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Diurnal photosynthesis, water use efficiency and light use efficiency of wheat under Mediterranean field conditions

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Abstract: *Photosynthesis and transpiration rates of wheat leaves (Triticum aestivum L.) were measured at 30 min intervals under Mediterranean field conditions, using Photosynthesis Monitor system (PM-48M). The dynamics of net photosynthetic rate (P_N), transpiration rate (E_T) , water use efficiency (WUE), light use efficiency (LUE), stomatal conductance (g_s), photosynthetically active radiation (PAR), air temperature (T), relative humidity (RH), and atmospheric CO_2 concentration (C_{atm}) were quantified at five rainfed wheat sites with the same stages of development (midflowering) along south-to-north and east-to-west transects for eight days in April. Diurnal P_N (3.6 to 6.6 $\mu mol\ m^{-2}\ s^{-1}$), PAR (392 to 564 $\mu mol\ m^{-2}\ sec^{-1}$), LUE (0.006 to 0.015) and WUE (0.0001 to 0.011) did not vary significantly across all five wheat sites ($p>0.05$). P_N and E_T were strongly coupled and highly correlated with PAR ($p<0.001$). Best multiple linear regression (MLR) models accounted for 92% of variations in P_N as a function of PAR and E_T, and 90% in E_T as a function of PAR and RH ($p<0.001$). P_N exhibited a peak at mid-morning, and a photosynthetic midday depression under the limiting effects of high evaporative demand. Diurnal variations in WUE and LUE showed a bimodal behavior with the maximum values in early morning and late afternoon. As the impacts of global climate change become increasingly felt, continuous measurements of climate-crop-soil-management interactions under natural conditions play a pivotal role not only in exploring changes in ecophysiological properties of strategic crops for food security such as wheat but also in devising preventive and mitigative management practices to ensure sustained agricultural productivity.*

Key words: *Photosynthesis, Light use efficiency, Transpiration, Water use efficiency, Wheat*
PDF of full length paper is available with author ***(*fevrendilek@yahoo.com)***

Introduction

Turkey is the centre of origin, diversification, and domestication for many progenitor crop species used in Mediterranean and temperate agricultural systems such as wheat, barley, oats, lentil, chickpea, apple, and pear (World Bank, 1993; Bennett *et al.*, 1998; Lev-Yadun *et al.*, 2000). Wheat is a significant stable food for majority of the world population, particularly in (semi)-arid zones of the world (Datta *et al.,* 2007). Turkey is one of the major wheat producers, with 3.3% (21 million metric tons) of world wheat production, 4.3% (9.4 million ha^{-1}) of global total wheat area, and an average yield of 2234 kg ha^{-1} (global average yield of 2906 kg ha^{-1}) in 2004 (FAO, 2005). Achieving future wheat yield increase through breeding and management practices requires a better understanding of the coupled dynamics of crop ecophysiological processes under natural conditions, particularly, given the projections of global climate change (Gupta *et al.,* 2007).

Changing global climate is most likely to further amplify not only uncertainties associated with the predictions of specific crop responses but also the importance of mitigative management measures for food security and agricultural sustainability, especially in the semi-arid regions. Unlike experimental studies done in controlled environments such as growth chambers, greenhouses, and plastic enclosures, few attempts in the field conditions have been made to explore concomitant interactions among photosynthetic rate (P_N), transpiration rate (E_T), photosynthetically active radiation (PAR), atmospheric CO_2 concentration (C_{atm}), relative humidity (RH), and air temperature (T) (Nielsen and Halvorson, 1991; Sadras *et al.*, 1991; Abbate *et al.*, 1995; Van den Boogaard *et al.*, 1995; Yang *et al.*, 2003; Evrendilek *et al.*, 2005). Such measurements are needed to understand interactions of these processes at the leaf scale and validate models of biogeochemical cycles. The objective of the study was to quantify diurnal patterns of variations of leaf P_N and E_T of wheat (*Triticum aestivum* L.) leaves and their interactions with PAR, C_{atm}, RH and T in Mediterranean field conditions of the Cukurova region (Adana, Turkey).

Materials and Methods

Study region: Study sites (37°04´-36°46´N, 35°20´-35°25´E) are located in the Cukurova region, a southern Mediterranean region of Turkey, at an altitude 6 to 150 m above sea level (Fig. 1.). A typical Mediterranean climate prevails in the study region with the long term mean annual temperature, precipitation, potential evapotranspiration and incident PAR of 18.7°C, 647 mm, 1320 mm and 284 MJ m^{-2}, respectively. Minimum and maximum air temperatures are -8.1°C in January and 45.6°C in August, respectively. About 87% of precipitation falls during the winter (November to May). Maximum incident PAR occurs in August (415 MJ m^{-2} $month^{-1}$) and the minimum in December (141 MJ m^{-2} $month^{-1}$).

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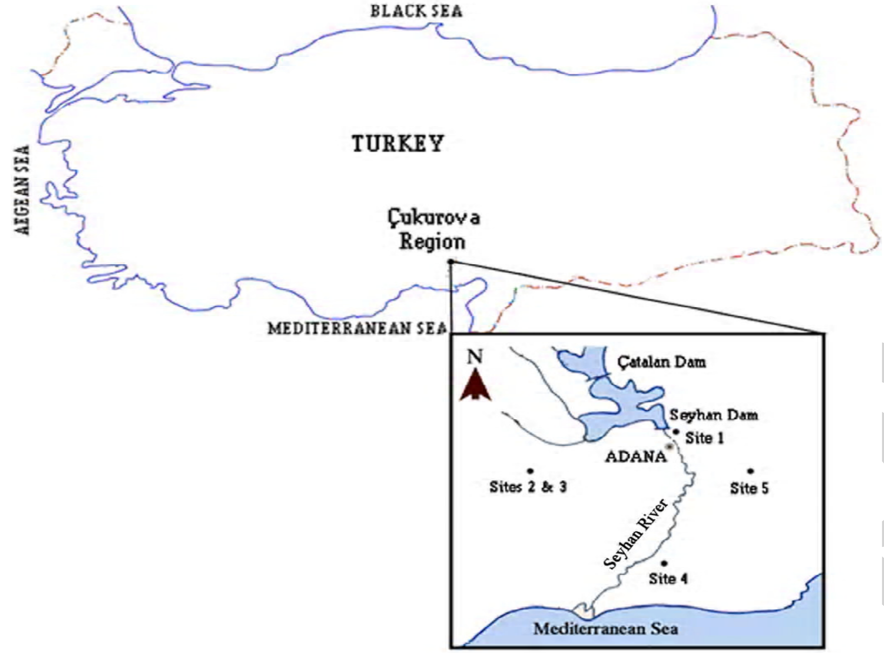

