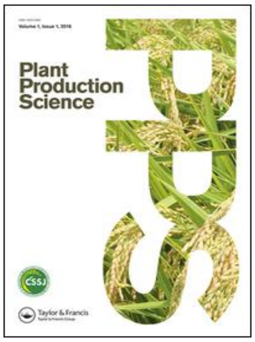

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Harvest index is a critical factor influencing the grain yield of diverse wheat species under rain-fed conditions in the Mediterranean zone of southeastern Turkey and northern Syria

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ABSTRACT

Environmental and plant factors critical to the grain yields of bread (*Triticum aestivum* L.), durum (*T. durum* L.) and emmer (*T. dicoccum* L.) wheat cultivars were investigated at two Mediterranean rain-fed field sites: Adana in southeastern Turkey (2009 and 2010) and Aleppo in northern Syria (2009). The grain yield (GY) and biological yield (BY) of most cultivars were higher in Adana than in Aleppo, and the lower GY in Aleppo resulted from lower harvest index (HI) and lower BY due to higher temperatures and lower rainfall. The variations in the HI among cultivars were greater in Adana than in Aleppo. The GY was closely related to the HI but not the BY across cultivars at each site, and a higher GY was accompanied by a superior conversion-efficiency of incident radiation during the grain filling period for grain yield [GY/Ra, where Ra is the cumulative radiation for 30 days after heading (D_{30})] across all observations. The GY/Ra correlated negatively with the average temperature for D_{30}, and higher HI values resulted in higher GY/Ra. In Adana, the time from anthesis to physiological-maturity decreased as the average temperature for D_{30} increased, resulting in a lower HI. Cultivars exhibiting the early heading trait can effectively escape the negative impacts of terminal high-temperature and water-shortage conditions on the HI. The results suggested that the HI is a critical factor for GY across diverse wheat cultivars under terminal high-temperatures and water-shortages in Mediterranean areas, and the BY is also an important factor under severe water-limitation conditions.

Abbreviations: BY, biological yield; D_{30}, 30 days after heading; GY, grain yield; HI, harvest index; Ra, cumulative radiation for D_{30}; GY/Ra, conversion-efficiency of incident radiation during the grain filling period for grain yield; T_{30}, average temperature for D_{30}

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With a global annual production of 730 million t in 2015, wheat is one of the world's most important food crops. Over the past 50 years, production has increased 3.2-fold, and grain yield has increased from 1.15 to 3.25 t ha^{-1} (USDA, 2015). Wheat can adapt to a wide range of growing conditions, from temperate and irrigated to dry and high-rainfall areas and from warm and humid to dry and cold environments (Curtis, 2002); thus, the production area has expanded from subtropical to high-altitude regions more than 3000 m above sea level (Percival, 1921). Bread wheat (*Triticum aestivum* L.) ($n = 42$) accounts for approximately 95% of the wheat grown worldwide, with most of the remainder being durum wheat (*T. durum*) ($n = 28$) (Peng et al., 2011); other types of wheat, such as emmer (*T. emmer*) ($n = 28$) and einkorn (*T. monococcum*) ($n = 14$), are only cultivated in limited areas in the Middle East and the Mediterranean (Stallknecht et al., 1996; Zaharieva & Monneveux, 2014). Although emmer and einkorn wheat are currently only minor crops, they are potentially important as resources to genetically improve bread wheat under environmental stresses (Zaharieva & Monneveux, 2014). In addition, the demand from consumers, bakers, and farmers for hulled emmer and einkorn wheat has recently increased due to the rediscovery of their use as food (Longin et al., 2016). However, the capacity of these diverse wheat species to adapt to environmental stressors, such as high temperature and limited water supply, has been less well studied than that of bread wheat (Zaharieva & Monneveux, 2014).

In the Mediterranean, which is one of the most dominant wheat-producing areas, wheat occasionally suffers from an increase in temperature and a decrease in rainfall at the end of the spring season (Turner, 1996). Moreover, global climate models predict an increase in the mean ambient temperatures in the range of 1.8 to 5.8 °C by the end of this century (IPCC, 2001; Kimura,

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2007) as well as increases in the temperature variability and frequency of hot days, resulting in reduced rainfall in the Mediterranean zone (Pittock, 2003). In fact, temperatures have increased over several decades in southeastern Turkey, which is one of the historically dominant wheat-producing areas (DMI, 2005). Therefore, wheat traits related to high-temperature and water-deficit resistance, particularly during the terminal growth season, will be increasingly important in the Mediterranean zone (Ludwig & Asseng, 2006).

The grain yield (GY) can be determined from the components of the biological (biomass) yield (BY) and harvest index (HI) (Passioura, 1977), and the potential yield of bread wheat has increased due to increases in the HI (Curtis, 2002; Gustavo & Andrade, 1989). Furthermore, high temperature and drought decrease the BY and GY in bread wheat, although they do not significantly affect the HI (Mondal et al., 2014). Under high-temperature conditions, the GY is related to the HI across bread wheat genotypes (Zhong-hu & Rajaram, 1993). However, the importance of the BY and HI on the GY if different wheat species with diverse phenotypes in rain-fed areas of the Mediterranean zone, where increases in temperature and water shortages are more severe, is not well known. Our objective in this study was to clarify the environmental and plant factors that are critical to the GY of cultivars of three background sources, bread (*Triticum aestivum* L.), durum (*T. durum* L.) and emmer (*T. dicoccum* L.) wheat, at two Mediterranean rain-fed field sites, southeastern Turkey and northern Syria. Einkorn wheat cultivars were grown but not included in the evaluation due to the difficulty associated with grain filling due to their late heading traits.

Materials and methods

Plant materials

Four cultivars from each of three wheat species were selected from the gene collection of the Laboratory of Crop Evolution at the Plant Germ-plasm Institute of the Graduate School of Agriculture, Kyoto University: bread (*Triticum aestivum* L., a hexaploid form of the ABD genomes) [Chinese Spring (origin: China), Norin 61 (Japan), Thatcher (UK) and Selkirk (UK)], durum [*T. turgidum* L. ssp. *durum* (Desf.) Husn., a tetraploid form of the AB genomes] [Pentad (Russia), Golden Ball (UK or France), Langdon (USA) and AC Navigator (Canada)] and emmer (*T. turgidum* L. ssp. *dicoccum* Schubler, a tetraploid form of the AB genomes) [*polonicum* (Polish), *turgidum* (Poulard) and *dicoccum* (French)]. One emmer wheat cultivar, pyramidale, was not included in the analysis due to the lack of data for this cultivar in Aleppo. The plant accessions of these cultivars were selected by Dr. Kawara of Kyoto University from 10,000 genotypes composed of land and improved races according to their localities and origins, and genetic diversity was retained as much as possible.

