

Morphological and Physiological Traits Associated with Canopy Temperature Depression in Three Closely Related Wheat Lines

Maria Balota,* William A. Payne, Steven R. Evett, and Troy R. Peters

ABSTRACT

Wheat (*Triticum aestivum* L.) cultivars with high canopy temperature depression (CTD) tend to have higher grain yield under dry, hot conditions. Therefore, CTD has been used as a selection criterion to improve adaptation to drought and heat. The CTD is a result of the leaf's energy balance, which includes terms determined by environment and physiological traits. We hypothesized that one or more of several physiological traits contributed to consistent CTD differences among three closely-related winter wheat lines grown under dryland conditions. For three years we measured several leaf traits, including CTD, leaf dimension, gas exchange rates, and carbon-13 isotope discrimination (Δ). Soil water content was also monitored. Data showed that daytime CTD was related to the leaf size in these wheat lines. The most drought-tolerant line, TX86A8072, had consistently smaller and narrower leaves than TX86A5606, the least drought tolerant. For TX86A8072, dryland and irrigated average noon CTD was -0.8°C , and average flag leaf area (LA) 11 cm^2 , for TX86A5606, values were -1.7°C and 12.5 cm^2 , respectively. However, TX86A8072 also had higher CTD (i.e., lower temperatures) than TX86A5606 at night, despite a theoretically greater sensible heat transfer coefficient, suggesting greater nighttime transpiration (T). Implications of these traits on nighttime leaf energy balance and possible adaptive roles of nighttime T are discussed.

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Abbreviations: A, CO_2 assimilation rate; $[\text{CO}_2]_i$, intercellular CO_2 concentration; CTD, canopy temperature depression; Δ , carbon-13 isotope discrimination; E, transpiration rate; g_{lw} , total leaf conductance to water vapor; IRT, infrared thermometer; LA, leaf area; RG, relative greenness; RH, relative humidity; RWL, rate of excised-leaf water loss; SLA, specific leaf area; T , transpiration; T_a , air temperature; T_c , canopy temperature; VPD, vapor pressure deficit.

CANOPY TEMPERATURE DEPRESSION, the difference between air temperature (T_a) and canopy temperature (T_c), is positive when the canopy is cooler than the air ($\text{CTD} = T_a - T_c$). It has been used in various practical applications including evaluation of plant response to environmental stress (Ehrler et al., 1978; Idso, 1982; Howell et al., 1986; Jackson et al., 1981; Singh and Kanemasu, 1983), irrigation scheduling (Hatfield, 1982; Pinter and Reginato, 1982; Evett et al., 1996; Wanjura et al., 1995), and to evaluate cultivars for water use (Pinter et al., 1990; Hatfield et al., 1987), tolerance to heat (Amani et al., 1996; Reynolds et al., 1994), and drought (Blum, 1980; Blum et al., 1989; Royo et al., 2002; Rashid et al., 1999). In general, CTD

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has been used to assess plant water status because it represents an overall, integrated physiological response to drought and high temperature (Blum, 1988; Amani et al., 1996).

The mechanisms by which plants maintain greater CTD (i.e., lower canopy temperature) have been studied less. Greater CTD of wheat in a hot irrigated environment of NW Mexico was linked to increased gas exchange rate (Amani et al., 1996; Fischer et al., 1998; Reynolds et al., 1994), leaf area index (Ayeneh et al., 2002), and assimilate translocation (Reynolds et al., 1999). In the semi-arid Texas High Plains, cooler cotton (*Gossypium hirsutum* L.) and wheat canopies were associated with greater leaf conductance (Hatfield et al., 1987) and photosynthetic enzyme activity (Burke and Hatfield, 1987; Burke et al., 1988; Wanjura et al., 1995). In the Sonora Desert of California, cooler leaves of desert plants resulted from higher transpiration rates and smaller leaf size (Smith, 1978). In Montana, cooler barley (*Hordeum vulgare* L.) canopies were due to light-colored and awned plants (Ferguson et al., 1973). Leaf orientation was shown to have a major role in soybean (*Glycine max* L.) canopy temperature in Ontario, Canada (Stevenson and Shaw, 1971). Soil water availability also affects canopy temperature (Campbell and Norman, 1998), and is influenced by root morphology and activity, especially under dryland conditions, e.g., for upland rice (*Oryza sativa* L.) (O'Toole et al., 1998). Overall, the existing literature suggests that dominant mechanisms that increase CTD vary with environment and crop species.