Fig. 1: Location of five wheat sites in the study region (Site $_1$ = the experimental station of the Department of Agricultural Structures and Irrigation of the Cukurova University; Site $_2$ = the Tarsus Agricultural Research Centre; Site $_3$ = the Topcu station of the Tarsus Agricultural Research Centre and Sites $_4$ and $_5$ = private wheat fields)

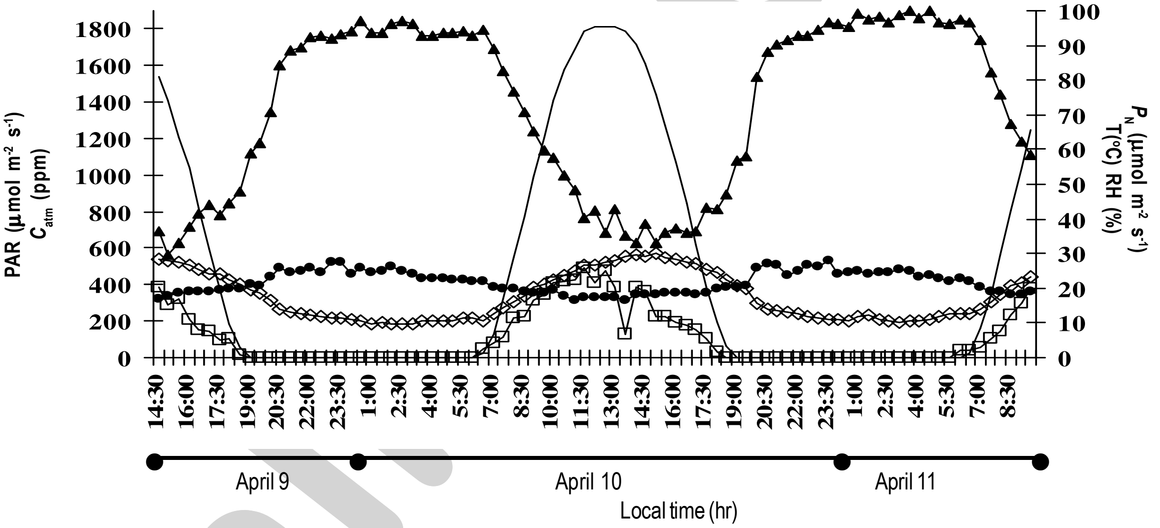

Fig. 2: Diurnal patterns of leaf net photosynthetic rate (P_N, □), photosynthetically active radiation (PAR, –), air temperature (T, ◇), relative humidity (RH, ▲), and atmospheric CO_2 concentration (C_{atm}, ●) measured at a wheat field of the experimental station of the Department of Agricultural Structures and Irrigation of the Cukurova University in the north on April 9 to 11, 2005

The surface soils (0-30 cm) with different proportions of sand, silt and clay fractions in the study locations were predominantly fine-textured soils. The soils of the wheat sites displayed a wide range of variation with respect to field capacity and permanent wilting point which corresponded to -0.03 MPa and -1.5 MPa, respectively in matric potential. Soil dry bulk densities ranged between 1.22 and 1.35 g cm^{-3}. The soils had no salinity problem and total soluble salt contents were under 0.1%. Soils of the study sites had slightly alkaline pH values of 7.5 to 7.7 and were determined to be poor in soil organic matter (1.18 to 2.37%) (Table 1).

Sampling: Under the detailed climatic and soil information given above for the five wheat sites, diurnal monitoring was carried out along south-to-north and east-to-west transects of the Cukurova region on April 9 to 16 of 2005 (north Site$_1$) the experimental station of the Department of Agricultural Structures and Irrigation of Cukurova

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Table - 1: Some physical and chemical properties of soil samples (0-30 cm) taken from wheat fields along south-to-north and west-to-east transects of the Cukurova region (n = 4)

Sites	Soil texture (clay-silt-sand %)	Field capacity (% vol.)	Wilting point (% vol.)	AWC (% vol.)	BD (g cm^{-3})	Salt (%)	pH	SOM (%)
1	Clay 56^{a}-24^{a}-20^{a}	0.45(0.01)^{a}	0.32(0.01)^{a}	0.13(0.02)^{a}	1.22(0.02)^{a}	0.07(0.02)^{a}	7.7(0.04)^{a}	1.70(0.29)^{ac}
2	Silty clay 49^{b}-42^{b}-9^{b}	0.31(0.01)^{b}	0.22(0.01)^{b}	0.09(0.01)^{b}	1.22(0.06)^{a}	0.07(0.01)^{a}	7.7(0.03)^{a}	1.56(0.05)^{ac}
3	Clay loam 28^{c}-40^{c}-32^{c}	0.29(0.03)^{b}	0.15(0.01)^{c}	0.14(0.04)^{a}	1.35(0.09)^{a}	0.04(0.01)^{b}	7.5(0.19)^{b}	1.18(0.23)^{a}
4	Clay loam 31^{d}-44^{b}-25^{d}	0.32(0.01)^{b}	0.22(0.02)^{b}	0.10(0.02)^{ab}	1.25(0.12)^{a}	0.04(0.01)^{b}	7.6(0.03)^{ab}	2.37(0.38)^{b}
5	Silty clay loam 35^{e}-50^{d}-15^{e}	0.32(0.03)^{b}	0.21(0.04)^{b}	0.11(0.01)^{ab}	1.33(0.15)^{a}	0.05(0.001)^{ab}	7.6(0.05)^{ab}	2.07(0.63)^{bc}
	$p<0.001$	$p<0.001$	$p<0.001$	$p<0.001$	$p<0.05$	$p<0.001$	$p<0.01$	$p<0.001$