These cultivars were compared in two locations (Adana and Aleppo) across two years (2009 and 2010). The experimental design was a randomized block with three (Adana and Aleppo 2009) or four replicates (Adana 2010), where 11 cultivars were randomly arranged in each replicate. The significance at the 0.10, 0.05 or 0.01 probability levels and LSD via Tukey's method at the 0.05 probability level were calculated through analysis of variance. The least-squares method was used to fit curves relating GY, BY and HI, and the correlation coefficient and the coefficient of determination (r and R^2) were calculated to assess the goodness-of-fit of the curve and correlation, respectively. The statistical analyses were performed in Microsoft Excel based on the methods described by Snedecor and Cochran (1967) and in Excel Statistic and Excel Multiple Analysis (ver. 7, Social Survey Research Information Co., Ltd., Tokyo).

Field sites

Adana in Turkey (2009 and 2010 seasons)

Eleven wheat cultivars (bread, durum and emmer) were grown in 2008 and 2009 at the experimental farm of Çukurova University (43 m above sea level, 35°21′ E and 37°01′ N) in Adana, Turkey. The soil was montmorillonitic, thermic, Vertic Xerofluvent with a low organic matter content and a pH that varied from 7.05 to 7.20. In each experimental plot, seeds of each genotype were sown at a density of 500 seeds m^{-2} on 18 November 2008 and 9 December 2009 in rows spaced 0.15 m apart in 5 × 8.4-m fields. Fertilizer was applied at sowing as follows: 200 kg N ha^{-1} as ammonium nitrate, 80 kg P ha^{-1} as P_2O_5, 80 kg K ha^{-1} as K_2O and 1 kg (the first year) or 5 kg (the second year) Zn ha^{-1}.

Aleppo in Syria (2009 season)

The same wheat genotypes (bread, durum and emmer) were grown at the experimental farm of the International Center for Agriculture Research in Dry Areas (ICARDA) (291 m above sea level, 36°56′ E and 36°01′ N) in Aleppo, Syria. The soil type was Chromic Luvisol consisting of 60% clay, 32% silt, 8% sand and 0.8% organic matter and having a pH of 8.1. The field soil was classified as thermic Chromic Calcixerert, which is a fine calcareous clay (Ryan et al., 1997). In each plot, seeds of each genotype were sown at a density of 400 seeds m^{-2} on 4 December 2008 in rows spaced 0.25 m apart in 2.5 × 1.0-m fields. Eighty-one days after sowing, fertilizer was applied as urea at a rate of 35 kg N ha^{-1}. The soil fertility in the experimental field was high, hence basal dressing was eliminated such that the wheat grain yields were scarcely changed by variations in the amounts of nitrogen fertilizer between 30 and 90 kg h^{-1} (Anderson, 1985). Following irrigation with a tube irrigation system on 15 December 2008 (66 mm) and 8 February 2009 (25 mm) to promote establishment, the plants were grown under rain-fed conditions.

Data collection and analysis

The daily temperature, short wave radiation, class A pan evaporation and precipitation were collected at a weather station located 4 and 1 km from the field site in Adana and Aleppo, respectively. The data were collected automatically and supplied as daily data. The cumulative rainfall minus evaporation serves as an indicator of the water supply and drought risk (Estamian & Eslamian, 2017). However, the cumulative rainfall minus evaporation can result in an underestimation of the water shortage because it ignores the loss of water through infiltration into deep soils or an overestimation because it ignores the reduction in soil surface evaporation due to soil drying (Nagler et al., 2007).

The plants were grown under rain-fed conditions, and the times of heading (Adana and Aleppo) and anthesis (Adana) were defined as the dates when 50% of the tillers headed and flowered, respectively. The time of physiological maturity was defined as the date when 50% of the peduncles were yellow and the glumes and grains were losing their colour (Bell & Fischer, 1994). Two weeks after physiological maturity was reached, two 0.5-m rows in Adana and two 1-m rows in Aleppo from each replicate were harvested, oven-dried at 80 °C for 48 h, the aboveground dry weight of the plants (BY) and their GY and yield components by dry weight basis were measured. The HI was calculated as GY/BY.

The conversion-efficiency of incident radiation during the grain filling period for grain yield [GY/Ra, where Ra is the cumulative radiation for 30 days after heading (D_{30})] was calculated. The base temperature (Tb) and cumulative temperature (CT) from emergence to heading for each cultivar were determined from the daily average temperatures (Sinclair, 1994).

$$CT = \Sigma(T - Tb) \tag{1}$$

The Tb for each cultivar was determined at the minimum coefficient of variation (cv) in the CT among data from three experiments in which increases in the temperature from 0 to 10 °C at a rate of 1 °C were inputted into the Tb of Equation (1).

Results

Meteorological conditions, grain yields and yield components

The average temperature decreased at the beginning of the growing season and then increased later in the growing season in the three fields. The temperature during the beginning of the season was lower in Aleppo, but the rate of increase in this area was higher than that in Adana in 2009 and 2010 (Figure 1). Shortwave radiation was lower approximately 50 days after sowing but then continuously increased, and during the last part of the season, higher shortwave radiation was observed in Aleppo than in Adana in 2009. The cumulative rainfall increased from sowing to approximately 150 days after sowing, and two- or threefold higher levels were detected in Adana than in Aleppo in 2009. The cumulative evaporation exceeded the cumulative rainfall beginning 200 days after sowing in Adana in 2009, 70 days after sowing in Adana in 2010 and 140 days after sowing in Aleppo in 2009. In this study, the cumulative rainfall minus evaporation showed that the conditions in Aleppo were dryer than those in Adana (Figure 1).

The heading time, which was averaged over the three observations, ranged from 120 to 160 days, and many durum and emmer wheat cultivars exhibited longer heading times than the bread wheat cultivars, although there were no significant differences between species (Table 1). The GY ranged from 53 to 481 10^{-3} kg m^{-2} across the cultivars and was significantly higher in the cultivars of bread and durum wheat than in those of emmer wheat (Table 1). The average GY of all cultivars showed significant differences across the observations in following order: Adana 2009 > Adana 2010 > Aleppo 2009. The grain number was lower in some of the emmer cultivars. The thousand-grain weight showed significant differences among the cultivars, but there were no trends among species. Across all cultivars and the three observations, the GY was more highly correlated with the grain number ($r = 0.767$, $p < 0.001$) than the single-grain weight ($r = 0.487$, $p < 0.005$). Although the BY of the emmer wheat cultivars was higher than that of the other cultivars, it was significantly lower in Aleppo than in Adana in 2009 and 2010 across the cultivars. The HI significantly differed among the cultivars during each observation: it was lower in many emmer wheat cultivars than in bread and durum wheat.