Experiments conducted by CIMMYT (Centro Internacional de Mejoramiento de Maiz y Trigo [International Maize and Wheat Improvement Center, Mexico]) at several locations across the globe suggested that CTD could be used as a selection tool for improved heat tolerance in wheat (Reynolds et al., 1994). Greater CTD has been associated with increased wheat yield under irrigated, hot environments (Amani et al., 1996; Reynolds et al., 1994; Reynolds, 2002; Fischer et al., 1998), but also under dryland environments, and has therefore been proposed as a selection criterion for drought tolerance (Blum, 1988; Balota et al., 2007). Under favorable soil-water conditions, greater CTD and yield have been attributed to increased stomatal conductance and crop water use (Amani et al., 1996; Fischer et al., 1998; Pinter et al., 1990), but physiological mechanisms determining greater CTD under water-limited environments are less clear. Identification of these mechanisms is needed for better understanding of the CTD-yield relationship and for more efficient genotypic selection under dry conditions.

In a previous paper, we identified consistent differences for CTD among three closely-related wheat lines during the day and the night (Balota et al., 2007), and found CTD was correlated with dryland yield. In this paper, we hypothesized that higher CTD was associated with rooting-soil water extraction patterns, or one or more of the following leaf traits: leaf conductance, carbon assimilation rate,

Δ , cuticular resistance, size, and relative greenness. We then discussed the phenomenon of nighttime CTD and the effects of these traits on the leaf energy balance.

MATERIALS AND METHODS

Plant Material and Growth Conditions

Three BC₃-generation sister lines (coefficient of parentage = 0.94) were planted at the Texas AgriLife Research Station (35° N. Lat., 102° W. Long., 1170 masl) near Bushland, TX, where soils are classified as Pullman Clay loam (fine, mixed, superactive, thermic Torrertic Paleustol). Based on multilocation dryland yield trials, the lines, TX86A5606, TX88A6880, and TX86A8072, had been classified as sensitive, moderately tolerant, and tolerant to drought, respectively (Lazar et al., 1996). Balota et al. (2007) demonstrated consistent differences among the lines for CTD, and correlated yield under dryland conditions with CTD. The lines have identical phenology, plant height, and tiller number (Balota et al., 2005).

Wheat was planted on 1 Oct. 2000, 13 Oct. 2001, and 19 Oct. 2002. In each year, both dryland and irrigated plots were used. Individual plot size was 4.6 m² in 2000, 3.3 m² in 2001, and 39 m² in 2002. Seeding rate was 6.5 g m⁻² in 2000 and 10 g m⁻² in the second and third years.

In 2000, no pre-plant fertilizer or irrigation was applied. In 2001, 18 g m⁻² N, 10 g m⁻² P₂O₅, and 76 mm of pre-plant irrigation were applied to all plots (including dryland plots, to ensure stand because of dry conditions) at the end of September. Similarly, in 2002, pre-plant fertilization of 17 g m⁻² N and 76 mm irrigation was applied to all plots. In all years, cultural operations for weed and pest control were applied as needed. Irrigated plots received a total of 180 mm of water in two irrigations on 20 Apr. and 18 May 2001. In 2002, they received a total of 462 mm in 4 irrigations on 27 March, 26 Apr., 10 May, and 6 June. In 2000, irrigated plots were plowed out at the end of March, before maturity, due to a severe greenbug (*Schizaphis graminum* Rondani) infestation; however, leaf measurements were taken. Otherwise, all plots were harvested mechanically at maturity, and the total numbers of heads, biomass, and grain yield were determined.

CTD and Environment Monitoring

Canopy temperature was measured from an area of approximately 0.7 m² in the middle of each plot with a thermocouple type infrared thermometer (IRT) (model IRT/c.2-T-80F, Exergen, Watertown, MA) mounted on a pole next to each plot, as described by Balota et al. (2007). Air temperature and relative humidity (RH) were measured with a temperature and RH probe (model HMP45C, Campbell Scientific Inc. (CSI), Logan, UT) in the middle of dryland and irrigated fields. All IRTs were calibrated at the beginning of measurements with a black body (model 1000, Everest Interscience Inc., Tucson, AZ). The temperature/RH sensor was factory-calibrated each year. Anemometers (model 03001-5 R.M., CSI Logan, UT) were placed in the middle of dryland and irrigated fields to monitor wind speed above the canopy. A single pyranometer (model CM3, CSI, Logan, UT) was used to record solar radiation. All instruments were connected to data loggers (models 21x and 23x, CSI, Logan, UT) for continuous readings taken at 50-s time intervals, and mean values were calculated and recorded at 10-min time intervals.

