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Evaluation of selection criteria for performance of wheat cultivars during high temperature stress in the field

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SUMMARY – Responses of crops to high temperatures are usually determined under controlled conditions that seldom duplicate field conditions. Our objectives were to devise a system and identify plant traits for evaluating responses to temperature in the field. Seven durum wheat (*T. turgidum* L. var. *durum*) cultivars were sown in Morocco during mid and late autumn and early winter to alter timing of maturation. Conditions other than temperature were held as constant as possible by fertilizing and irrigating plants and controlling pests. Plant traits – photosynthesis, stomatal conductance, yield components, and harvest index – and their ratios of late versus early plantings were measured during maturation. Mean daily high temperature from anthesis to maturity was 25, 28, and 31°C for the first, second, and third plantings, respectively. The ratio of harvest indices from the third planting relative to the first planting ranged from 0.42 to 1.31, indicating considerable genetic variation among cultivars. Photosynthetic rates and grain yields of third planting relative to the first planting were highly correlated, and the ratio of harvest indices and yields were closely associated, indicating that current assimilation and efficient translocation were important for yield under stress. Low stomatal conductance showed that senescence was accelerated by high temperature. Altering planting dates exposed plants to different temperature regimes during maturation, affected variability among cultivars, and elucidated traits related to yield under stress.

Key words: Heat stress, durum wheat, photosynthesis, stomatal conductance, harvest index.

RESUME – “Evaluation de critères de sélection pour les performances de cultivars de blé pendant le stress des hautes températures aux champs”. L’effet du stress thermique est habituellement déterminé sous des conditions contrôlées, qui rarement reflètent les conditions des champs. Notre objectif était d’envisager un système qui nous permette d’identifier et d’évaluer les critères morpho-physiologiques liés au stress thermique aux champs. Sept variétés de blé dur (*T. turgidum* L. var. *durum*) ont été semées au Maroc. Trois dates de semis ont été utilisées, semis précoce, de saison et tardif, pour imposer des degrés différents de stress au printemps. Des critères morpho-physiologiques ont été mesurés, en l’occurrence la photosynthèse, la conductance stomatique, le rendement, les composantes de rendement et l’indice de récolte. La moyenne des températures journalières de la floraison à la maturité physiologique était de 25, 28, et 31°C pour la première, la deuxième, et la troisième date de semis, respectivement. Le rapport des indices de récolte du semis tardif par rapport au semis précoce oscillait entre 0,42 à 1,31, ce qui est indicatif d’une variabilité entre les différentes variétés. Les rapports de la photosynthèse et ceux des rendements du semis tardif par rapport au semis précoce étaient bien corrélés, ce qui suggère que l’assimilation courante ainsi que la translocation était primordiale pour le rendement final sous stress thermique. En altérant les dates de semis, on peut exposer les plantes à un régime croissant de température pendant la maturité ce qui permet d’identifier les critères morpho-physiologiques pouvant servir à sélectionner pour la tolérance au stress thermique.

Mots-clés : Stress thermique, blé dur, photosynthèse, conductance stomatique, indice de récolte.

Introduction

High-temperature effects on field-grown wheat have been investigated by several systems that had advantages and disadvantages. Different temperature regimes were imposed by growing plants under air-conditioned canopies (Johnson and Kanemasu, 1983), at low and high elevations (Midmore *et al.*, 1984), and during cool and hot seasons (Shpiler and Blum, 1986). These approaches yielded valuable information regarding adverse effects of high temperature, but they had disadvantages of limited space and high cost; variability in solar radiation, diurnal temperature range, and disease incidence; and difference in photoperiod, respectively. Many wheat-producing regions lack adequate differences in elevation and multiple growing seasons to apply the latter methods.

The need for methods of growing plants at different temperature regimes under field conditions and for information on responses of wheat to these regimes prompted the following investigations. Altering

the dates of planting changed the time of maturation and exposed plants to increasing stress as temperatures rose during spring. The method had few apparent disadvantages and the important advantages of providing conditions that were more natural than those in controlled environments.