Critical effects of meteorological factors on the BY and GY

There were significant single positive corrections ($p < 0.05$) between the BY and cumulative rainfall or average temperature from sowing to D_{30} (entire season) in most species

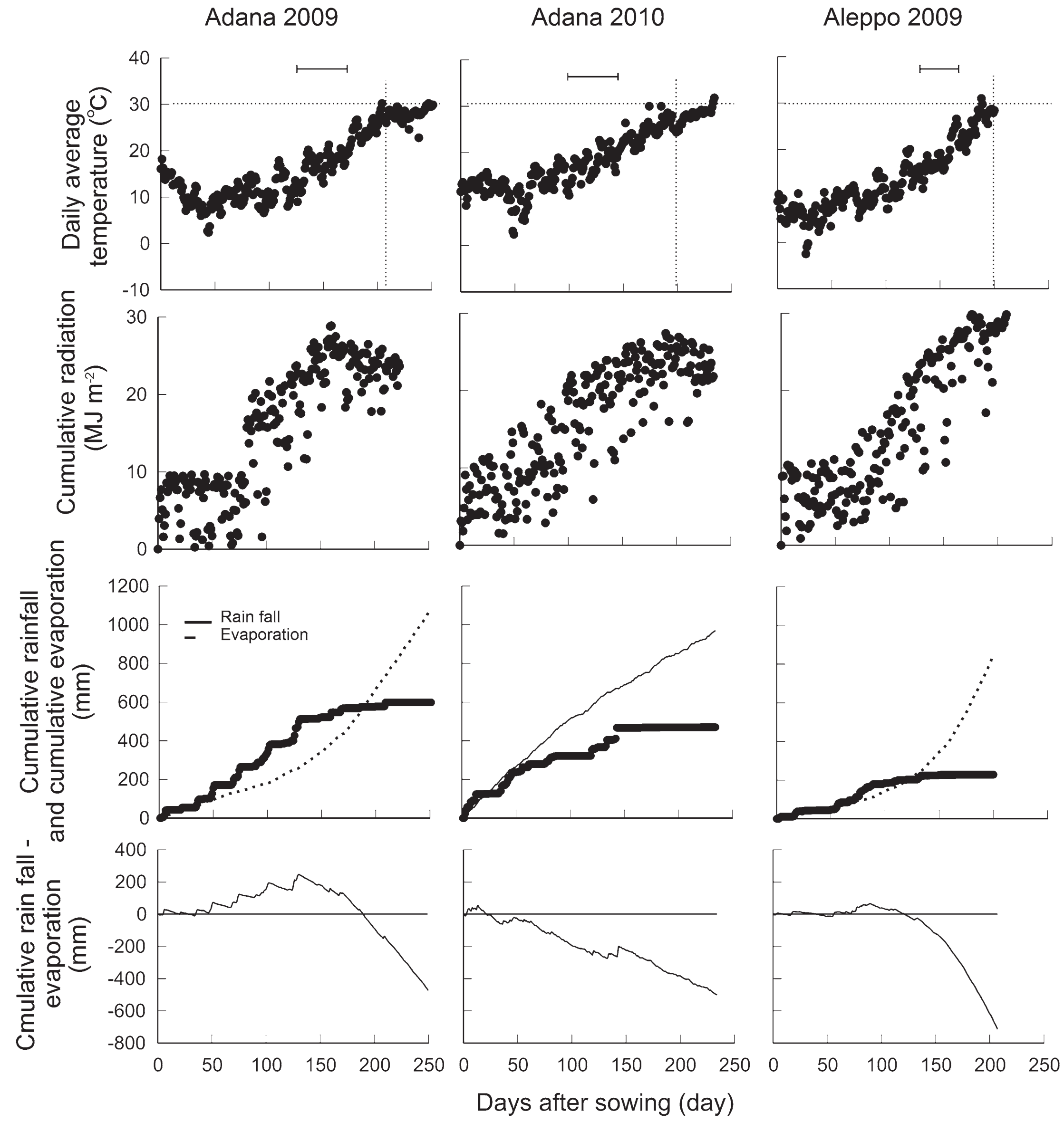

Figure 1. Daily average temperature, shortwave radiation, cumulative rainfall (R) and cumulative evaporation (E) by pan-evaporation and cumulative R-E during the wheat-growing seasons in Adana, Turkey, in 2009 and 2010 and Aleppo, Syria, in 2009. The lateral bars indicate the ranges of heading times in the investigated wheat genotypes.

except emmer wheat, but almost no correlations were found between BY and cumulative radiation (Table 2). Correlations were detected between the GY and cumulative rainfall in bread wheat and the combined data-set and between the GY and cumulative radiation in durum wheat and the combined data. The GY was positively correlated with the cumulative rainfall after heading (D_{30}) in the combined data-set, negatively correlated with the average temperature in most species except emmer wheat and negatively correlated with the cumulative radiation in the combined data-set. The partial correlation coefficient showing the effect of single meteorological factors on the BY and GY indicated that the BY and GY were significantly positively correlated with the cumulative rainfall during the entire season in most species except emmer wheat, and the BY and GY were positively and negatively correlated with the average temperature, respectively. The GY was significantly negatively correlated with the average temperature after heading in most species.

A multiple regression analysis revealed that the BY and GY were associated with three independent factors of meteorological data (cumulative rainfall, average temperature and cumulative radiation) (Table 3). Throughout the growing season, the cumulative rainfall and average temperature exerted positive effects on the BY in most species and the combined data-set, but the cumulative radiation had negative effects. The average temperature and cumulative radiation after heading had negative

Table 1. Grain yield, biological yield and harvest index of different wheat species under rain-fed conditions in Adana, Turkey, in 2009 and 2010 and Aleppo, Syria, in 2009.