Means with different letters for each of the variables in the columns denote significant differences determined by Tukey's test at $p<0.05$. Values in parentheses refer to standard deviations. AWC, BD, and SOM refer to available water content, bulk density, and soil organic matter, respectively. 1 = the experimental station of the Department of Agricultural Structures and Irrigation of the Cukurova University in the north, 2 = the Tarsus Agricultural Research Centre in the west, 3 = the Topcu station of the Tarsus Agricultural Research Centre in the west, 4 = a private wheat field in the south and 5 = a private wheat field in the east

University in the north for 43 hr (14:30-09:30) on April 9 to 11 (west Site$_2$) the Tarsus Agricultural Research Centre in the west for 24 hr (13:00-13:00) on April 11 to 12 (west Site$_3$), the Topcu station of the Tarsus Agricultural Research Centre in the west for 24 hr (15:30-15:00) on April 12 to 13 (south Site$_4$), a private wheat field in the south for 24 hr (18:00-18:00) on April 13 to 14 and (east Site$_5$) a private wheat field in the east for 23 hr (10:30-09:30) on April 15 to 16. Continuous time series data were collected by an automatic 4-channel open type monitoring system (PM-48M photosynthesis monitor 1.0, PhyTech, Israel) for P_N (µmol m^{-2} sec^{-1}) and E_T (mg m^{-2} sec^{-1}) of wheat leaves, C_{atm} (ppm), T (°C), RH (%) and PAR (µmol m^{-2} sec^{-1}) at 30 min intervals. In the north Site, *in-situ* E_T data and thus, WUE and g_s values could not be recorded due to a technical problem. All five wheat sites were at the same stages of development in midflowering under rainfed conditions without supplemental irrigation before the measurements.

Soil samples were taken from each of the wheat sites to depth of 0 to 30 cm in four replicates and analyzed for some physical and chemical properties (Table 1). Soil samples for analysis of soil bulk density were taken by using a steel cylinder of a 100-cm^3 volume (5 cm in diameter, and 5 cm in height). The soil samples were sieved through a 2 mm meshed sieve for chemical analyses. Bulk density was determined by the core method (Blake and Hartge, 1986), particle size distribution by the hydrometer method (Gee and Bauder, 1986), soil organic matter by the Walkey Black method (Schnitzer, 1982), soil pH according to Page *et al.* (1982), and available water capacity (AWC) by the difference between field capacity and permanent wilting point (Klute and Dirksen, 1986).

Light use efficiency (LUE), water use efficiency (WUE) and stomatal conductance (g_s) were estimated as follows:

LUE = P_N (µmol m^{-2} sec^{-1}) / incident PAR (µmol m^{-2} sec^{-1})....... (1)

WUE = P_N (µmol m^{-2} sec^{-1}) / E_T (µmol m^{-2} sec^{-1}) .... (2)

g_s = LUE / WUE .... (3)

Stomatal conductance is a measure of transpiration per unit intercepted PAR where soil evaporation is a negligible part of evapotranspiration (Sadras *et al.*, 1991; Caviglia and Sadras, 2001).

Statistical analyses: Data analyses were carried out, using the statistical software Minitab 13.32. A correlation matrix was performed for the environmental variables, using Pearson correlation coefficient. Following one-way analysis of variance (ANOVA), Tukey multiple comparison test was used to determine significant differences among mean hourly P_N and E_T values of the five wheat sites. Simple and multiple linear regression (MLR) models of the response variables were performed as a function of the explanatory variables of PAR, T, and RH. Dummy variable regression was used to compare intercepts and slopes of simple linear regression models for the wheat sites. The best subset regression procedure was used to select MLR models with the highest adjusted coefficient of determination (R^2_{adj}) and smallest C_p:

$$C_p = (SSE_p / MSE_m) - (n\text{-}2p) \quad (4)$$

where SSE_p is the sum of squared errors (SSE) for the best model with *p* parameters including the intercept, *p* is the number of parameters in the model; MSE_m is the mean of squared errors (MSE) for the model with all *m* predictors and *n* is the sample size.

Results and Discussion

Spatial patterns of diurnal trends: Microclimatic conditions during the dates of the measurements in the wheat sites were typical of spring months of the Cukurova region. As presented in the correlation matrix, the five independent wheat sites show a close concordance in terms of the direction and shape of the relationships among the measured variables (Table 2). The matrix of correlation coefficients revealed that P_N, E_T, PAR, T, LUE, WUE and g_s were positively correlated for all the sites. A negative correlation was detected both

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Table - 2: A correlation matrix of net photosynthetic rate (P_N), transpiration rate (E_T), light use efficiency (LUE), water use efficiency (WUE), stomatal conductance (g_s), photosynthetically active radiation (PAR), air temperature (T), relative humidity (RH), and atmospheric CO_2 concentration (C_{atm}) for each of the five wheat sites

	C_{atm}	T	RH	PAR	P_N	E_T	LUE	WUE
T	-0.85*** -0.88*** -0.81*** -0.30* -0.78***							
RH	0.83*** 0.91*** 0.81*** 0.20 0.82***	-0.98*** -0.97*** -0.98*** -0.90*** -0.98***						
PAR	-0.80*** -0.77*** -0.73*** -0.56*** -0.65***	0.84*** 0.88*** 0.87*** 0.68*** 0.83***	-0.78*** -0.83*** -0.86*** -0.69*** -0.85***					
P_N	-0.77*** -0.84*** -0.88*** -0.70*** -0.83***	0.76*** 0.84*** 0.82*** 0.65*** 0.86***	-0.70*** -0.84*** -0.82*** -0.69*** -0.91***	0.93*** 0.88*** 0.81*** 0.95*** 0.85***				
E_T	- --0.69*** -0.76*** -0.43** -0.66***	- -0.83*** 0.89*** 0.65*** 0.89***	- --0.76*** -0.88*** -0.66*** -0.89***	- -0.87*** 0.94*** 0.92*** 0.90***	- -0.76*** 0.80*** 0.83*** 0.81***			
LUE	-0.33** -0.32* -0.17 -0.39** -0.33*	0.16 0.25 0.02 0.32* 0.17	-0.14 -0.33* -0.02 -0.34* -0.27	0.20 0.01 -0.04 0.23 0.14	0.29** 0.26 0.18 0.40** 0.39*	 -0.03 -0.02 0.11 0.13		
WUE	- -0.13 -0.63*** -0.37** -0.41**	- -0.09 0.50*** 0.13 0.10	- --0.13 -0.50*** -0.15 -0.20	- -0.12 0.38** 0.21 0.15	- -0.30* 0.68*** 0.39** 0.42**	- -0.08 0.34* 0.07 0.02	- -0.34* 0.52*** 0.63*** 0.50**	
g_s	- -0.54*** -0.21 -0.49*** -0.68***	- -0.62*** 0.13 0.61*** 0.82***	- --0.65*** -0.14 -0.68*** -0.86***	- -0.27 0.10 0.71*** 0.60***	- -0.41** 0.21 0.70*** 0.77***	- -0.43** 0.17 0.76*** 0.78***	- -0.70*** 0.91*** 0.46** 0.49**	- 0.17 0.34* 0.23 0.13

