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Root and shoot growth, water use and water use efficiency of spring durum wheat under early-season drought

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Abstract – One of the common features of the Mediterranean climate of North Africa is the uncertainty of rainfall immediately after durum wheat (*Triticum durum* Desf.) emergence, leading to early-season drought. Impacts of drought during wheat reproductive development have been thoroughly investigated, while studies of early-season drought are lacking. The objectives of the research reported here were to examine genotypic differences for some morphological traits in response to early-season drought, and to determine the association of these traits with water use, water use efficiency in producing grain (WUE_g) and dry matter (WUE_{dm}). Experiments were conducted under field conditions on a Vertic Calicixerol. Four cultivars and two advanced lines of spring durum wheat were subjected to four water regimes, including a well-irrigated control and three water stress treatments. The three water stress treatments were imposed by withholding water during the period from emergence to either the onset, middle or the end of tillering. Subsequently, irrigation was used to provide adequate soil moisture for the remainder of the growing season. Total water use, WUE_g, and WUE_{dm} were weakly associated with root length density. Under drought stress conditions WUE_g and WUE_{dm} were positively associated with relative growth rate under stress, relative growth rate upon recovery and shoot dry matter yields early in the season. To develop new cultivars with improved early vigor, vegetative biomass and WUE_g, as proved in this study, wheat breeders need to utilize parent materials with considerable improvements in these characteristics. (© Inra/Elsevier, Paris.)

wheat / early-season drought / shoot and root growth / water use efficiency

Résumé – Croissance racinaire et aérienne, utilisation de l'eau et efficience de l'utilisation de l'eau chez le blé dur de printemps en conditions de sécheresse de début de cycle. Une des caractéristiques du climat Méditerranéen de l'Afrique du Nord est l'incertitude des précipitations immédiatement après l'émergence du blé dur (*Triticum durum*

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Desf.), entraînant une sécheresse de début de cycle (SDC). L'impact de la sécheresse durant la phase reproductive du blé a suscité beaucoup d'études, alors que très rares sont les études qui se sont intéressées à la SDC. Les objectifs de cette étude étaient d'examiner des différences génotypiques concernant certains traits morphologiques en réponse à une SDC et de determiner l'association de ces traits avec l'utilisation de l'eau (WU), l'efficience d'utilisation de l'eau pour la production du grain (WUE_g) et de la matière séche totale (WUE_{dm}). Les expérimentations ont été conduites au champ sur un sol Vertic Calicixerol. Quatre cultivars et deux lignées avancées du blé dur de printemps ont été soumis à quatre régimes hydriques, incluant un témoin adéquatement irrigué et trois niveaux de stress hydriques. Les niveaux de stress hydrique ont été imposés en empêchant l'alimentation hydrique durant la période s'étalant de l'emergence jusqu'au début, mi-, ou la fin du travail du sol. Des irrigations ont été apportées ultérieurement aprés la fin de chaque période de stress pour maintenir une alimentation hydrique adéquate tout au long de la saison de croissance. La quantité d'eau totale utilisée, WUE_g, and WUE_{dm} ont été faiblement associées à la densité racinaire. Sous des conditions de stress hydrique, WUE_g et WUE_{dm} ont été positivement associées avec le taux de croissance relative(RGR) sous stress, RGR durant la reprise, et la production de matière séche au début de cycle. Pour développer de nouvaux cultivars capables de tolérer une SDC et ayant une vigueur de départ , une biomasse végétative, et une WUE_g élevées, comme cette étude le montre, les améliorateurs du blé auront besoin de matériel parental possédant ces caractéristiques. (© Inra/Elsevier, Paris.)

blé / sécheresse de début de cycle / croissance aérienne / croissance racinaire / utilisation efficace de l'eau

1. INTRODUCTION

Under the rainfed farming systems of the arid and semiarid areas of the Mediterranean basin, economic and stable gains in food production should be achieved through more efficient use of water. Improved drought resistance should, therefore, be a major objective in plant breeding programs for crops grown in these regions.

In rainfed systems, research on individual crops has shown that the efficiency of water use can be considerably enhanced by manipulating the balance between the two components of water use, transpiration and evaporation, through agronomic management [7–9], and germplasm modification [28, 29].

In water-limited Mediterranean environments, direct soil evaporation is a major source of water loss, and losses as high as 75 % of the seasonal evapotranspiration have been reported in northern Syria [9], and as high as 48 % in semiarid regions of Morocco [30]. Most of this evaporative loss occurs early in the season, when the crop biomass and ground cover are limited [8, 25]. It may be that the best approach to improving drought resistance in this context is to select plants with the ability to establish rapidly in cool temperatures under appropriate agronomic management techniques [8, 19]. Consequently, yields may be increased by increasing the proportion of water transpired during winter, and this can be achieved genetically through early vigor. Turner and Nicholas [27] found that vigorous early growth results in high dry matter yields at anthesis and improved grain yields with no decrease in harvest index (HI). Similar results were found by Van Oasterom and Acevedo [27, 28] and Whan et al. [31]. Other studies suggest no consistent relationship between early vigor and grain yield depending on the prevailing environment conditions [1, 24, 25, 10].

Certainly, root characteristics are largely influenced by the prevailing edaphic and climatic conditions. Nevertheless, many of these characteristics have been shown to be under genetic control, and they are quantitatively inherited [20].