				Biological yield			Grain number			Thousand grain weight			Grain yield			Harvest index		
Cultivar	ID NO.	Species	Heading (day)	Adana 2009	Adana 2010 (g m^{-2})	Aleppo 2009	Adana 2009	Adana 2010 (m^{-2})	Aleppo 2009	Adana 2009	Adana 2010 (g)	Aleppo 2009	Adana 2009	Adana 2010 (g m^{-2})	Aleppo 2009	Adana 2009	Adana 2010 (%)	Aleppo 2009
Norin-61	260	Bread	120	977	783	633	10,510	10,662	11,262	39.6	33.9	24.2	415	313	273	42.7	40.1	43.1
Chinese	184-2	Bread	132	1291	1428	511	14,092	8625	6501	28.2	23.1	18.3	390	374	119	30.3	26.2	23.1
Thatcher	325	Bread	143	1240	1639	860	8791	4654	12,648	33.9	17.1	17.6	296	268	223	24.0	16.2	25.9
Selkerk	333	Bread	143	1389	1471	759	11,802	5050	8740	28.0	21.2	23.5	337	239	201	24.2	16.2	26.3
ACNavigator	PI 610666	Durum	128	1119	1323	745	11,024	20,885	9564	41.0	43.3	23.6	445	481	224	39.8	36.4	30.1
Langdon	Kobe U.	Durum	146	1436	1320	664	9291	8481	8174	31.6	28.5	19.4	290	295	158	20.3	22.7	23.8
Golden	328	Durum	148	1098	1221	816	7592	5228	6258	36.6	29.1	35.4	262	179	221	23.9	14.7	27.1
Pentad	135	Durum	150	1314	1348	863	8130	3166	9114	35.6	17.4	18.0	290	181	164	22.3	13.3	19.1
Polonicum (Polish)	143	Emmer	149	1462	1634	775	4161	7108	4354	44.9	37.8	46.1	183	188	201	12.5	11.6	25.8
Turgidum (Poulard)	148	Emmer	149	1130	1949	801	6708	2903	8553	27.9	18.0	19.9	186	154	168	16.5	8.7	21.0
Dicoccum (French 64)	118	Emmer	160	1137	1892	522	8163	780	2174	29.4	12.9	28.7	241	53	62	21.2	2.7	12.0
LSD$_{0.05}$			13	556	804	275	4843	3934	3700	16.6	6.3	4.8	116	106	78	5.6	5.0	4.6
ANOVA	Cultivar		****		***			***			****			****			+	
	Location & Year		****		****			****			****			****			****	
	Cultivar×Location & Year		–		***			****			****			****			ns	
Average Cultivar																		
	Norin 61				798	(0.22)		10,811	(0.04)		32.6	(0.24)		334	(0.22)		42.0	(0.04)
	Chinese				1077	(0.46)		9739	(0.4)		23.2	(0.21)		294	(0.52)		26.5	(0.14)
	Thatcher				1246	(0.31)		8698	(0.46)		22.9	(0.42)		262	(0.14)		22.0	(0.23)
	Selkerk				1206	(0.32)		8531	(0.4)		24.2	(0.14)		259	(0.27)		22.2	(0.24)
	ACNavigator				1063	(0.28)		13,824	(0.45)		36.0	(0.3)		383	(0.36)		35.4	(0.14)
	Langdon				1140	(0.37)		8649	(0.07)		26.5	(0.24)		248	(0.31)		22.2	(0.08)
	Golden				1045	(0.20)		6359	(0.20)		33.7	(0.20)		221	(0.19)		21.9	(0.29)
	Pentad				1175	(0.23)		6804	(0.47)		23.7	(0.44)		212	(0.32)		18.2	(0.25)
	polonicum (Polish)				1290	(0.35)		5208	(0.32)		42.9	(0.1)		191	(0.05)		16.6	(0.48)
	Turgidum (Poulard)				1294	(0.46)		6055	(0.48)		21.9	(0.24)		169	(0.09)		15.4	(0.40)
	Dicoccum (French 64)				1183	(0.58)		3705	(1.06)		23.7	(0.39)		119	(0.89)		12.0	(0.77)
	LSD$_{0.05}$				362			2280			5.3			57			ns	
Location & Year	Adana 2009		151		1236			9115			34.3			303			25.2	
	Adna 2010		127		1455			7049			25.7			248			19.0	
	Aleppo 2009		150		723			7940			25.0			183			25.2	
	LSD$_{0.05}$		9		136			857			2.1			21			6.7	
ANOVA	Species		****		****			ns			***			*			**	
	Location and Year		****		ns			+			ns			***			+	
	Species×Location and Year		ns		*			ns			ns			ns			ns	
Average Species																		
	Bread		134		1082			9445			25.7			287			28	
	Durum		143		1106			8909			30.0			266			24	
	Emmer		152		1256			4989			29.5			160			15	
	LSD$_{0.05}$		ns		184			ns			5.6			69			5.1	

Notes: Each data point shows the mean of three replicates from Adana and Aleppo in 2009 and four replicates from Adana in 2010. The number of days from sowing to heading is the average of the three observations from Adana in 2009 and 2010 and Aleppo in 2009. LSD$_{0.05}$ indicates a least significant difference with a probability level of 0.05, and ns indicates no significance according to Tukey's test. +, *, **, ***, **** and ns indicate significant probabilities of 0.10, 0.05, 0.01, 0.005, 0.001 and no significance, respectively. The values in parentheses following the average for each cultivar are the coefficients of variation.

Table 2. Single and partial correlation coefficients between each meteorological parameter (cumulative rainfall, average temperature and cumulative radiation) and the biological or grain yield throughout the season and after heading in cultivars of the three species of wheat.

		Single correlation coefficient			Partial correlation coefficient		
Term	Species	Cumulative rainfall	Average temperature	Cumulative radiation	Cumulative rainfall	Average temperature	Cumulative radiation
Entire season							
Biological yield	Bread	0.785**	0.828**	−0.020	0.708*	0.847**	0.619
	Durum	0.834**	0.834**	−0.341	0.743*	0.611	−0.301
	Emmer	0.629	0.903**	−0.677*	0.601	0.652	−0.772*
	Combined	0.711**	0.836**	−0.177	0.458**	0.703**	−0.051
Grain yield	Bread	0.735**	0.270	−0.412	0.856**	−0.603	−0.696*
	Durum	0.445	0.098	−0.578*	0.883**	−0.845**	−0.900**
	Emmer	0.333	−0.152	0.212	0.624	−0.560	−0.266
	Combined	0.414*	−0.040	−0.527**	0.771**	−0.705**	−0.768**
After heading							
Grain yield	Bread	0.507	−0.674*	−0.436	0.728*	−0.826**	0.468
	Durum	0.346	−0.897**	−0.509	−0.055	−0.847**	−0.085
	Emmer	0.213	−0.399	−0.137	−0.156	−0.387	−0.185
	Combined	0.432*	−0.762**	−0.450**	0.209	−0.714**	0.013

Notes: These correlations were obtained from the combined data in Adana (2009 and 2010), Turkey, and Aleppo, Syria (2009). * and ** indicate significant correlations with a probability level of 0.05 and 0.01.

Table 3. Partial regression coefficients of three independent factors (cumulative rainfall, average temperature and cumulative radiation from sowing to 30 days after heading or 30 days after heading), intercepts and significance (p) from a multiple regression analysis of the biological yield at harvest and grain yield of 11 cultivars of three wheat species in Adana (2009 and 2010), Turkey, and Aleppo, Syria (2009).