*, ** and *** refer to $p \leq 0.05$, $p \leq 0.01$ and $p \leq 0.001$, respectively. No asterisk means "not significant". Pearson correlation coefficients (r values) in each of the matrix cells refer to the wheat sites1, 2, 3, 4 and 5, respectively

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between RH and T and between C_{atm} and P_N, E_T, PAR, T, LUE, WUE and g_s. However, differences among the wheat sites were noticed in the strength of the relationships among the variables as shown by the values of the correlation coefficients (r) in Table 2.

Mean diurnal values of P_N (3.6 to 6.6 μmol m^{-2} s^{-1}), PAR (392 to 564 μmol m^{-2} sec^{-1}), LUE (0.006 to 0.015), and WUE (0.0001 to 0.011) did not vary significantly across the wheat sites ($p > 0.05$) (Table 3). Mean diurnal minimum and maximum values ranged from 6.2 mg m^{-2} s^{-1} in the east $Site_5$ to 16 mg m^{-2} s^{-1} in the west $Site_2$ for E_T ($p < 0.01$); from 0.3 in the south and east sites to 1.3 in the west $Site_2$ for g_s ($p \leq 0.001$); from 373 ppm in the south $Site_4$ to 413 ppm in the north $Site_1$ for C_{atm} ($p < 0.001$), from 17.2°C in the east $Site_5$ to 24.6°C in the west $Site_3$ for T ($p < 0.001$) and from 41.5% in the west $Site_3$ to 72.7% in the north $Site_1$ for RH ($p < 0.001$), respectively.

Table - 3: Spatial comparison of mean diurnal changes in net photosynthetic rate (P_N), transpiration rate (E_T), light use efficiency (LUE), water use efficiency (WUE) and stomatal conductance (g_s) of wheat leaves and in photosynthetically active radiation (PAR), air temperature (T), relative humidity (RH) and atmospheric CO_2 concentration (C_{atm}) at five sites

Variables	**Sites**					***p***
	1	**2**	**3**	**4**	**5**	
	1(n = 87)	**2(n = 49)**	**3(n = 48)**	**4(n = 49)**	**5(n = 41)**	
P_N (µmol m^{-2} s^{-1})	5.3 ± 8.2^{a}	6.6 ± 8.5^{a}	3.6 ± 4.6^{a}	4.7 ± 6.7^{a}	4.9 ± 7.3^{a}	>0.05
E_T (mg m^{-2} s^{-1})	-	16.0 ± 23.6^{a}	13.3 ± 15.9^{ab}	6.8 ± 8.8^{b}	6.2 ± 7.9^{b}	<0.01
PAR (µmol m^{-2} s^{-1})	440 ± 625^{a}	436 ± 605^{a}	444 ± 584^{a}	564 ± 723^{a}	392 ± 551^{a}	>0.05
T (°C)	17.4 ± 6.8^{a}	21.8 ± 6.5^{bc}	24.6 ± 6.4^{b}	20.6 ± 3.5^{cd}	17.2 ± 5.3^{ad}	<0.001
RH (%)	72.7 ± 24.4^{a}	59.2 ± 15.7^{b}	41.5 ± 12.8^{c}	65.4 ± 19.4^{ab}	69.0 ± 19.1^{ab}	<0.001
C_{atm} (ppm)	413 ± 60^{a}	395 ± 57^{ab}	376 ± 26^{b}	373 ± 37^{b}	386 ± 36^{b}	<0.001
LUE	0.008 ± 0.01^{a}	0.015 ± 0.02^{a}	0.009 ± 0.018^{a}	0.006 ± 0.008^{a}	0.011 ± 0.017^{a}	>0.05
WUE	-	0.002 ± 0.04^{a}	0.0001 ± 0.01^{a}	0.007 ± 0.04^{a}	0.011 ± 0.09^{a}	>0.05
g_s	-	1.3 ± 1.8^{a}	1.2 ± 2.4^{a}	0.3 ± 0.3^{b}	0.3 ± 0.5^{b}	≤ 0.001

Means with different letters for each of the variables in the rows denote significant differences determined by Tukey's test. 1 = the experimental station of the Department of Agricultural Structures and Irrigation of the Çukurova University in the north, 14:30-9:30 April 9-11, 2 = the Tarsus Agricultural Research Centre in the west, 13:00-13:00 April 11-12, 3 = the Topcu station of the Tarsus Agricultural Research Centre in the west, 15:30-15:00 April 12-13, 4 = a private wheat field in the south, 18:00-18:00 April 13-14 and 5 = a private wheat field in the east, 10:30-9:30 April 15-16

Table - 4: Simple linear regression models of net photosynthetic rate (P_N) as a function of photosynthetically active radiation (PAR), air temperature (T), relative humidity (RH), and transpiration rate (E_T) (p<0.001)