Breeding for increased WUE is frequently suggested as a desirable characteristic for drought tolerance [4], although Sinclair et al. [26] questioned the extent to which exploitable variation exists in this variable. Siddique et al. [25] showed that WUE_g, defined as the amount of dry grain mass produced per unit of water transpired, increased substantially from old to modern wheat cultivars in Mediterranean environments. The improved WUE_g in modern wheat cultivars was associated with faster development, earlier flowering, longer duration of grain filling, improved canopy structure and high HI. Similarly López-Casteñada and Richards [18] found genotypic differences in bread wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.) in WUE_g and WUE_{dm}. More dry matter partitioned to the shoots at the expense of roots, and cool-temperature vigor have been advocated as promising traits for improving WUE [21, 22].

In water-limited Mediterranean environments, information on changes in root pattern and shoot growth in spring durum wheat under early-season drought stress are lacking, especially under field conditions. The relationships of root and shoot growth to water use and water use efficiency of spring durum wheat under early-season drought is not fully understood.

The objectives of this study were to determine the effect of variation in the duration of drought stress during the period from emergence to the end of tillering on shoot and root growth, water use and water use efficiency in spring durum wheat.

2. MATERIAL AND METHODS

Field experiments were conducted during the 1994–1995 (1995) and 1995–1996 (1996) growing seasons at the National institute of agricultural research experiment station at Sidi El Aydi (31° 15' N latitude, 7° 30' W longitude) near Settat, Morocco. The plot sites had been in a wheat-fallow rotation for the previous 6 years and were considered generally typical of semi-arid regions of Morocco. The soil type was a Vertic Calcixerol and had a depth of 120 cm.

In each experiment the field design was a split-plot arrangement of treatments within a randomized complete block with three replications. Water regimes were allocated to the main plots and cultivars to the subplots. Each experimental unit consisted of 12 rows, 2 m in length. The inter-row spacing was 17 cm. The distance between two subplots within the main plot was 0.5 m. The experiments included six spring durum wheat (*Triticum durum* Desf.) cultivars representing a range of phenotypic variation in maturity, date to heading, height, adaptation zone, yield potential and date of release. 'Keyperounda' is tall, late cultivar more adapted to irrigated and more favorable dryland environments. 'Karim', 'ACSAD 65' and 'Marzak' were released more recently. Karim is more adapted to favorable conditions; and ACSAD 65 is an early cultivar adapted to semiarid conditions, where terminal drought is frequent; Marzak is also an early maturing cultivar, which has a wide adaptation. LA V17 and LA V18 are advanced breeding lines recommended for arid and semiarid conditions and both have resistance to some insects and plant diseases. Four water regimes including a control, which was frequently irrigated, and three stress treatments were included in this study.

The planting dates were 12 December 1994 and 1 November 1995. Variation in seed weight and germination among cultivars was used to adjust seeding rates to 250 viable seed m^{-2} for each cultivar so that near uniform stands could be obtained. A small-plot grain drill was used in seeding all the plots. To avoid a Hessian fly (*Mayetiola destructor* Say) infestation, Furadan 5G (2,3-dihydro-2,2-dimethyl-7-benzofuranyl methyl-carbamate) was used at a rate of 25 kg ha^{-1}. Weed control was accomplished using Certrol H (4-hydroxy-3,5 diiodonezontrile) at a rate of 3 L ha^{-1}. Fertilizers at a rate of 40 kg ha^{-1} of nitrogen as ammonium nitrate and 60 kg ha^{-1} of phosphorus as super triple phosphate were applied at planting time, and 30 kg ha^{-1} of nitrogen as urea was top dressed at the end of the tillering stage. To achieve a near uniform emergence and stand establishment for all cultivars, all plots received an irrigation of 50 mm after planting on 13 December in 1994 and on 6 November in 1995.

The three water stress regimes consisted of applying the first post-emergence irrigation at either the onset of tillering (low stress), mid-tillering (medium stress), or the end of tillering (severe stress). The onset of tillering was determined visually by observing the appearance of a tiller at the axil of the first leaf of the main shoot. The end of tillering was considered achieved when the first node was detectable at the base of the main shoot. The onset, middle and end of tillering correspond approximately to stages 2, 3 and 4 of the Feeckes scale [16], respectively. Water-stressed plots were shielded from precipitation by polyethylene sheets, placed on iron frames, when needed. Subsequent irrigations were used to provide adequate amount of available soil water for the remainder of the growing season after the end of the water stress period in each water stress regime. The low, medium and severe treatment plots were first rewatered on 10 and 26 January, and 7 February in the 1995 growing season, and on 28 November and 6 and 18 December in the 1996 growing season, respectively.

Soil water content, to a depth of 120 cm in 30-cm increments, was determined gravimetrically at planting, just prior to the first rewatering for each treatment, at anthesis, and at physiological maturity. The water balance method [18] was used to calculate evapotranspiration (ET), and the related water use efficiency (WUE). Runoff was ignored because plots were level, and no drainage below the root zone was also assumed. Capillary rise was neglected because the water table is deep (20 m). Total ET was computed as the sum of total rainfall received during the period considered, the amount of irrigation water applied, and the change in soil water content in the 120-cm profile that occurred between the start and the end of the considered period. Most of the root system was found in the 120-cm soil profile.