		Partial regression coefficient					Standard partial regression coefficient		
		Cumulative rainfall	Average temperature	Cumulative radiation	Intercept		Cumulative rainfall	Average temperature	Cumultive radiation
		(10^{-3} m)	(°C)	(MJ m^{-2})	(g m^{-2})	*p*	R	T	Ra
Entire season									
Biological yield	Bread	1.05*	162.68**	0.32	−2089.68**	**	0.41	0.70	0.28
	Durum	1.00*	76.37	−0.10	−79.19	**	0.56	0.42	−0.13
	Emmer	1.11	145.13	−0.85*	988.11	**	0.34	0.44	−0.46
	Combined	0.84**	153.89**	−0.03	−1168.50*	**	0.32	0.63	−0.03
Grain	Bread	0.56**	−25.24	−0.13*	650.88**	**	0.96	−0.47	−0.49
	Durum	0.68**	−62.48**	−0.26**	1427.67**	**	0.96	−0.89	−0.90
	Emmer	−0.31	25.14	0.15	−449.79		−0.76	0.64	0.76
	Combined	0.58**	−45.09**	−0.18**	1029.53**	**	0.82	−0.69	−0.66
After heading									
Grain	Bread	1.55*	−38.85**	0.50	584.88*	**	0.81	−0.81	0.43
	Durum	−0.16	−62.30**	−0.12	1649.82**	**	−0.06	−0.87	−0.09
	Emmer	−0.47	−23.25	−0.22	852.15		−0.27	−0.53	−0.27
	Combined	0.56	−35.73**	0.06	909.39**	**	0.22	−0.71	0.04

Note: *, ** and *** indicate significance with a probability level of 0.05, 0.01 and 0.001.

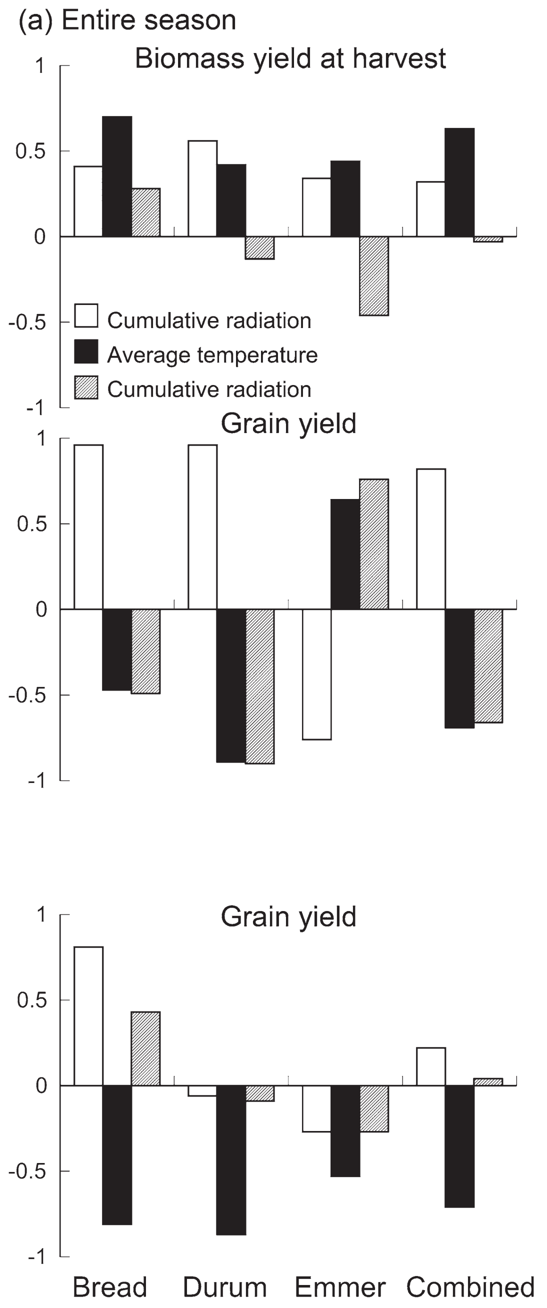

Figure 2. Standard partial regression coefficient for three meteorological factors (cumulative rainfall, average temperature and cumulative radiation) throughout the season (a) and after heading (b). The coefficients were obtained from a multiple regression analysis of the biological yield and grain yield shown in Table 2.

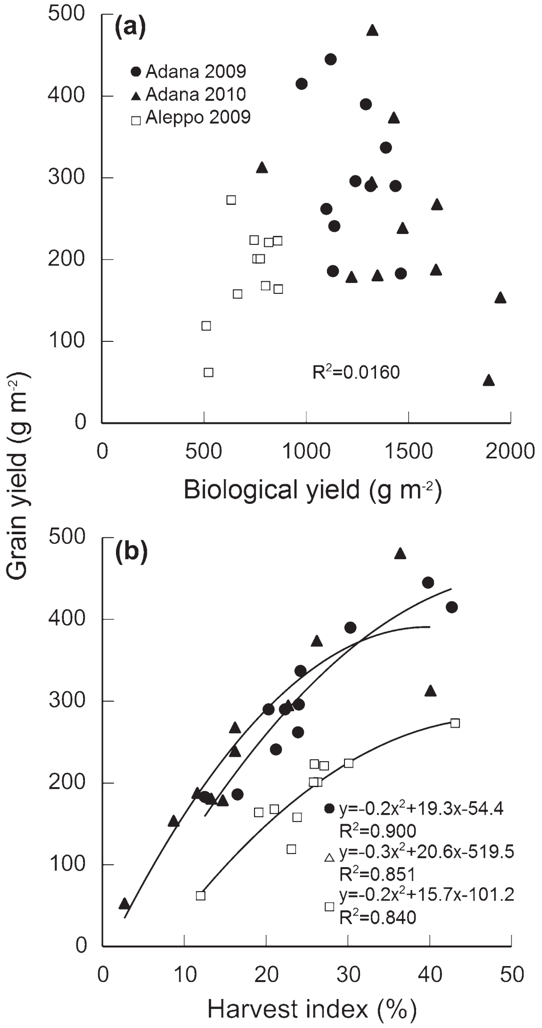

Figure 3. (a) Grain yield vs. biological yield and (b) grain yield vs. harvest index for diverse cultivars of three wheat species in Adana in 2009 and 2010 and Aleppo in 2009. Each data point is the average from three or four replicates of each genotype.

effects on the GY in most species. The standard partial regression coefficients for the parameters of these multiple regressions (Table 2) were calculated to compare the contributions of each meteorological factors on the BY and GY (Figure 2). The coefficient for the cumulative rainfall and average temperature throughout the seasons indicated higher positive contributions to the BY than the cumulative radiation and the radiation had negative contributions to the BY in almost species (Figure 2(a)). The coefficient for the cumulative rainfall throughout the seasons indicated a higher positive contribution on the GY only in bread and durum wheat, but the average temperature and cumulative radiation showed higher negative contributions in all species except emmer wheat. The coefficient for cumulative rainfall after heading indicated a higher contribution on the GY only in bread wheat, even though the average temperature had a higher negative contribution on all wheat species, and the coefficient for cumulative radiation indicated a small or negative contribution in durum and emmer wheat (Figure 2(b)).