Response variable P_N (µmol m^{-2} s^{-1})	**Intercept**	**Explanatory variable**				***R^2* (%)**
		PAR (µmol m^{-2} s^{-1})	**T (°C)**	**RH (%)**	**E_T (mg m^{-2} s^{-1})**	
P_{N1}	-0.12^{a}	0.012a				87.9
P_{N2}	1.18^{a}	0.012a				78.6
P_{N3}	0.70^{a}	0.006b				66.8
P_{N4}	-0.26^{a}	0.008c				90.3
P_{N5}	0.51^{a}	0.011a				72.4
P_{N1}	-10.8^{a}		0.92^{a}			58.4
P_{N2}	-17.6^{b}		1.11^{a}			72.0
P_{N3}	-11.0^{a}		0.59^{b}			67.2
P_{N4}	-20.7^{b}		1.23^{a}			42.3
P_{N5}	-15.4^{ab}		1.18^{a}			74.1
P_{N1}	22.6^{ad}			-0.23^{a}		49.9
P_{N2}	33.9^{b}			-0.46^{b}		71.9
P_{N3}	16.1^{c}			-0.30^{ac}		68.3
P_{N4}	19.6^{cd}			-0.22^{a}		42.7
P_{N5}	29.2^{ab}			-0.35^{c}		84.4
P_{N2}	2.22^{a}				0.27^{a}	58.2
P_{N3}	0.44^{a}				0.23^{a}	64.7
P_{N4}	0.35^{a}				0.63^{b}	68.9
P_{N5}	0.28^{a}				0.75^{b}	66.2

Means with different letters for intercepts and slopes of the variables in the columns denote significant differences determined by dummy variable regression at p <0.05. 1 = the experimental station of the Department of Agricultural Structures and Irrigation of the Çukurova University in the north, 14:30-9:30 April 9-11, 2 = the Tarsus Agricultural Research Centre in the west, 13:00-13:00 April 11-12, 3 = the Topcu station of the Tarsus Agricultural Research Centre in the west, 15:30-15:00 April 12-13, 4 = a private wheat field in the south, 18:00-18:00 April 13-14 and 5 = a private wheat field in the east, 10:30-9:30 April 15-16

Across the related sites, E_T and g_s were positively associated in the same decreasing order of the west Site$_2$ > west Site$_3$ > south Site$_4$ > east Site$_5$. Mean diurnal g_s values of the west sites$_{2-3}$ were significantly higher than those of the south and east sites ($p \leq 0.001$). High ratios of P_N to E_T and low g_s values observed in the south and east sites indicated an increase in WUE. Increasing order of mean leaf E_T and g_s in the east Site$_5$ < south Site$_4$ < west Site$_3$ < west Site$_2$ was reflected in decreasing order of mean soil available water content (AWC) in the west Site$_3$ > east Site$_5$ > south Site$_4$ > west Site$_2$. The reason for the difference in the corresponding inverse relationship between mean leaf E_T and g_s and mean soil AWC of the wheat sites may be that the west Site$_3$ had the lowest wilting point among the

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Table - 5: Simple linear regression models of transpiration rate (E_T) as a function of photosynthetically active radiation (PAR), air temperature (T), relative humidity (RH), and net photosynthetic rate (P_N) (p <0.001)

Response variable E_r (mgol m^{-2} s^{-1})	Intercept	Explanatory variable				R^2 (%)
		PAR (µmol m^{-2} s^{-1})	T (°C)	RH (%)	P_N (µmg m^{-2} s^{-1})	
E_{T2}	1.17^a	0.034^a				76.1
E_{T3}	1.99^a	0.025^b				88.6
E_{T4}	0.52^a	0.011^c				85.7
E_{T5}	1.08^a	0.013^c				82.3
E_{T2}	-49.8^a		3.02^a			69.2
E_{T3}	-40.7^{ac}		2.20^b			79.2
E_{T4}	-26.7^{bc}		1.63^{bd}			43.5
E_{T5}	-16.8^b		1.34^{cd}			80.6
E_{T2}	84.2^a			-1.15^a		58.6
E_{T3}	58.8^b			-1.09^a		78.2
E_{T4}	26.5^c			-0.29^b		43.5
E_{T5}	31.9^c			-0.37^b		80.4
E_{T2}	2.03^a				2.11^a	58.2
E_{T3}	3.50^a				2.74^a	64.7
E_{T4}	1.76^a				1.08^b	68.9
E_{T5}	1.85^a				0.88^b	66.2

Means with different letters for intercepts and slopes of the variables in the columns denote significant differences determined by dummy variable regression at p<0.05. 1 = the experimental station of the Department of Agricultural Structures and Irrigation of the Cukurova University in the north, 14:30-9:30 April 9-11, 2 = the Tarsus Agricultural Research Centre in the west, 13:00-13:00 April 11-12, 3 = the Topcu station of the Tarsus Agricultural Research Centre in the west, 15:30-15:00 April 12-13, 4 = a private wheat field in the south, 18:00-18:00 April 13-14 and 5 = a private wheat field in the east, 10:30-9:30 April 15-16

Table - 6: Multiple linear regression models of net photosynthetic rate(P_N) and transpiration rate (E_T) as a function of photosynthetically active radiation (PAR), air temperature (T), relative humidity (RH), net photosynthetic rate (P_N), and transpiration rate (E_T) (p<0.001)

Response variable	Intercept	Explanatory variable					R^2_{adj} (%)
		PAR (µmol m^{-2} s^{-1})	T (°C)	RH (%)	E_T (mg m^{-2} s^{-1})	P_N (%)	
P_{N1}	1.53	0.0135	-0.12				87.9
P_{N2}	14.5	0.0083		-0.194			81.8
P_{N3}	9.32	0.0032		-0.172			71.4
P_{N4}	-0.127	0.0119			-0.269		91.7
P_{N5}	88.0	0.0030	-1.81	-0.770			90.9
E_{T2}	-102	0.0225	2.94	0.750			78.0
E_{T3}	19.6	0.0189		-0.352			90.3
E_{T4}	0.346	0.0173				-0.672	87.8
E_{T5}	-8.60	0.0075	0.690				88.1

1 = The experimental station of the Department of Agricultural Structures and Irrigation of the Cukurova University in the north, 14:30-9:30 April 9-11, 2 = the Tarsus Agricultural Research Centre in the west, 13:00-13:00 April 11-12, 3 = the Topcu station of the Tarsus Agricultural Research Centre, 15:30-15:00 April 12-13, 4 = a private wheat field in the south, 18:00-18:00 April 13-14 and 5 = a private wheat field in the east, 10:30-9:30 April 15-16

wheat sites and a field capacity similar to those of the other sites, thus having the maximum AWC (p <0.001) (Table 1).