Plant density was determined 2 weeks after emergence on two 1-m sections of row for each subplot. Plants were harvested from a 0.5-m section of row at selected dates during the growing season for aerial dry matter yield determination. Plant samples were oven-dried to constant dry weight at 70 °C for 48 h and weighed. Aerial dry matter yield harvests were conducted at the stages coinciding with the termination of the three stress treatments in each plot to assess the relative growth rate (RGR). Subsequent harvests were taken at booting, anthesis and maturity. RGR was calculated as the rate of dry matter accumulation per unit of existing mass. Average RGR was calculated on a thermal time basis. Average RGR was calculated from time t_1 to t_2 as:

$RGR = (\log_e W_2 - \log_e W_1) / (t_2 - t_1)$ where W_1 and W_2 are the values of dry mass yields (g m^{-2}) at t_1 and t_2, respectively [14]. Daily thermal unit (TU) was calculated from daily maximum (T_{max}) and minimum (T_{min}) air temperatures as follows:

$TU = [(T_{max} + T_{min})/2] - T_b$. The base temperature ($T_b$) was 0 °C [2]. Daily thermal units were summed to provide accumulated TU.

At the beginning, middle and end of tillering, and at anthesis, soil samples were taken with a 7.6-cm diameter probe at depths of 0–30, 30–60 and 60–90 cm. Roots in each sample were separated from soil by washing. Root length was estimated with a root image analyzer (Decagon Devices, Inc., Pullman, Washington 99163). Root length density was calculated as root length per unit of soil volume. Soil samples for root measurements were from within the row in the same 0.5-m sections where shoot plant samples were taken.

Grain and straw yields were determined from a harvested area of 1 m^2. WUE_g was calculated as the amount of dry grain mass produced per unit of water evapotranspired. WUE_{dm} was calculated as the amount of total above-ground dry matter per unit of water evapotranspired.

Analysis of variance was used to evaluate the effects of treatments and their interaction. Statistical differences among treatment means for all variables were evaluated using Fisher's least significant difference test ($\alpha = 0.05$ confidence level). Associations among variables were determined using Pearson's simple correlation test.

3. RESULTS

3.1. Climatic conditions

Rainfall during the period from December through May of the 1995 cropping season was 80 mm, 30 % of the long-term average. Almost half of this seasonal precipitation was received during April, and no rain fell during the period between planting and end of tillering. Mean temperatures were relatively high during the first 2 months of the growing season, averaging 17 °C, compared to the long-term average (12 °C). Reference ET, calculated based on the FAO version of the Blaney-Criddle method, during the 1995 growing season was relatively low early in the season averaging 3.5 mm day^{-1}, then increased steadily and reached a maximum of 6.7 mm day^{-1} during the reproductive phase.

The 1996 growing season was more favorable for wheat growth and development. Rainfall during the period from November through April was 398.5 mm, 35 % above the long-term average. Seventy five millimeters were received during the period from planting to the end of tillering, and 63 % of total rainfall was concentrated during December and January. The 1996 growing season was relatively warmer during the vegetative growth, and both minimum and maximum temperatures were favorable for vegetative production. Reference ET during the 1996 growing season was relatively low during the entire vegetative growth period averaging 3.8 mm day^{-1}, then increased steadily and reached a maximum of 5.3 mm day^{-1} during the reproductive phase.

3.2. Soil moisture conditions

Profiles of volumetric water content of the soil in 30-cm depth increments at the end of each period of water stress in 1995 and 1996 are presented in *figure 1*. At the end of the low water