Measurements were taken from 15 April to 15 May in 2000, from 26 April to 13 June in 2001, and from 5 April to 2 June in 2002. In each plot, neutron access tubes were placed to a 2.3-m depth. These were read with a field-calibrated neutron probe (model 503DR, Campbell Pacific Nuclear Int., Inc., Martinez, CA) at 0.2-m intervals throughout the growing season in 2002.

Plant Measurements

Leaf characteristics were measured at various vegetation stages in all years (Table 1). Sample size was between 10 and 30 newest, fully expanded leaves per plot from 10 to 30 individual plants. Leaf area (LA, cm²) was measured with an area meter (model LI-3100 LICOR, Lincoln, NE). Leaf dry-weight was then determined, and specific leaf area (SLA, cm² g⁻¹) calculated. Total leaf length and maximum leaf width were also measured. A hand-held meter (model SPAD 502, Minolta, Spectrum Technologies Inc., Plainfield, IL) was used to measure relative greenness (RG) in arbitrary absorbance, or SPAD units, in flag leaf and first leaf below the flag leaf (flag-1). The rate of water loss (RWL, g g⁻¹ h⁻¹) of the flag leaf was estimated by the excised-leaf method as described by Clarke and McCaig (1982a). Ten leaves per plot were randomly excised at their base, placed in plastic bags, and transported in the laboratory as quickly as possible. Fresh weight was determined, and leaves were placed in a dark growth cabinet at 25°C and 50% RH for 5 h, and weighed again. They were then oven-dried for 24 h at 45°C, and weighed to determine dry mass. Leaf water content was calculated from these weights.

In 2002, gas exchange rates of the flag leaf were measured using a portable photosynthesis system (model LI-6200, LICOR, Lincoln, NE) equipped with a 0.5-L assimilation chamber. Nine plants were measured per plot on 2 May, and 8 May, between

1000 and 1500 h. Photosynthetically active radiation under these conditions was at least 1800 μmol m⁻² s⁻¹. In addition, pre-dawn measurements of total leaf conductance to water vapor (g_{lw}, mol m⁻² s⁻¹) were taken using the LI-6200 on 2 May, 8 May, and 14 May. The infrared gas analyzer of the LI-6200 was calibrated each day of measurement against a standard CO₂ gas at a concentration of 500 ppm (Praxair Distribution Inc., Amarillo, TX). Water flux was measured from a saturated piece of No. 2 Watman filter paper that was approximately the same size and shape as a wheat flag leaf to estimate boundary layer conductance, which was set to 1.47 mol m⁻² s⁻¹ for LI-6200 software calculations. A high flow rate of 900 μmol s⁻¹ was used to circulate chamber air through the desiccant to keep humidity variation inside the chamber to less than ±2%. To ensure that chamber CO₂ concentration (Ca) was similar for all measurements and close to the air CO₂, before each measurement, fresh air was circulated for 3 to 5 s through an open and empty chamber, and circulated again through a closed and empty chamber for 3 to 5 s until constant Ca and RH; thereafter, leaves were placed inside the chamber. This way, average Ca was 354 μmol mol⁻¹ during day and 386 μmol mol⁻¹ during nighttime gas exchange readings. Each leaf was allowed to equilibrate for 60 s before taking readings of carbon assimilation rate (A, μmol m⁻² s⁻¹), g_{lw}, transpiration rate (E, mmol m⁻² s⁻¹), and intercellular CO₂ concentration ([CO₂]_i, mmol m⁻² s⁻¹).

Carbon-13 isotope discrimination (Δ) was determined on dried ground flag leaf samples collected at approximately flowering stage in 2001 and at 2 wk after flowering in 2002. Ten leaves per plot were collected and ground together to constitute a sample. Measurement of Δ was done by mass spectroscopy at the International Atomic Energy Agency in Vienna, Austria. Results were expressed as Δ values, calculated assuming a carbon-13 isotope composition of air of -8‰ (Farquhar et al., 1989).