According to these results, the rainfall and temperature generally positively affected the BY, but temperature had negative effects on the GY, particularly after heading. The negative effect of radiation on the GY was due to the increase in the average temperature with increases

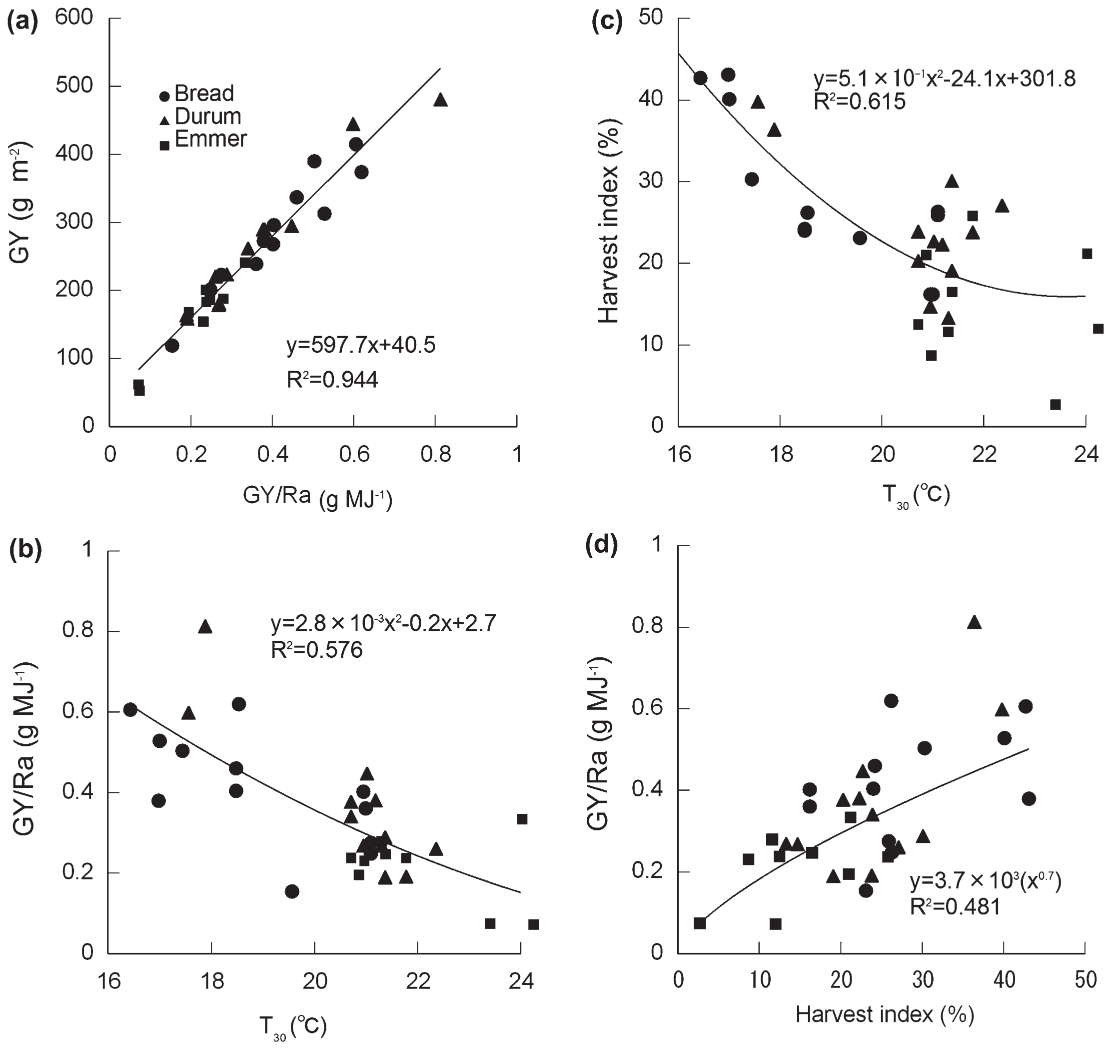

Figure 4. (a) Grain yield (GY) and radiation-use efficiency of grains [GY/Ra, where Ra is the cumulative radiation for 30 days after heading (D_{30})], (b) GY and average temperature for D_{30} (T_{30}), (c) harvest index (HI), average temperature for D_{30} (T_{30}) and GY/Ra in diverse cultivars of bread, durum and emmer wheat. All data from Adana in 2009 and 2010 and Aleppo in 2009 were combined. Each data point is the average of three (Adana in 2009 and 2010) or four (Aleppo in 2009) replicates.

in the radiation. Significant relationships were found between the average temperature and cumulative radiation throughout the entire growing seasons: r = 0.675 (p < 0.005) in bread, r = 0.851 (p < 0.001) in durum and r = 0.828 (p < 0.001) in emmer wheat.

Biological yield, grain yield and harvest index

There were no significant relationships between the GY and BY during the three observations. In Adana in 2009 and 2010, the GY was widely distributed within a narrow BY range, but the distribution was smaller in Aleppo in 2010 than in Adana in both years (Figure 3(a)). However, the GY was closely positively related to the HI across all cultivars in each observation, where the slope showing the relationship between the GY and HI was clearly lower in Aleppo than in Adana in 2009 and 2010 (Figure 3(b)).

The GY/Ra was highly correlated with the GY across all cultivars (Figure 4(a)) and was negatively correlated with the average temperature for D_{30} (Figure 4(b)). The HI decreased with an increase in the average temperature for D_{30} (Figure 4(c)); thus, GY/Ra was strongly related to the HI (Figure 4(d)).

Based on the day of flowering and physiological maturity recorded for Adana in 2009 and 2010, a low HI accompanied the reduction in the number of days from flowering to maturity, i.e. the effective grain filling period (Figure 5(a)). The grain filling period was negatively related to the temperature post anthesis (Figure 5(b)).