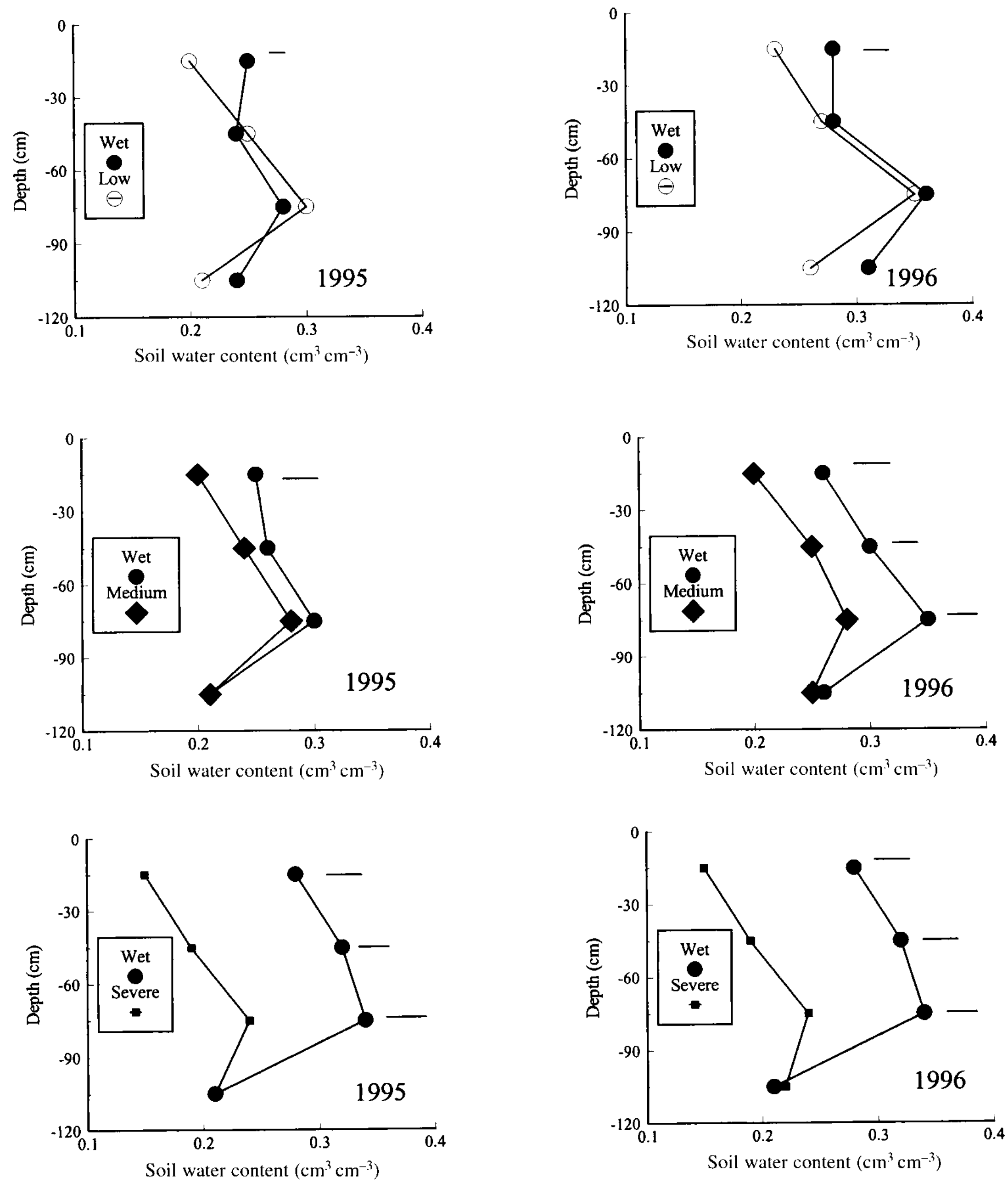

Figure 1. Soil water content at four different depths at the end of each period of water stress during the 1995 and 1996 growing seasons.

stress period the major differences among water regimes were detected at the top soil layer (0–30 cm). Relatively higher soil moisture levels were observed at depths below 30 cm. The reduction in soil moisture content in the upper soil layer between the wet and low water-stress treatments was significant and quite similar in both growing seasons averaging a value of 16%. At the end of the medium-stress period, differences between water regimes became more pronounced especially at the 0–30 and 30–60 cm depths. Results from both years were quite similar. Volumetric soil water content at the top soil layer approached the wilting point of 0.17 g g^{-1}, determined using the pressure plate apparatus method [6], at the end of the severe stress period. At this period, soil water content in all three upper soil layers under severe water stress conditions were significantly below those under the wet regime.

3.3. Phenology

Thermal time to reach each development stage was similar in both 1995 and 1996 growing seasons for each cultivar. Within each year, thermal time to reach the onset of tillering and mid-tillering were the same for all cultivars. Differences among cultivars were observed at the end of tillering and revealed two contrasting groups. ACSAD 65, Marzak, and LA V18 reached the end of tillering earlier than Keyperounda, Karim and LA V17. Consistent differences among cultivars became larger and more apparent thereafter. ACSAD 65 showed early phenological development compared with the other cultivars, while Keyperonda, the earlier-released tall cultivar, exhibited late phenological development.

3.4. Vegetative growth

3.4.1. Shoot dry matter accumulation and relative growth rate

In both growing seasons, the accumulation of above-ground dry matter and the relative growth rate (RGR) were significantly sensitive to the varying water stress treatments imposed (*tables I* and *II*). Values of RGR were in general higher in 1996 than in 1995. The magnitude of the reduction in above-ground dry matter yields was positively associated with the duration of the drought stress period. In both growing seasons variation in vegetative growth among cultivars was substantial. Although cultivars responded differently to the water regimes imposed, several consistent patterns emerged. Keyperounda and LA V18 accumulated more dry matter under the wettest conditions, compared to the other cultivars. LA V17 and Marzak accumulated more dry matter under the driest conditions compared with the other cultivars. In general, ACSAD 65 accumulated the least dry matter under both well-watered and stressed conditions. Marzak and LA V17 maintained the highest RGR under water stress conditions, while the lowest RGR values were recorded for Keyperounda and LA V18.

In both years rewatering resulted in recovery of dry matter accumulation (*tables II* and *III*). The magnitude of recovery was negatively associated with the duration of water stress. Thus RGR in the low and medium water stress treatments were similar to that in the wet treatment. RGR values of plants that had experienced drought stress during the period from emergence to the end of tillering were markedly below those observed under the wet treatment. Thus a severe stress resulted in a significant reduction in RGR not only during the water stress period, but during the recovery period as well. Marzak and LA V17, the two cultivars that exhibited the highest RGR and dry mass yields under the severe stress, were able to maintain the highest RGR and dry mass yields after rewatering. ACSAD 65 and LA V18, the two cultivars that were the most adversely affected by the severe water stress, exhibited the lowest values of RGR and dry matter yields after rewatering.