Materials and methods

The experiment was conducted at the Agriculture Research Experiment Station at Sidi El Aydi (31° 15'N, 7° 30'W), near Settat, Morocco during the 1993-1994 season. Temperature conditions during the growing season for wheat were characterized by large contrasts. Maximum and minimum temperatures decreased from autumn to January and then increased to high daily levels that reached 43°C during April and May. Rainfall was above normal until the end of December, near normal and uniformly distributed through March, and deficient during April and May. Ample irrigation was provided as needed to establish the wheat stands and maintain them through physiological maturity.

Seven durum wheat cultivars were planted at early, normal, and late dates during 1993. The experiment was planted at the recommended seeding rate of 100 kg/ha. Each cultivar was planted in six rows, each 5.0 m long and 0.25 m apart. Three plantings, 24 October 1993, 24 November 1993, and 24 December 1993, represented early, mid-season and late dates, respectively. The experiment was managed for optimum production and minimum differences other than temperature among planting dates, including fertilization, and complete weed and disease control.

Net photosynthetic rates and stomatal conductances were measured with a Li-6200 portable photosynthesis system (Li-Cor, Inc., Lincoln, NE). Readings were taken on flag leaves of main stems of four plants in each of four replications on each cultivar. Gas exchange was measured weekly in all cultivars from anthesis to physiological maturity.

The experimental design was a split-plot with four replications. Sowing dates were main plots, and cultivars were sub-plots. Data analysis used SAS (1988) procedures.

The ability of plants to maintain high physiological activities and high grain yield at late planting relative to early planting was considered a measure of tolerance to high temperatures. Pearson rank correlations were calculated among these ratios to determine any associations.

Results

Altering the dates of planting in 1994 successfully changed the temperature regime during maturation of the wheat cultivars. Cultivars planted on the first date reached anthesis on a mean date of 3 March and physiological maturity on 4 April. Those planted on the second date flowered on 28 March and matured on 18 April. Planting on the third date delayed mean dates of anthesis to 18 April and physiological maturity to 5 May. The mean daily high temperature from anthesis to physiological maturity was 25, 28, and 31°C for the first, second, and third plantings, respectively, and cultivars planted on the three dates accumulated nearly the same number of degree day units between two developmental stages. Physiological measurements were initiated on the mean date of anthesis of all cultivars in each planting.

Photosynthetic rates of all seven durum wheat cultivars that were planted early decreased gradually from anthesis to physiological maturity (Fig. 1A). Rates were similar among cultivars the first week after anthesis but began to differ two weeks after anthesis. Sarif and several other cultivars had high photosynthetic rates, whereas Acsad 65 had a low rate the second week. Differences among cultivars disappeared as the plants approached physiological maturity the last date. Durum wheats planted the second date had net photosynthetic rates that were almost stable from anthesis to the second week and then declined at physiological maturity (Fig. 1B). Some cultivars such as Sarif maintained a high photosynthetic rate, whereas Acsad 65, Cocorit, and Karim had low rates at one or more sampling dates. Photosynthetic rates of durum wheats planted late in the season declined as the spring progressed but ranged more among cultivars (Fig. 1C). Sarif maintained a high rate, especially at maturity, and Cocorit was often low.

Stomatal conductance declined from anthesis to maturity in durum wheats that were planted early (Fig. 1D). Although Acsad 65 was often low, there were few significant differences among the cultivars. Durum

wheats from the second planting date ranged widely in stomatal conductance at anthesis (Fig. 1E). Kyperounda had higher conductance than most other cultivars, and Acsad 65 was low. Stomatal conductance values and differences among cultivars decreased gradually to maturity. Durum wheat planted at the late date varied inconsistently (Fig. 1F). Sarif often had high conductance, however, and Acsad 65 often had low values.