Across all cultivars, the GY and HI decreased with increases in the time from sowing to heading for each

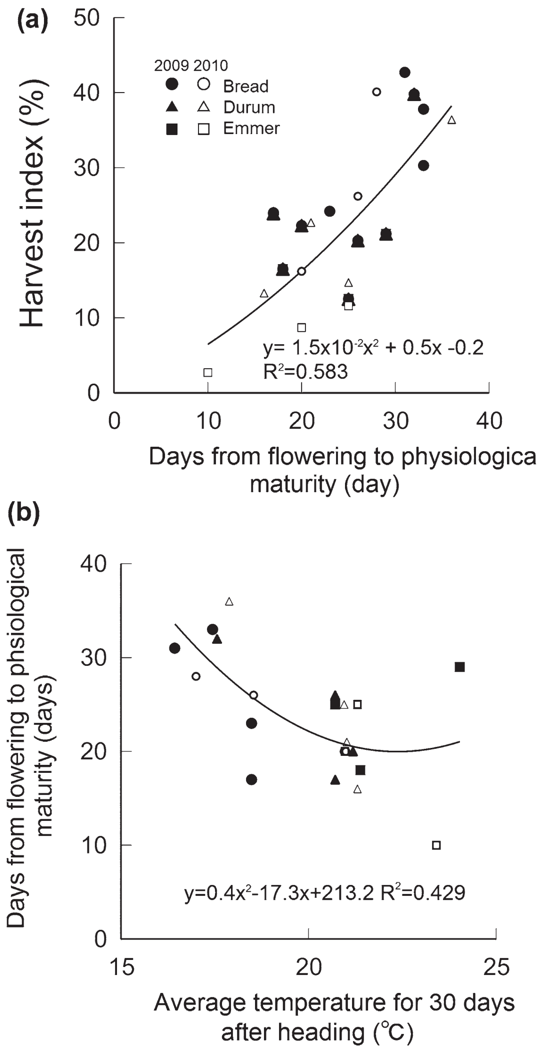

Figure 5. (a) Harvest index vs. days from heading to physiological maturity (D_{FM}) and (b) D_{FM} vs. the average temperature for D_{30} for different species of wheat in Adana in 2009 and 2010.

observation (Figure 6(a) and (b)). The late heading date resulted in a higher average temperature for D_{30} (T_{30}) and a greater plant water shortage, as provided by the cumulative rainfall minus evaporation (Figure 6(c) and (d)). The delay of heading day accompanied a decrease in the cumulative rainfall minus evaporation for D_{30}, and there was a significant correlation between the GY and the cumulative rainfall minus evaporation ($r = 0.608$, $p < 0.001$).

The cv for the BY and particularly the HI of each cultivar increased with delays in the heading time (Figure 7). The cv for the BY and the HI in most of the emmer wheat cultivars was greater than that in the bread and durum wheat cultivars. As a result, the GY of the late-heading cultivars, such as most of the emmer wheat cultivars, having higher instability of the BY and the HI, was lower.

The cv for CT was higher in the late-heading cultivars than in the early-heading cultivars (Table 4). The Tb of most cultivars, except several of the early-heading cultivars, ranged near 0; thus, the CT of the cultivars used in this study ranged widely from 1070 to 1870 °C.

Discussion

The HI is an important factor influencing the GY rather than the BY in diverse wheat cultivars in each cultivated site in these Mediterranean zones due to the close relationship between the GY and BY across cultivars in each cultivated site (Figure 3). Furthermore, the HI was closely negatively related with T_{30} (Figure 4), which suggested that high temperature was closely related to suppression of the HI; thus, high temperatures after anthesis decreased the available grain-filling period across cultivars and the HI (Figure 5). Furthermore, escaping high temperatures maintains the HI by avoiding sterility. Sterility can be avoided in wheat if the temperatures do not exceed 24 °C during the week before flowering (Vara Prasad & Djanaguiraman, 2014). In fact, at Aleppo, some wheat cultivars might have suffered temperatures exceeding the critical temperature during the sensitive time (Figure 1). As a result, early heading traits contributed to the more effective use of water and radiation resources to enhance the GY (Figure 6). Thus, the heading time of each cultivar is one of the key traits determining the HI. More early heading cultivars of bread and durum than of emmer allowed realization of the potential GY under terminal stress conditions (Table 1). However, even within the same cultivar, the HI varied among the observed sites, particularly in the late-heading cultivars (Figure 7); thus, the risk of a decrease in the HI is higher in the late-heading cultivars. The high-yield benefit of the early heading trait has been shown in bread wheat under irrigated conditions in heat-stressed areas of South Asia (Mondal et al., 2013). However, within the same HI range, the GY in Aleppo was lower than that in Adana due to the low BY; thus, the BY is an additional factor determining the GY under severe environmental stress (Table 1 and Figure 3).

In the Mediterranean, water shortage due to low rainfall is one of the most dominant environmental factors determining the wheat yield (Turner, 1996). Water deficit due to the cessation of rainfall during the terminal growth stage decreases resource assimilation, resulting in decreases in the GY and BY (Kobata et al., 1992, 2012; Turner, 1996). In our results, rainfall exerted a positive effect on BY (Table 2 and Figure 2), whereas a high BY did not result in a higher GY in all cases (Figure 3). Radiation had a negative effect on the BY (Tables 2 and 3 and Figure 2); plants can receive adequate radiation after the winter season, but the