The signs of the rate of changes (the slope coefficients of the explanatory variables) were consistent in the simple linear regression models of P_N and E_T for all the wheat sites (Table 4-5). Most of the variations in P_N values were accounted for by PAR in the north, west and south sites ($R^2_{\text{north Site 1}}$ = 0.88, $R^2_{\text{west Site 2}}$ = 0.79, $R^2_{\text{south Site 4}}$ = 0.90); by RH in the east and west sites ($R^2_{\text{east Site 5}}$ = 0.84, $R^2_{\text{west Site 3}}$ = 0.68) (p<0.001) (Table 4). Least of the variations in P_N values were explained by T in the south Site$_4$ (R^2 = 0.42); by RH in the north Site$_1$ (R^2 = 0.50); and by E_T in the west and east sites ($R^2_{\text{west Site 2}}$ = 0.58, $R^2_{\text{west Site 3}}$ = 0.65, $R^2_{\text{east Site 5}}$ = 0.66) (p<0.001) (Table 4).

Incident PAR accounted for most of the variations in E_T in all the wheat sites (p<0.001) (Table 5). Least important factors of the simple linear regression models in accounting for the variations in E_T were T and RH in the southSite$_4$ (R^2 = 0.44); and P_N in the west and east sites ($R^2_{\text{west Site 2}}$ = 0.58, $R^2_{\text{west Site3}}$ = 65, $R^2_{\text{east Site 5}}$ = 0.66) (p <0.001) (Table 5). The highest R^2_{adj} values for the MLR models of P_N and E_T were 0.92 as a function of PAR and E_T in the south Site$_4$

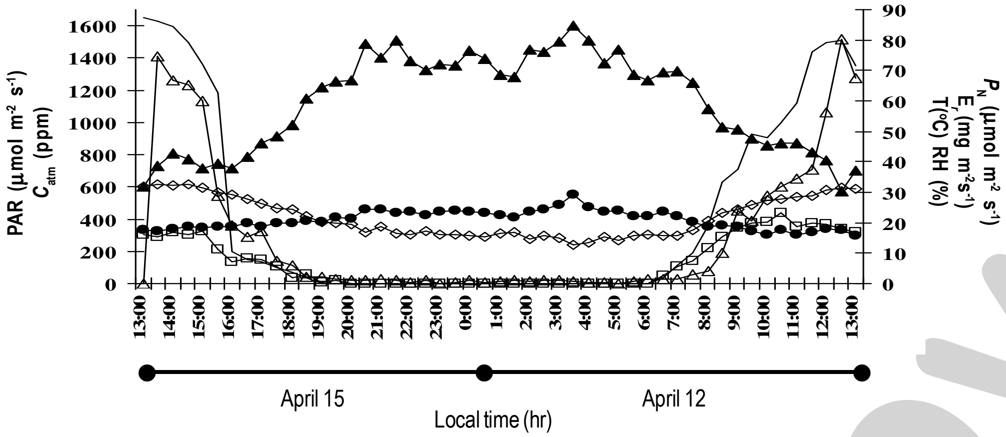

Fig. 3: Diurnal patterns of leaf net photosynthetic rate (P_N □), leaf transpiration rate (E_T △), photosynthetically active radiation (PAR –), air temperature (T ◇), relative humidity (RH ▲), and atmospheric CO_2 concentration (C_{atm} ●) measured at a wheat field of the Tarsus Agricultural Research Centre in the west on April 11 to 12, 2005

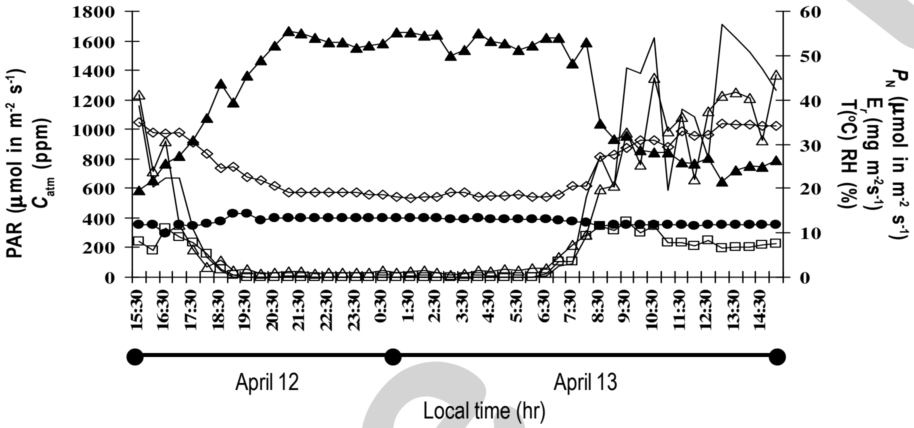

Fig. 4: Diurnal patterns of leaf net photosynthetic rate (P_N □), leaf transpiration rate (E_T △), photosynthetically active radiation (PAR –), air emperature (T ◇), relative humidity (RH ▲), and atmospheric CO_2 concentration (C_{atm} ●) measured at a wheat field of the Topcu station of The Tarsus Agricultural Research Centre in the west on April 12 to 13, 2005