Table 1. Heading days of three close-related wheat lines and dates for physiological measurements. LA is leaf area, SLA specific leaf area, CT cuticular transpiration, and Δ carbon-13 isotope discrimination. Days after sowing are provided between the parenthesis.

Year	Heading day	LA	Leaf width	Leaf length	SLA	RG [†]	CT	Plant height	Gas exchange	Δ
Dryland										
2000	112 [‡] (204)	54 (146)			54 (146)	54 (146)				
2001	120 (199)	123 (202)			123 (202)	123 (202) 138 (217) 143 (222) 150 (229)	124 (203)			123 (202)
2002	118 (191)	101 (174) 133 (206)	133 (206)	133 (206)	101 (174) 133 (206)	101 (174) 116 (189) 126 (199) 133 (206)		120 (193) 130 (203) 143 (216)	122 (195) 128 (201) 134 (207)	133 (206)
Irrigation										
2000		54 (146)			54 (146)	54 (146)				
2001	120 (199)	123 (202)			123 (202)	123 (202) 138 (217) 143 (222) 150 (229)	124 (203)			123 (202)
2002	122 (195)	101 (174) 141 (214)	141 (214)	141 (214)	101 (174) 141 (214)	101 (174) 116 (189) 126 (199) 141 (214)		120 (193) 130 (203) 143 (216)	122 (195) 128 (201) 134 (207)	141 (214)

[†]Relative greenness in relative units of the Minolta SPAD meter.

[‡]Day of year.

Experimental Design and Statistical Analysis

In each environment (i.e., irrigated and dryland), the experimental design was a randomized complete block with genotype as the only treatment. Year was treated as a random effect for combined analyses. There were four replications in 2000 and 2001, and three in 2002. Statistical analyses, including ANOVA and linear regression, were made using SYSTAT 10.2 (SYSTAT Software Inc. San Jose, CA).

RESULTS AND DISCUSSION

CTD and Grain Yield

Variation among Genotypes

The three cropping seasons contrasted one another in terms of air temperature, precipitation, and vapor pressure deficit (VPD). The coolest season was in 2000, the most humid in

2001, and the driest in 2002. During CTD measurements, mean and maximum air temperatures were 17 and 26.2°C in 2000, 19.3 and 27.3°C in 2001, and 18.4 and 27.3°C in 2002. Occasionally days with air temperatures as high as 36°C were recorded in all years. Cropping season precipitation was 178 mm in 2000, 389 mm in 2001, and 152 mm in 2002. During CTD measurements, average noon VPD was 2.1 kPa in 2000, 1.8 in 2001, and 2.6 in 2002, with values up to 6 kPa on several days in June in all years. More detailed weather information was reported by Balota et al. (2007).

Under both water regimes, genotype and year significantly influenced seasonal noon CTD with no interaction (Table 2). The drought sensitive line, TX86A5606, (Lazar et al., 1995), consistently had the smallest CTD (i.e., warmest canopy) during midday. In dryland, TX86A8072 had