3.4.2. Root length density

Similar trends were observed in both growing seasons (*tables IV* and *V*). At the onset of tillering

Table I. Total dry matter yields of six durum wheat cultivars at the end of tillering under severe water stress, and at anthesis after rewatering for well-irrigated control and water stress treatments during the 1995 and 1996 growing seasons.

	1995				1996			
	End of tillering		Anthesis		End of tillering		Anthesis	
	†Control	Stress	Control	Stress	Control	Stress	Control	Stress
	g m^{-2}							
Keyperounda	107.5	44.1	892.6	352.2	154.1	76.4	967.3	496.5
Karim	94.3	37.9	759.6	371.2	98.1	68.1	903.1	508.7
ACSAD 65	96.4	34.5	558.1	231.3	120.3	73.7	706.9	421.8
Marzak	104.3	48.3	695.5	420.3	117.3	81.7	920.5	534.3
LA V17	90.6	48.5	641.6	500.1	110.0	82.9	885.1	593.7
LA V18	104.2	34.4	668.0	268.9	109.7	78.0	854.5	446.1
$LSD_{0.05}$ WR	4.7***		146.6**		4.6***		87.1***	
$LSD_{0.05}$ C	3.6***		46.6***		8.1***		28.1***	
$LSD_{0.05}$ WRxC‡	7.1***		93.2*		16.1***		56.2***	

*, **, *** Significant at the 0.05, 0.01 and 0.001 probability levels, respectively.
† Water stress treatment was imposed by withholding water during the period from emergence through the end of tillering.
‡ Indicates LSD values for comparison of cultivar means within a water regime.

Table II. Relative growth rates (RGR) of six wheat cultivars at two different development stages for well-irrigated control and water stress treatments during the 1995 and 1996 growing seasons.

	1995				1996			
	Onset of tillering		End of tillering		Onset of tillering		End of tillering	
	†Control	Stress	Control	Stress	Control	Stress	Control	Stress
	g g^{-1} (100 degree $d)^{-1}$							
Keyperounda	0.40	0.09	0.47	0.29	0.43	0.32	0.52	0.35
Karim	0.29	0.20	0.44	0.31	0.46	0.33	0.42	0.34
ACSAD 65	0.58	0.14	0.57	0.31	0.51	0.37	0.55	0.38
Marzak	0.72	0.39	0.58	0.38	0.63	0.51	0.51	0.41
LA V17	0.68	0.35	0.52	0.36	0.60	0.47	0.47	0.40
LA V18	0.39	0.11	0.52	0.28	0.43	0.32	0.44	0.39
$LSD_{0.05}$ WR	0.09***		0.02***		0.05***		0.05**	
$LSD_{0.05}$ C	0.12***		0.02***		0.01***		0.03**	
$LSD_{0.05}$ WRxC‡	NS		0.04***		0.01**		0.06*	

*, **, *** Significant at the 0.05, 0.01 and 0.001 probability levels, respectively.
† Water stress treatment was imposed by withholding water during the period from emergence through the indicated stage of development.
‡ Indicates LSD values for comparison of cultivar means within a water regime.

Table III. Relative growth rates of six wheat cultivars during the recovery period for well-irrigated control and water stress treatments during the 1995 and 1996 growing seasons.

	1995 growing season				1996 growing season			
	RGR end of Tillering - Boot stage							
	†Control	WSot	WS_{mt}	WS_{et}	Control	WS_{ot}	WS_{mt}	WS_{et}
	$g\ g^{-1}$ (100 degree d)$^{-1}$							
Keyperounda	0.24	0.19	0.17	0.09	0.27	0.20	0.25	0.20
Karim	0.20	0.26	0.21	0.13	0.32	0.26	0.30	0.24
ACSAD 65	0.20	0.21	0.20	0.07	0.23	0.23	0.27	0.23
Marzak	0.22	0.23	0.22	0.10	0.32	0.32	0.27	0.22
LA V17	0.25	0.26	0.22	0.14	0.33	0.25	0.29	0.22
LA V18	0.19	0.25	0.15	0.10	0.31	0.30	0.25	0.21
$LSD_{0.05}$ WR		0.05***				0.04**		
$LSD_{0.05}$ C		0.04***				0.02**		
$LSD_{0.05}$ WR*C‡		0.07***				0.03*		

*, **, *** Significant at the 0.05, 0.01 and 0.001 probability levels, respectively.
† WS_{ot}, WS_{mt} , WS_{et} denote water stress treatments imposed by withholding water during the period from emergence to either the onset, middle, or the end of tillering, respectively.
‡ Indicates LSD values for comparison of cultivar means within a water regime.

(end of the low water stress period) water stress did not significantly affect root length density; but significant differences were found among cultivars. Results obtained at the end of tillering (end of the severe water period) root length density in the top soil layer was greatly reduced for Keyperounda and Karim, slightly reduced for LA V17, and unchanged for ACSAD 65, Marzak and LA V18 as compared to well-watered conditions. LA V17 tended to maintain the highest root length density across all water regimes in the 0–30-cm zone. Differences among cultivars and among water regimes in the deeper soil layer (30–60 cm), even though statistically significant, were quite small with a general tendency for all cultivars to have higher root length density under severe water stress conditions as compared to wet and low water stress conditions.