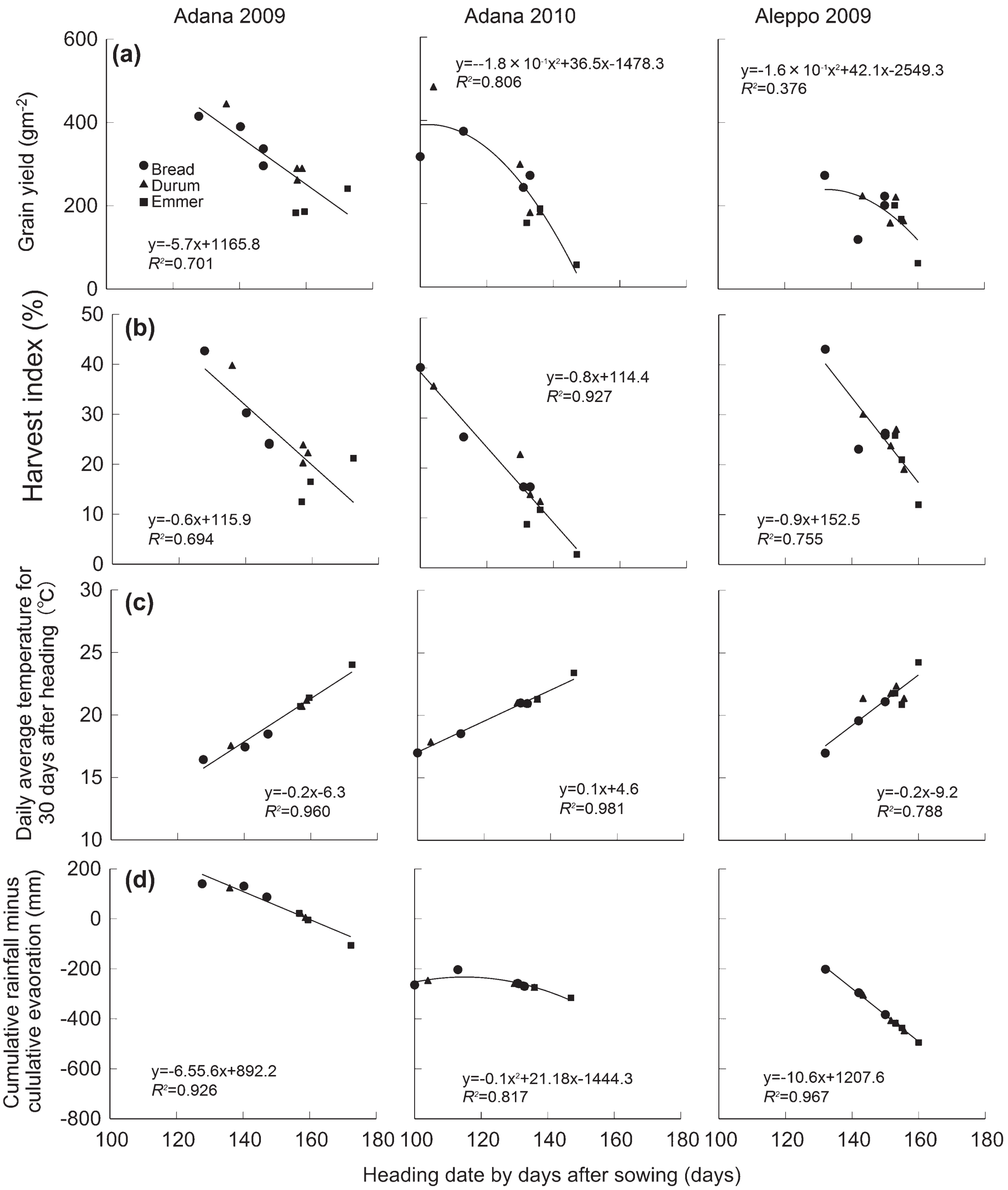

Figure 6. (a) Grain yield, harvest index, (b) average temperature for D_{30} and (c) R – E cumulative rainfall minus evaporation for D_{30} vs. number of days between sowing and heading across wheat species in Adana in 2009 and 2010 and Aleppo in 2009.

higher temperature due to high radiation at the terminal stage can reduce the HI. As a result, a higher HI would increase radiation use during the grain-filling period (Figure 4).

Across diverse cultivars in the studied areas, our results suggested that the partitioning of assimilates to grains is more important for a high GY than total biomass productivity. Although direct stress resistance is important among genotypes with similar flowering habitats (Kramer, 1980; Turner, 1996), early flowering in wheat can effectively avoid terminal stresses under future conditions of elevated temperature and decreased rainfall due to the stability of the HI and BY. The breeding of landrace genetic resources is suggested to yield increases in resistances to high temperature and drought induced by climate changes (Lopes et al., 2015). The late-flowering traits sometimes observed in old cultivars such as emmer wheat should be removed to develop more stress-resistant cultivars under terminal high-temperature and water-deficit conditions when these landrace genotypes will be used for breeding.

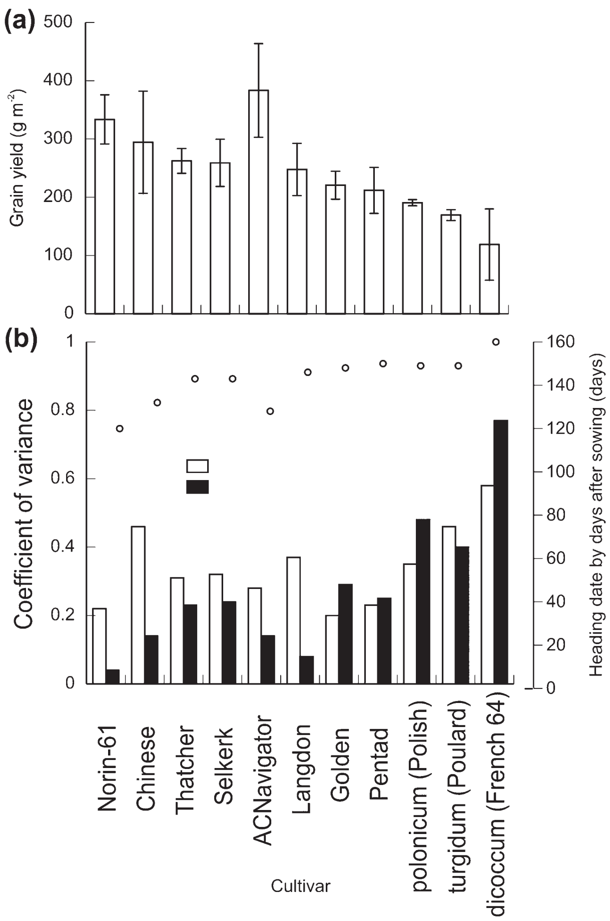

Figure 7. (a) Average grain yield and standard error and (b) heading date (open circle) and coefficient of variation of the biological yield and harvest index of 11 diverse cultivars of bread, durum and emmer wheat in Adana in 2009 and 2010 and Aleppo in 2009. The data used in the analysis are shown in Table 1.

Table 4. Base temperature (Tb) from emergence to heading for cultivars of different wheat species and coefficient of variation (cv) for the cumulative temperature (CT), calculated as Σ(T – Tb), for Adana in 2009, Adana in 2010 and Aleppo in 2009. T is the daily temperature (°C).

Cultivar	Tb (°C)	cv	CT (°C)
AC Navigator	2.0	0.01	1030
Norin	1.0	0.08	1069
Chinese	1.0	0.08	1243
Shelkerk	0.0	0.12	1537
Thatcher	0.0	0.13	1552
Golden	0.0	0.11	1650
Langdon	0.0	0.12	1654
Polanicum	0.0	0.12	1663
Turgidum	0.0	0.10	1666
Pentad	0.0	0.10	1691
Dicoccum	0.0	0.14	1867
Average	0.4	0.10	1511
cv	1.9	0.3	0.2

Note: The minimum cv for the Tb was obtained when a Tb from 0 to 10 °C was inputted into Σ(T – Tb).

Conclusion

Under rain-fed conditions in the Mediterranean zone of Turkey and Syria, the HI was identified as an important factor determining the GY across cultivars of diverse species of wheat under terminal high-temperature and water-shortage conditions.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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