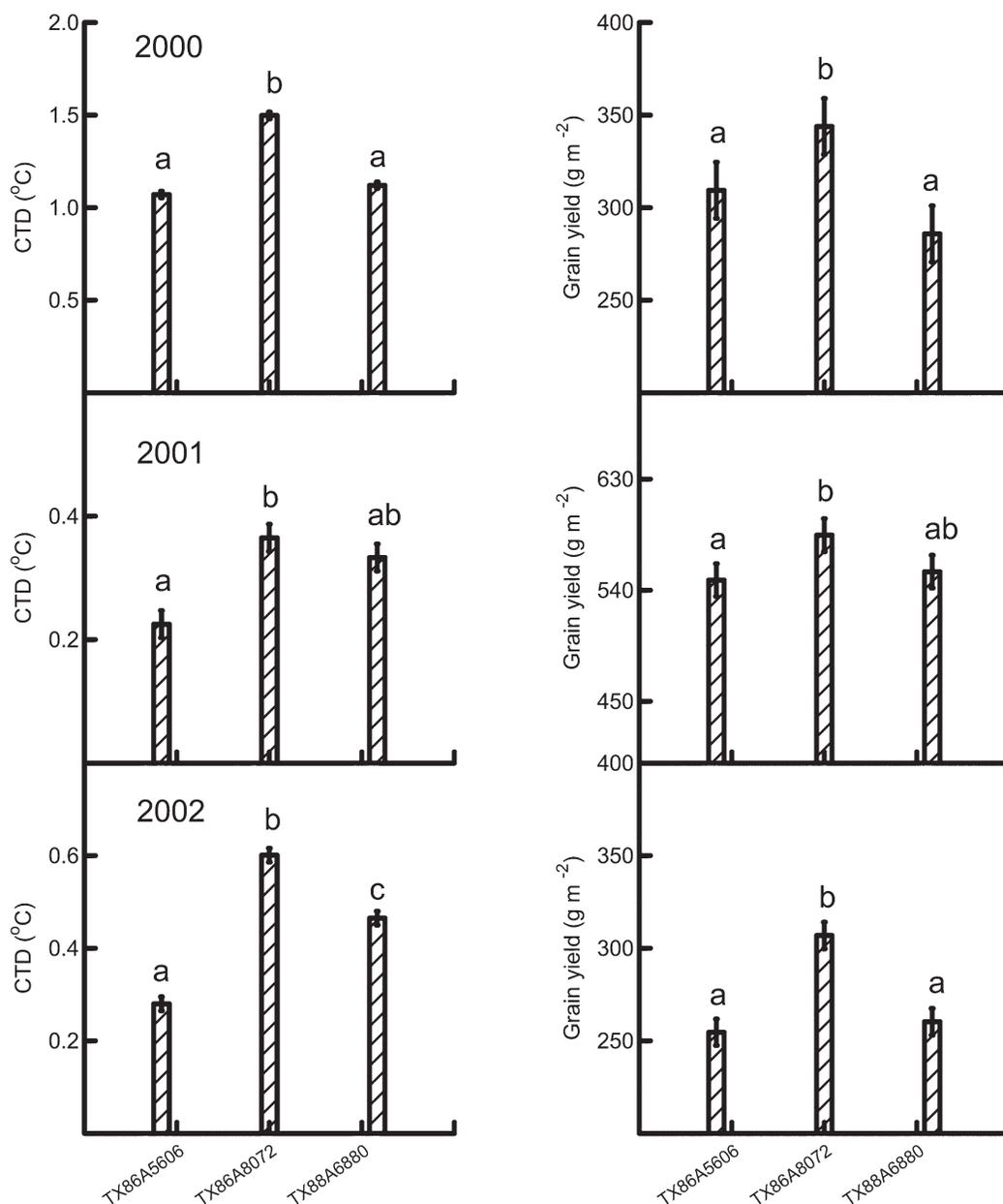


Figure 1. Seasonal mean CTD and grain yield of three closely-related wheat lines under dryland environment. Vertical bars are ± 1 SE. Means with different letters are significantly different using LSD test $P < 0.05$.

the coolest canopy and the largest grain yield, whereas TX86A5606 had the warmest canopy and smallest yield (Fig. 1). Greater yield of TX86A8072 was associated with increased harvest index (Table 2). Except for the irrigated plots in 2002, grain yield was significantly correlated with seasonal mean noon CTD in all other years and environments at the 0.10 probability level or smaller (Table 2). Around noon, seasonal mean CTD varied from negative values (i.e., the canopy was warmer than air) in dryland to positive values under irrigation except for TX86A5606 (Fig. 2). In dryland, average noon CTD was -2°C and values as low as -10°C were recorded for individual days in May and June every year. At night, only positive values of CTD were recorded, i.e., canopies were cooler than air (Fig. 2). Under our conditions, genotypic differentiation for CTD was better for dryland than irrigated wheat. More detailed yield and CTD results were reported by Balota et al. (2007).

Soil Water Content and CTD

There were no significant effects of genotype on soil profile water distribution in dryland plots for any date of measurement in 2002 (Fig. 3). Nor were there any differences in total profile water storage (Fig. 4) on any day of measurement, suggesting no differences among genotypes for plant water availability or root activity at lower depths. Nonetheless, TX86A8072 consistently had greater CTD than did TX86A5606 and TX88A6880 at noon on days that neutron probe readings were taken (Fig. 4).

