 ^{ab}	35.33 ^a ±3.54	29.67 ^{bcd} ±0.64	15.67 ^{abc}	39.33 ^a ±9.29	34.89 ^{ab} ±7.23	11.33 ^a ±1.77
Tomouh	39.33 ^{bc} ±1.20	26.00 ^{cd} ±1.48	32.67 ^{bc}	32.33 ^a ±2.52	27.33 ^{bc} ±0.56	15.33 ^{abcd}	40.67 ^{ab} ±1.44	25.67 ^b ±0.95	36.67 ^d	37.44 ^a ±4.58	26.33 ^{ab} ±8.50	28.22 ^a ±13.61
Vitron	48.67 ^c ±4.00	41.67 ^h ±0.57	14.67 ^a	35.00 ^{abc} ±1.69	30.33 ^{bcd} ±0.32	13.33 ^{abc}	43.67 ^{abc} ±3.22	39.33 ^e ±2.39	10.00 ^{ab}	42.44 ^a ±5	37.11 ^{ab} ±3.60	12.66 ^a ±2.53
Waha	38.00 ^b ±3.76	24.33 ^c ±1.54	35.33 ^{bc}	40.33 ^{cdef} ±0.92	29.00 ^{bc} ±2.03	28.33 ^d	38.33 ^{ab} ±3.37	27.00 ^{bc} ±1.63	29.67 ^{cd}	38.88 ^a ±2.30	26.77 ^{ab} ±2.08	31.11 ^a ±2.05
Yassmine	35.33 ^{ab} ±3.04	n.a.	n.a.	37.33 ^{bcd} ±2.51	30.67 ^{bcd} ±1.34	17.00 ^{abcd}	41.00 ^{ab} ±8.57	33.67 ^d ±0.95	17.00 ^{abc}	37.88 ^a ±3.05	32.17 ^{ab} ±2.12	17.0 ^a ±0

*Mean on years 2 and 3 only; n.a.: no grain in T2 plants due to fungal infection; Same letter indicates no difference between varieties with significance level $\alpha=5\%$.