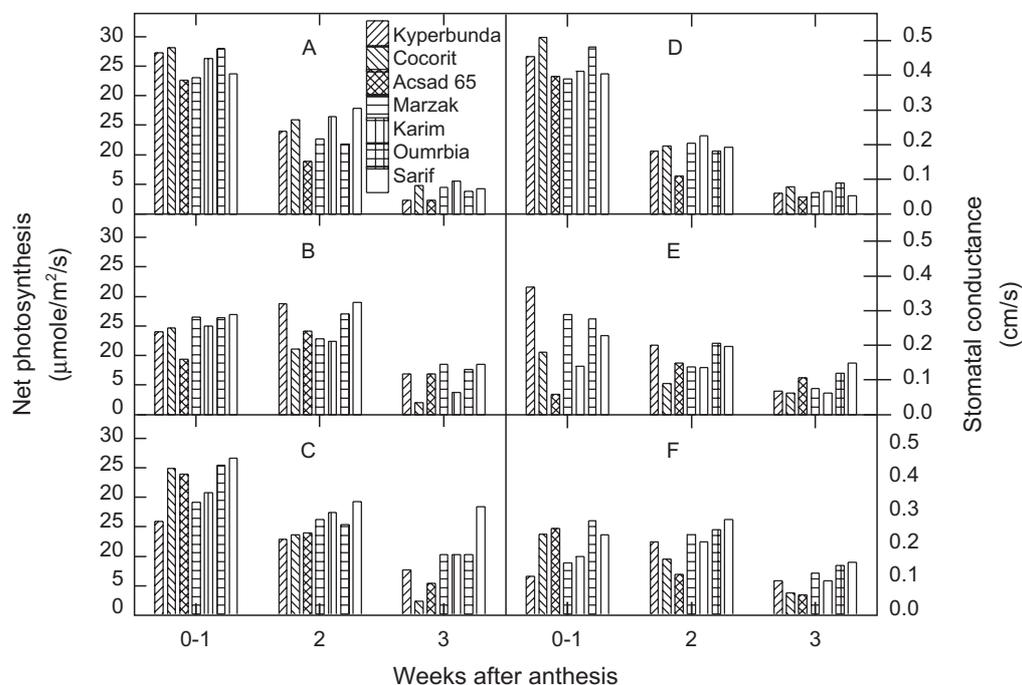


Fig. 1. Net photosynthetic rates (A,B,C) and stomatal conductance (D,E,F) of seven durum wheat cultivars after different dates of planting (A,D = early dates; B,E = normal dates; C,F = late dates).

Stepwise regression analysis of grain yields of durum wheat cultivars identified harvest index as the most important parameter and as one that increased as planting was delayed (Table 1). Spike density accounted for significant variance in yield but decreased in importance from early to late planting. Grain yields were positively correlated with harvest indices and the yield components at most dates (Table 2). Delaying sowing date increased the correlation between yields and harvest indices and between kernel weights and harvest indices (Table 2).

Table 1. Stepwise regression analysis of durum wheat cultivar grain yields for three planting dates

Variable added [†] to equation	Planting dates, partial r^2			Planting dates, model r^2		
	1	2	3	1	2	3
Harvest index (%)	0.125	NS ^{††}	0.916	0.893	NS ^{††}	0.916
Kernel weight (mg/grain)	0.071	0.742	0.004	0.985	0.742	0.959
Spike density (no./m ²)	0.768	0.144	0.039	0.768	0.973	0.955
Kernel number (no./spike)	0.021	0.087	0.025	0.914	0.829	0.983

[†]All variables met the $P = 0.05$ significance level for entry into the model.

^{††}Not significant at $P = 0.05$ for entry into the model.