Gas Exchange

On 2 May, 8 May, and 14 May 2002, noon and pre-dawn gas exchange measurements were taken on the two most contrasting lines for CTD and grain yield, TX86A5606 and TX86A8072. Recorded average Ca was $354 \mu\text{mol mol}^{-1}$ during day and $386 \mu\text{mol mol}^{-1}$ during night gas exchange readings without significant differences between the two lines within each water treatment. The difference between day and nighttime Ca is expected. Nobel (1999) estimated that during daytime a transpiring and photosynthesizing plant community has a vertical flux density of CO_2 (J_{CO_2}). At midday, J_{CO_2} can vary from -15 to $-44 \mu\text{mol mol}^{-1}$, depending on species, canopy size and health, and environment. Thus CO_2 , which might have $380 \mu\text{mol mol}^{-1}$ at 20°C well into the turbulent air, e.g., 30 m above vegetation, could be at 336 to $365 \mu\text{mol mol}^{-1}$ just above the canopy where the flag leaves are positioned. At night,

Table 2. Mean canopy temperature depression (CTD) at noon, grain yield, biomass, head number, and harvest index in dryland and irrigated plots at Bushland, TX, and their correlation with CTD.

Genotype	Noon CTD $^{\circ}\text{C}$	Grain yield g m^{-2}	Biomass g m^{-2}	Harvest index %	Heads m^{-2}
Dryland					
TX86A5606	-3.3	367	1198	30.6	821
TX86A8072	-1.7	407	1206	33.9	738
TX88A6880	-2.4	365	1244	29.4	848
SE	0.112	8.5	58	1.3	40.3
Genotype effect (P)	0.0001	0.0001	NS	0.061	NS
Year effect (P)	0.0001	0.0001	0.0001	NS	0.002
Genotype \times year (P)	NS	NS	NS	NS	NS
Correlation with CTD: 2000 $n = 12$	1.00	0.75**	0.75**	NS	
2001 $n = 12$	1.00	0.75**	NS	NS	NS
2002 $n = 9$	1.00	0.59***	0.73**	0.89**	0.71**
Irrigation					
TX86A5606	-0.2	556	1756	31.9	880
TX86A8072	0.1	545	1720	32.4	881
TX88A6880	0.3	551	1735	31.3	957
SE	0.124	18.5	112	1.7	37.6
Genotype effect (P)	0.033	NS	NS	NS	NS
Year effect (P)	0.001	0.0001	0.0001	NS	0.0001
Genotype \times year (P)	NS	NS	NS	NS	NS
Correlation with CTD:					
2001 $n = 12$	1.00	0.67*	NS	NS	NS
2002 $n = 9$	1.00	NS	NS	NS	NS
Correlation with CTD when dryland and irrigation were combined:					
2000 $n = 12$	1.00	0.75**	0.75**	NS	NS
2001 $n = 24$	1.00	0.66*	0.61*	NS	NS
2002 $n = 18$	1.00	0.92**	0.67*	NS	NS

*Correlation coefficient significant at the 0.05 probability level.

**Correlation coefficient significant at the 0.01 probability level.

***Correlation coefficient significant at the 0.10 probability level.

respiration occurs, so vegetation then acts as a source of CO_2 . Thus the mole fraction of CO_2 just above the canopy at night is usually a few $\mu\text{mol mol}^{-1}$ greater than in the well-above turbulent air (Nobel, 1999).

The coolest line, TX86A8072, had significantly greater A and noon g_{lw} than did TX86A5606 under both dryland and irrigated conditions (Table 3). However, under dryland conditions, E was not significantly different ($P = 0.077$) among lines. Correlations of CTD were significant with noon A, g_{lw} , and E (Table 3).

Burke et al. (1988) found that T_c less than 23°C allowed optimal enzymatic activity in wheat leaves. When seasonal $T_c > 23^{\circ}\text{C}$ was summed, TX86A8072 had cooler temperatures than the other lines in all years under dryland conditions, suggesting overall better status for physiological processes, e.g., carbon assimilation (Burke and Oliver, 1993). The carboxylation efficiency, $A:[\text{CO}_2]_i$ (Krieg and Hutmacher, 1986), of TX86A8072 was also greater than in the other lines (Table 3). Under