During the recovery period, root length density at anthesis was highest for the top soil layer where significant cultivars and water regime differences were detected (*table V*). Thus, at this depth, root length density was significantly reduced only by a severe water stress. Differences in root length density between the latest (Keyperounda, Karim and LA V17) and the earliest flowering cultivars (ACSAD 65, Marzak and LA V18) were clearly detected especially under wet, low and medium water regimes. In considering the deeper soil layers (30–60 cm), cultivar and water regime effects were in general not significant.

3.5. Water use and water use efficiency

Similar trends in water use and water use efficiency were observed in both years (*table VI*). With increasing water stress duration, there was a significant reduction in total water consumption, with relatively small differences among cultivars. In both years, WUE_g and WUE_{dm} were significantly

Table IV. Root length density at different soil depths for six durum wheat cultivars at two different stages of developement for well-irrigated control and water stress treatments during the 1995 and 1996 growing seasons.

	Stage of development					
	†Onset of tillering		End of tillering			
	¶ Control	Stress	Control		Stress	
	Depth (cm)					
	0–30	0–30	0–3	30–60	0–30	30–60
	$cm\ cm^{-3}$					
	1995 growing season					
Keyperounda	0.54	0.55	1.06	0.04	0.76	0.10
Karim	0.51	0.52	1.11	0.04	0.78	0.06
ACSAD 65	0.45	0.45	0.86	0.02	0.85	0.03
Marzak	0.49	0.55	0.82	0.06	0.82	0.04
LA V17	0.63	0.65	1.17	0.02	1.10	0.06
LA V18	0.30	0.30	0.75	0.03	0.69	0.07
$LSD_{0.05}$ WR	NS		0.05***			0.01**
$LSD_{0.05}$ C	0.03***		0.03***			0.01***
$LSD_{0.05}$ WR*C‡	0.06*		0.06*			0.02**
	1996 growing season					
Keyperounda	0.60	0.57	1.10	0.06	0.81	0.07
Karim	0.63	0.60	1.17	0.06	0.86	0.07
ACSAD65	0.52	0.50	0.92	0.03	0.89	0.06
Marzak	0.57	0.57	0.90	0.01	0.86	0.04
LA V17	0.72	0.73	1.20	0.03	1.27	0.07
LA V18	0.39	0.35	0.79	0.05	0.79	0.07
$LSD_{0.05}$	NS		0.05***			0.01**
$LSD_{0.05}$ C	0.02***		0.03			0.01***
$LSD_{0.05}$ WR*C‡	0.03*		0.059			0.01**

*, **, *** Significant at the 0.05, 0.01 and 0.001 probability levels, respectively.
† Meaurements were taken at the end of each period of water stress.
¶ Water stress treatments were imposed by withholding water during the period from emergence through the indicated stage of development.
‡ Indicate LSD values for comparison of cultivar means within a water regime.

ly lower for the severe stress level as compared to the other treatments. Overall results from both years showed that the highest yielding cultivars across all levels of water stress (LA V17, Marzak and Karim) showed the highest WUE_g and WUE_{dm}. Under extreme soil water shortage, LA V17 and Marzak had the highest WUE_g and WUE_{dm} and showed the least reductions in both variables as compared to the other cultivars.

4. DISCUSSION

Cultivars used in this study were classified in two groups. LA V17, Marzak and Karim were relatively drought resistant. Keyperounda, ACSAD 65 and LA V18 were relatively drought susceptible. Greater WUE_g for LA VI7 and Marzak across all levels of water stress appeared to be the result of a

Table V. Root length density at anthesis at different depths, after rewatering, for well-irrigated control and water stress treatments during the 1995 and 1996 growing seasons.

	Depth							
	0–30 cm				30–60 cm			
	†Control	WS_{ot}	WS_{mt}	WS_{et}	Control	WS_{ot}	WS_{mt}	WS_{et}
	cm cm^{-3}							
	1995 growing season							
Keyperounda	3.33	2.86	3.09	1.84	0.08	0.37	0.14	0.10
Karim	2.96	2.98	3.21	1.97	0.12	0.28	0.13	0.14
ACSAD 65	1.68	1.60	2.04	1.48	0.69	0.28	0.18	0.07
Marzak	1.36	1.50	1.55	1.19	0.27	0.08	0.12	0.11
LA V17	2.83	2.99	2.04	2.07	0.10	0.19	0.26	0.20
LA V18	2.02	1.88	1.99	1.39	0.44	0.12	0.28	0.14
$LSD_{0.05}$ WR		0.42				NS		
$LSD_{0.05}$ C		0.14***				NS		
$LSD_{0.05}$ WR*C‡		0.28**				NS		
	1996 growing season							
Keyperounda	3.85	3.42	3.20	2.79	0.15	0.32	0.23	0.13
Karim	3.87	3.60	3.48	2.82	0.17	0.27	0.21	0.15
ACSAD 65	2.31	2.38	2.44	2.12	0.43	0.24	0.21	0.09
Marzak	2.25	2.23	2.13	1.86	0.20	0.11	0.15	0.11
LA V17	3.77	3.44	3.22	2.85	0.14	0.20	0.25	0.17
LA V18	2.58	2.72	2.39	2.31	0.33	0.19	0.29	0.16
$LSD_{0.05}$ WR		0.19*				NS		
$LSD_{0.05}$ C		0.14***				NS		
$LSD_{0.05}$ WR*C‡		0.27**				NS		