Table 2. Pearson's correlation coefficients of yield, yield components, and harvest index of 7 durum wheat cultivars

	Planting date	Harvest index	Kernel weight	Spike density	Kernel number
Yield (kg/ha)	1	0.79**	0.18	0.88**	0.27
	2	0.83**	0.86**	-0.09	0.45*
	3	0.96**	0.81**	0.82**	0.40*
Harvest index (%)	1		0.28	0.57**	0.26
	2		0.80**	-0.31	0.49**
	3		0.84**	0.71**	0.47*
Kernel weight (mg/grain)	1			0.03	-0.64**
	2			-0.16	0.18
	3			0.51**	0.12
Spike density (no./m ²)	1				0.03
	2				-0.73**
	3				0.03

***Significant at P = 0.05 and 0.01, respectively.

Grain yield ratio of late-planted cultivars to early-planted cultivars and the ratio of photosynthetic rates of late- to early-planted cultivars were significantly correlated (Table 3). There was no correlation between yield ratios and photosynthetic ratios for other dates or the ratios of stomatal conductance. Yield ratio was highly correlated with the ratio of late- to early-harvest index and the ratio of late- to early spike density (Table 3).

 Table 3. Pearson's correlation coefficients of ratios of net photosynthesis (P), conductance (C), F_v, harvest index (HI), yield (Y), spike density (SD), kernel number (KN), and kernel weight (KW)

Grain yield	P3/P1	P3/P2	C3/C1	C3/C2
Y3 [†]	0.293	0.272	-0.063	-0.172
Y3/Y1	0.602**	0.502**	0.180	0.091
Y3/Y2	0.186	0.020	-0.01	-0.234
	HI3/1	HI3/2	SD3/1	SD3/2
Y3	0.811**	0.669**	0.459*	0.795**
Y3/Y1	0.893**	0.320	0.872**	0.571**
Y3/Y2	0.643**	0.704**	0.372*	0.851**
	KN3/KN1	KN3/KN2	KW3/KW1	KW3/KW2
Y3	0.427*	-0.148	0.389*	0.324
Y3/Y1	0.645**	-0.069	0.037	-0.031
Y3/Y2	0.287	-0.070	0.331	0.411*

[†]Number 1, 2, and 3 represent early, mid-season, and late sowing dates.

***Significant at P = 0.05 and 0.01, respectively.

Discussion

Altering planting dates while holding other conditions as constant as possible provided ample area, eliminated differences in soil types and pest incidence and, the latitude of Morocco, had little variation in solar radiation and photoperiod. Few disadvantages of other methods were apparent (Johnson and Kanemasu, 1983; Midmore *et al.*, 1984; Shpiler and Blum, 1986). Most importantly, the method caused

adequate differences in temperature during maturation to observe plant traits that were affected and to identify genetic variability among cultivars.

Two major factors of those investigated were important determinants of grain yields of the durum wheat cultivars. Maintenance of photosynthetic activity favored yields of resistant cultivars as delayed planting increased temperatures during maturation (Paulsen, 1994). High harvest index, which is indicative of efficient utilization of photosynthate (Gifford *et al.*, 1984; Blum *et al.*, 1994) was also associated with high yields under the stress.

An association between relative photosynthetic rates and relative yields of the cultivars reflected the importance of the relationship. The highly significant correlation between photosynthesis and yields of the last planting relative to the first planting showed that current assimilation is as important under stress conditions as under normal conditions. The magnitude of the coefficient (0.60^{**}), however, indicated that other factors were involved. Most wheats possess some tolerance to high temperature (Rawson, 1986), and differences are likely less distinct among cultivars in the field than between the extreme cool and hot environments in controlled chambers. The shortened interval between anthesis and maturity also obscured the association between photosynthesis and productivity. Wheat cultivars differ constitutively in mobilization of reserves from the stem to the grain (Blum *et al.*, 1994), for instance, and those that efficiently translocate stem contents at high temperature depend less on current photosynthesis for high yield.

Stomatal conductance had no association with cultivar yields, probably because it was not limiting. Kernel weight and either or both of the two components of kernel number per area, spike density and kernel number per spike, contributed about equally to yield of all plantings. The significant correlations between kernel numbers and yield of the last planting relative to the first planting suggested that setting and retaining tillers and caryopses were important for productivity under stress conditions. Any of these measures would be appropriate for developing or identifying cultivars that are resistant to those conditions.

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