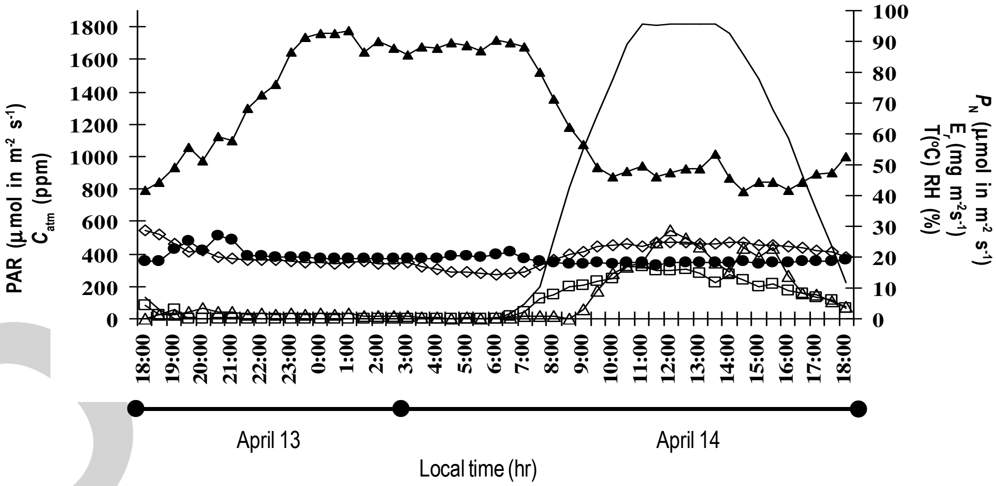

Fig. 5: Diurnal patterns of leaf net photosynthetic rate (P_N □), leaf transpiration rate (E_T △), photosynthetically active radiation (PAR –), air temperature (T ◇), relative humidity (RH ▲), and atmospheric CO_2 concentration (C_{atm} ●) measured at a private wheat field in the south on April 13 to 14, 2005

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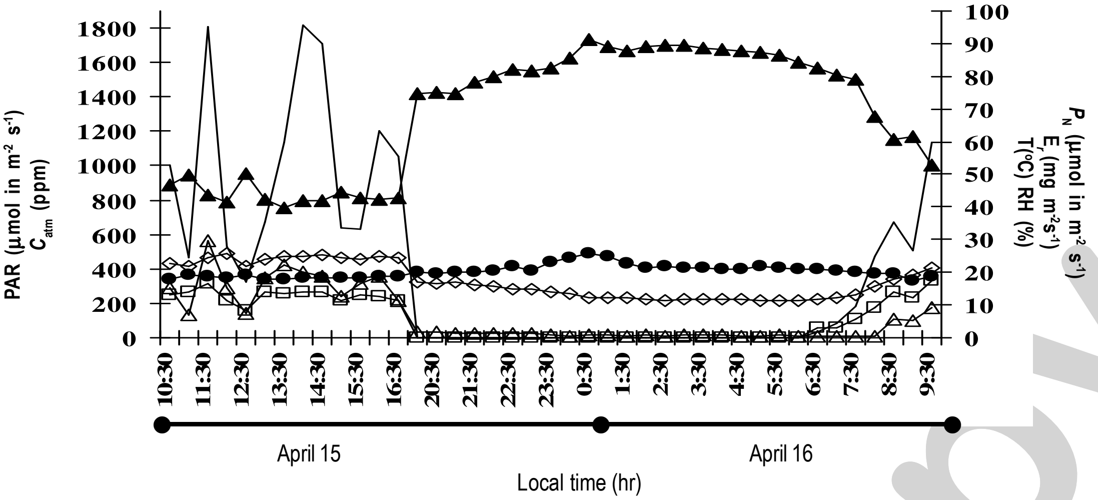

Fig. 6: Diurnal patterns of leaf net photosynthetic rate (P_N □), leaf transpiration rate (E_T △), photosynthetically active radiation (PAR –), air temperature (T ◇), relative humidity (RH ▲) and atmospheric CO_2 concentration (C_{atm} ●) measured at a private wheat field in the east on April 15 to 16, 2005

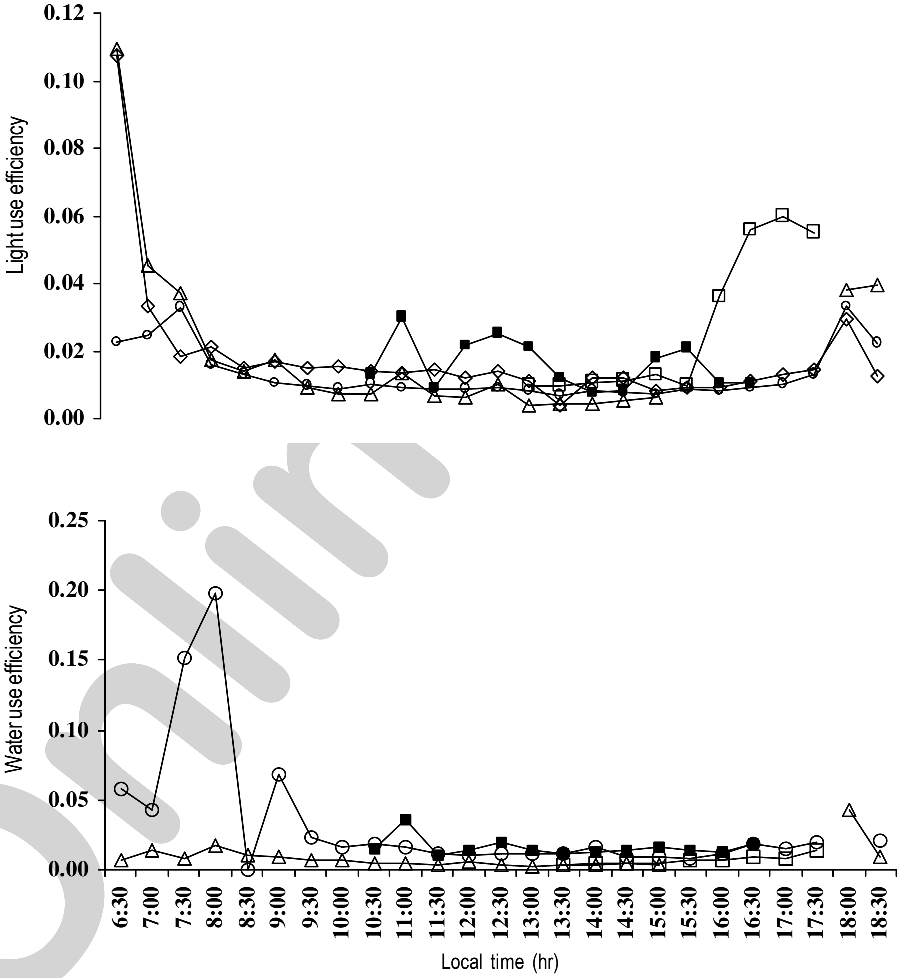

Fig. 7: Diurnal patterns of light use efficiency (LUE = P_N/PAR) and water use efficiency (WUE = P_N/E_T) of wheat leaves measured at five wheat fields for the period of 06:30 to 18:30 hr ($Site_1$ = ◇, $Site_2$ = □, $Site_3$ = △, $Site_4$ = O and $Site_5$ = ■)

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and 0.90 as a function of PAR and RH in the west Site$_3$, respectively (p <0.001) (Table 6). Unexplained variability was most likely to be attributable to heterogeneity in crop characteristics, heterogeneity in management practices and to errors in measurements (Lobell *et al.*, 2002; Deng *et al.*, 2005).