*, **, *** Significant at the 0.05, 0.01 and 0.001 probability levels, respectively.
† WS_{ot}, WS_{mt} , WS_{et} denote water stress treatments imposed by withholding water during the period from emergence to either the onset, middle or the end of tillering, respectively.
‡ Indicates LSD values for comparison of cultivar means within a water regime.

high kernel number per spike, high spike number and more efficient dry matter distribution [12]. Under stressed conditions, grain yield was more strongly associated with WUE_g (r = 0.95, $P < 0.001$) than with total water use (r = 0.67, $P < 0.05$). Similarly, biological yield was more strongly associated with WUE_{dm} (r = 0.96, P < 0.0.01) than with total water use (r = 0.58, $P < 0.05$). Therefore, the main factor contributing to the greater above-ground dry matter and grain yields of the resistant cultivars [12] was a greater WUE; thus confirming earlier results reported by López-Castañeda and Richards [18].

Higher WUE was principally achieved through high RGR and early vigor, and optimal flowering date. Actually, the drought-resistant cultivars, compared with the susceptible ones, were characterized by a higher RGR and dry matter accumulation during the early vegetative growth period under stress and upon rewatering. Thus the results support the

Table VI. Total water consumption (WU), water use efficiency for grain yield (WUE_g), and water use efficiency for total above-ground dry matter (WUE_{dm}) of six durum wheat cultivars for well-irrigated control and severe water stress treatments during the 1995 and 1996 growing seasons.

	Water regimes					
	†Control	WS_{ot}	Control	WS_{ot}	Control	WS_{ot}
Cultivar	WU		WUEg		WUEdm	
	mm		kg ha^{-1} mm^{-1}		kg ha^{-1} mm^{-1}	
			1995 growing season			
Keyperounda	457	373	7.4	2.9	25.7	13.7
Karim	480	362	8.3	2.9	22.3	11.5
ACSAD 65	466	349	5.2	2.2	15.1	09.6
Marzak	467	345	7.8	3.9	20.1	13.2
LA V17	450	338	8.5	4.5	22.1	16.6
LA V18	451	340	7.1	2.0	22.6	09.6
$LSD_{0.05}$ WR	5.5***		0.27***		1.70***	
$LSD_{0.05}$ C	NS		0.38***		1.79***	
$LSD_{0.05}$ WR*C ‡	NS		0.76**		NS	
			1996 growing season			
Keyperounda	480	343	7.7	4.2	23.4	16.6
Karim	459	329	10.0	5.8	27.4	22.1
ACSAD 65	487	312	7.1	3.5	19.8	14.2
Marzak	462	291	9.8	6.7	26.4	24.5
LA V17	476	314	10.0	6.6	26.7	24.9
LA V18	475	316	8.5	5.1	24.2	19.8
$LSD_{0.05}$ WR	2.6***		0.69***		2.0**	
$LSD_{0.05}$ C	11.6**		0.62***		1.9***	
$LSD_{0.05}$ WR*C	NS		NS		NS	

*, **, *** Significant at the 0.05, 0.01 and 0.001 probability levels, respectively.
† WS_{ot}, WS_{mt}, WS_{et} denote water stress treatments imposed by withholding water during the period from emergence to either the onset, middle or the end of tillering, respectively.
‡ Indicates LSD values for comparison of cultivar means within a water regime.

contention of De Detta et al. [11] and Lilley and Fukey [17] that the ability of a cultivar to recover quickly from water deficit is as important to grain production as drought tolerance during water deficit. Exceptions to this general relationship were noted. For instance, Marzak and ACSAD 65, whose RGRs during the recovery period were similar (*table III*), displayed very large differences in grain yield under both well-watered and drought conditions [12]. LA V17, the highest yielding cultivar, across all levels of water stress, displayed the ability of recovering quickly and was relatively drought resistant during the water deficit.

Higher RGR and dry matter accumulation during the early vegetative period across all soil water conditions in general and under medium and severe water stress in particular resulted in rapid early ground cover, and consequently, relatively less soil water loss through evaporation. However, unless anthesis is earlier in this water-limited environment, the faster early growth may also result in greater water use before anthesis and, therefore, lower yields. This may be counterbalanced, to some extent at least, by the saving in soil evaporation and the availability of additional assimilates for retranslocation to the grain.

Furthermore, the drought-resistant cultivars were charcterized by a high RGR not only under drought conditions but under optimal soil moisture conditions as well. This is an important feature since in environments with variable water availability, cultivars with high physiological and/or morphological plasticity with respect to RGR are better adapted. This kind of adaptation is of particular significance for crops grown in the semi-arid tropics. Therefore, it is important to identify the association of morphological and physiological components of RGR that can easily be used in plant breeding programs for drought resistance. One possible reason for the significant genotypic variation in RGR could be that the balance between the amount of roots and leaf area may have influenced the water status of the leaves and as a result photosynthesis and, therefore, RGR. In fact our results [12] demonstrated that the resistant cultivars maintained significantly higher leaf area and net photosynthesis rate under early-season drought conditions. Cultivar differences in RGR were also associated, to some extent, with development pattern. The slowest increase in RGR under stress was observed for the latest cultivar, i.e. Keyperounda, confirming previous results for wheat [15].