Temporal patterns of diurnal trends: On any given day in any wheat site during the measurement dates, the coupled diurnal trajectories of PAR, T, RH and C_{atm} followed the same pattern in that PAR peaked at noon with both peak of T and trough of RH lagging behind by about two hours. Relative humidity and T were negatively correlated with high r values ranging from -0.90 to -0.98 (p <0.001) (Table 2).

Except for C_{atm}, P_N was positively correlated with all the variables measured. Net photosynthetic rates in the wheat sites were lower in the afternoon than in the morning. The diurnal course of P_N exhibited a peak in the morning and a photosynthetic midday depression. As shown in Table 2, in proportion to an increase (a decrease) in P_N, C_{atm} decreased (increased) during the day and peaked at midnight under the influence of soil and plant respiration. Maximum values of P_N and their corresponding local times were 25.7 µmol m^{-2} s^{-1} at 11:30 in the northSite$_1$ (Fig. 2); 23.2 µmol m^{-2} s^{-1} at 10:30 in the west Site$_2$ (Fig. 3); 12.7 µmol m^{-2} s^{-1} at 09:30 in the west Site$_3$ (Fig. 4); 17.1 µmol m^{-2} s^{-1} at 10:30 in the south Site$_4$ (Fig. 5) and 17.5 µmol m^{-2} s^{-1} at 09:30 in the east Site$_5$ (Fig. 6). Effect of water stress on the wheat sites was visible in the middle of the days. The midday depressions in P_N have been reported as a consequence of a stomatal control of photosynthesis as air temperature, vapor pressure deficit (VPD), and soil dryness increase, especially, in arid and mediterranean climates (Tenhunen *et al.*, 1987; Whitfield, 1990; Olioso *et al.*, 1996; Kumar *et al.*, 2000; Evrendilek *et al.*, 2005).

Most P_N and PAR curves were quite regular and symmetrical, with slight irregularities reflecting the influence of intermittent clouds on the PAR and P_N curves during the measurement days. Diurnal dynamics of leaf P_N and E_T were strongly coupled and highly correlated with PAR (P <0.001). Leaf P_N values increased with increasing PAR in a curvilinear manner in the wheat sites ($R^2_{\text{Site 1}}$ = 0.76, $R^2_{\text{Site 2}}$ = 0.89, $R^2_{\text{Site 3}}$ = 0.59, $R^2_{\text{Site 4}}$ = 0.91, $R^2_{\text{Site 5}}$ = 0.78). Similarly, leaf E_T and PAR values were strongly coupled in a curvilinear way ($R^2_{\text{Site 2}}$ = 0.89, $R^2_{\text{Site 3}}$ = 0.78, $R^{2S}_{\text{Site 4}}$ = 0.82, $R^2_{\text{Site 5}}$ = 0.68). The peaks and troughs of E_T corresponded closely with those of PAR ($r_{\text{min to max}}$ = 0.87 to 0.94) (Fig. 2-6).

Mean leaf LUE computed on the basis of incident PAR for the period between 06:30 and 18:30 ranged between 0.01 and 0.09 which are in general agreement with data obtained from C$_3$ and C$_4$ agricultural crops (Biscoe *et al.*, 1975; Baldocchi *et al.*, 1987; Gower *et al.*, 1999). Mean leaf WUE values were of the order of 0.003 to 0.2, directly related to mean LUE values and inversely related to g_s values (Caviglia and Sadras, 2001). Both mean LUE and WUE values for the period between 06:30 and 18:30 exhibited a bimodal behavior, with peaks in early morning as well as in late afternoon (Fig. 7). Mean LUE peaked both at 0.9 at 07:00 and at 0.03 at 18:00, while mean WUE peaked at 0.2 at 09:00 and at 0.04 at 18:00 (Fig. 7). Similarly, Vadell *et al.* (1995) reported that leaves of *Trifolium subterraneum* L. under drought conditions of late spring days in Australia improved WUE by taking advantage of morning and evening hours with high RH.

Stomatal conductance was negatively correlated with C_{atm} (r = -0.21 to -0.68) and positively correlated with T (r = 0.13 to 0.82) in the wheat sites monitored. It was reported that elevated C_{atm} increased P_N in C$_3$ species more than in C$_4$ species, but decreased g_s and E_T in both C$_3$ and C$_4$ species and greatly improved WUE in all the crops (Morrison and Gifford, 1984; Field *et al.*, 1995). On average, a 29% increase in P_N, and reductions by 34% in g_s and 23% in E_T were found under double CO$_2$ levels in the literature survey of agricultural crops (Cure and Acock, 1986).

Adverse effects from future climate change are projected for wheat production in many (semi-arid) regions, with important economic and social implications from local to national levels. For example, the most likely range of median grain yield decrease (“32 to “13.5%) were quantified for eight sites representative of the south Australian wheat belt, based on downscaled climate change outputs of nine global and regional climate models regarding atmospheric CO$_2$ concentration, regional temperature and regional rainfall for 2080 (Luo *et al.*, 2005). Wheat production provides a vital source of food and income for millions of people throughout the developing countries. Further investigations about ecophysiological characteristics of wheat are needed to understand magnitude of climate change impacts on its potential productivity and thus, to improve WUE and LUE at the local scale in all Mediterranean agricultural regions, where multiple interacting stress factors such as concentration of rainfall in winter, a distinct summer drought, warm-to-hot summers, cool-to cold winters, and a long history of human-induced disturbances prevail. As the impacts of global climate change become increasingly felt, continuous measurements of climate-crop-soil-management interactions under natural conditions play a pivotal role not only in exploring changes in ecophysiological properties of strategic crops for food security such as wheat but also in devising preventive and mitigative management practices to ensure sustained agricultural productivity.

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