Results from these trials suggest that early in the season, when the vapor pressure deficit (VPD) between the leaf and the air is low, and the efficiency of transpiration and WUE are high, the drought-resistant cultivars (Marzak and LA V17) used water more efficiently compared with the susceptible cultivars (Keyperounda and LA V18). The fact that Marzak and LA V17 used less water under stress, compared to Keyperounda and LA V18 would confirm this finding. Physiological responses of these cultivars to early-season drought [12] also support this finding. Actually, Marzak and LA V17 maintained the highest instantaneous leaf transpiration efficiency, defined as the ratio of leaf net photosynthesis rate to leaf transpiration rate. The higher WUE for the drought-resistant cultivars could be attributed to their higher instantaneous leaf transpiration efficiency, as evidenced by the strong association observed between these variables under early-season drought conditions [12]. Consequently, the results suggest that yields may be increased by increasing the proportion of water transpired early in the season when the VPD is low, and this can be partly achieved genetically through improved early vigor and RGR.

In the experiment reported here, sowing density and nutrition was better than is current farmer practice in these dryland regions. Therefore, under conditions similar to those reported in this experiment, increases in nitrogen or planting density are unlikely to greatly improve the early vigor of wheat in these regions. The potential to genetically increase vigor in the slower growing cereals would, therefore, seem to be large and this is likely to be advantageous in regions where rainfall is confined mainly to the period between sowing and anthesis. However, in rainfed low-input systems, both agronomic management (mulching, residue management, fertilization, sowing density, etc.) and germplam modification should be important in enhancing the efficiency of water use through the manipulation of the balance between the two components of water use, transpiration and evaporation from the soil surface.

Under drought stress conditions, WUE_g and WUE_{dm} were weakly associated with root length density early in the season (*table VII*). Thus, although grain yield responses can not be attributed only to the different root systems characterizing these genotypes, we may anticipate that the carbon cost to produce the larger root system of LA V17 and Karim had no negative influence on yield.

As stated by Brown et al. [5], for barley in Syria, high root density in the upper layers of the soil profile may ensure that a larger proportion of water is transpired rather than lost by evaporation from the soil surface. In these trials, the greater extension of LA V17 and Karim root systems in the upper layer of the soil may have ensured a better utilization of

Table VII. Linear correlation coefficients among various traits under drought stress conditions during the 1995 and 1996 growing seasons.

	WUEg†		WUEdm†		Total water use	
	1995	1996	1995	1996	1995	1996
Shoot dry matter at:						
onset of tillering	0.27	0.11	0.51*	0.03	0.12	0.35
end of tillering	0.86***	0.68**	0.89***	0.55*	0.69**	0.60**
anthesis	0.79***	0.88***	0.71**	0.77***	0.72***	0.68**
Root length density at:						
onset of tillering	0.21	0.33	0.27	0.41	0.06	0.09
end of tillering	0.46	0.44	0.52*	0.46	0.19	0.22
anthesis	0.49*	0.34	0.68**	0.34	0.33	0.43
Relative growth rate						
three leaves-end tillering	0.89***	0.78***	0.83***	0.63**	0.71**	0.62**
end tillering-booting	0.80***	0.49*	0.75***	0.40	0.85***	0.53*

*, **, *** Significant at the 0.05, 0.01 and 0.001 probability levels, respectively.
For each growing season cultivar and water stress regime treatment means were used (n = 18 in 1995 and 1996).
† WUE_g and WUE_{dm} represent water use efficiency for grain yield and water use efficiency for the above-ground dry matter, respectively.

the amount of water applied immediately after planting. Furthermore, LA V17 had a large root system under drought and under optimal moisture (*tables IV* and *V*). As pointed out by O'Toole and Bland [20], such flexibility in root system development is to be considered a valuable trait in terms of adaptability of a genotype to an unpredictable stress such as drought in these Mediterranean regions where rainfall is highly erratic.

We examined the relationship between root growth and water use. Our results point out a weak relationship between root length density and water use (*table VII*). Others have shown similar results [13]. At anthesis, across all levels of water stress treatments, the earliest genotypes (i.e. ACSAD 65, Marzak and LA V18) showed the lowest total root length densities (*table V*) possibly due to the reduced duration of their vegetative growth, confirming earlier results reported by Benlaribi et al. [3] and Rosella et al. [23].

High WUE_g and WUE_{dm} yields in this environment under early-season drought were attributed to high RGR and aerial dry matter yield under water stress, and high capability of recovery. To develop new cultivars with improved early vigor and vegetative biomass, and consequently grain yield, as shown in this study, breeders need access to parents with considerable improvements in these characteristics. In this respect, LA V17 and Marzak appear to be the most promising candidates.

Moreover, it is worth noting that high yields under early-season drought can rise from different combinations of traits. High RGR and early vigor were identified in this study as potential traits associated with improved resistance to early-season drought. However, these traits can only be incorporated successfully if they are considered as part of an entire plant ideotype. Furthermore, the combination of a plant ideotype and appropriate agronomic management techniques can contribute to reduce the negative impact of early-season drought on wheat production in this semi-arid Mediterranean environment.

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