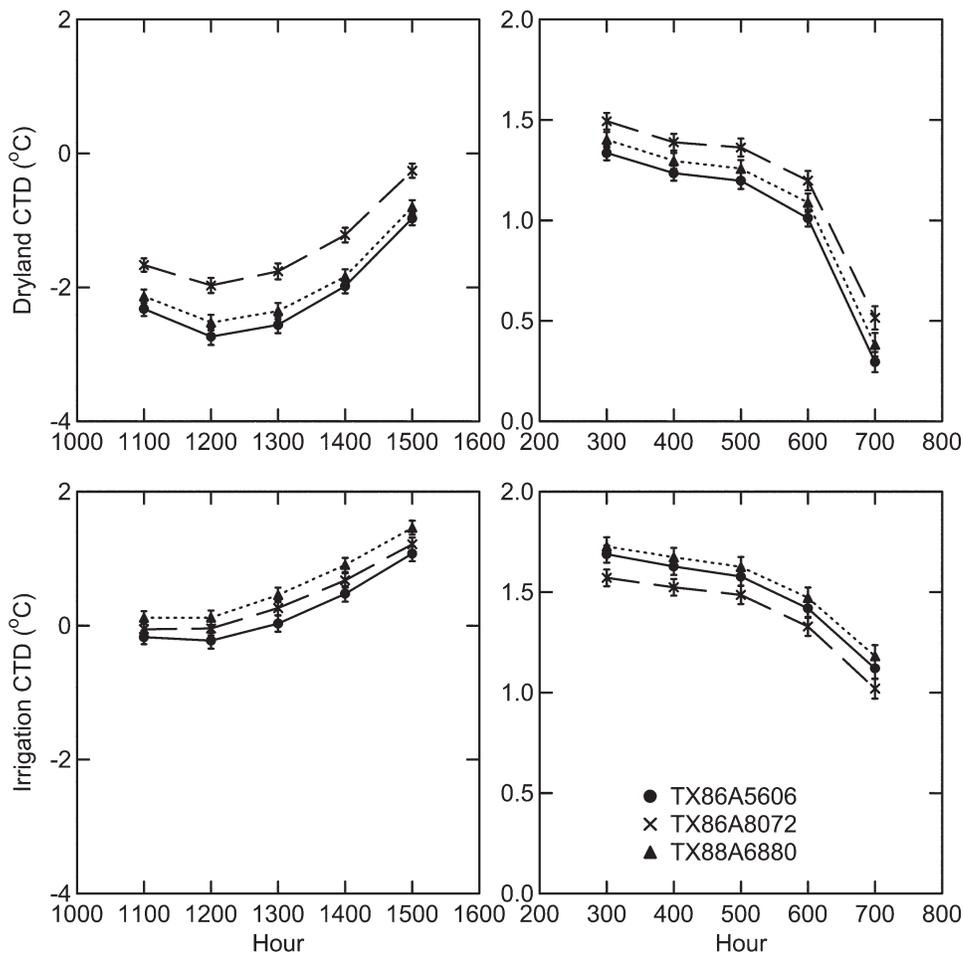


Figure 2. Genotypic effect on CTD during midday and nighttime hours in dryland and irrigated wheat for years combined. Points represent hourly means over the entire measurement periods: 15 Apr. to 15 May in 2000, 26 Apr. to 13 June in 2001, and 5 Apr. to 2 June in 2002. Vertical bars are ± 1 SE.

dryland conditions, the moderately tolerant line TX88A6880 accumulated an average of 95 more degrees centigrade, and the sensitive line TX86A5606 accumulated 584 more degrees centigrade, than did TX86A8072 over the entire measurement period relative to 23°C. A significant negative correlation between cumulative noon $T_c > 23^\circ\text{C}$ and grain yield was found (Fig. 5), suggesting that heat stress limited yield in addition to moisture stress, and reinforcing earlier conclusions (Balota et al., 2007) that cultivars with cooler canopies (larger CTD) are more suitable for dryland cultivation in this region.

Carbon Isotope Discrimination

Wheat lines exhibited significantly different flag leaf Δ ($P = 0.01$) with no main or interactive effects due to year under dryland conditions. There was no genotype effect on flag leaf Δ under irrigated conditions. TX86A8072 had mean Δ values of 18.2% in dryland and 19.1% under irrigation. The drought sensitive line, TX86A5606, had mean Δ values of 18.1% in dryland and 19.3% under irrigation, while the

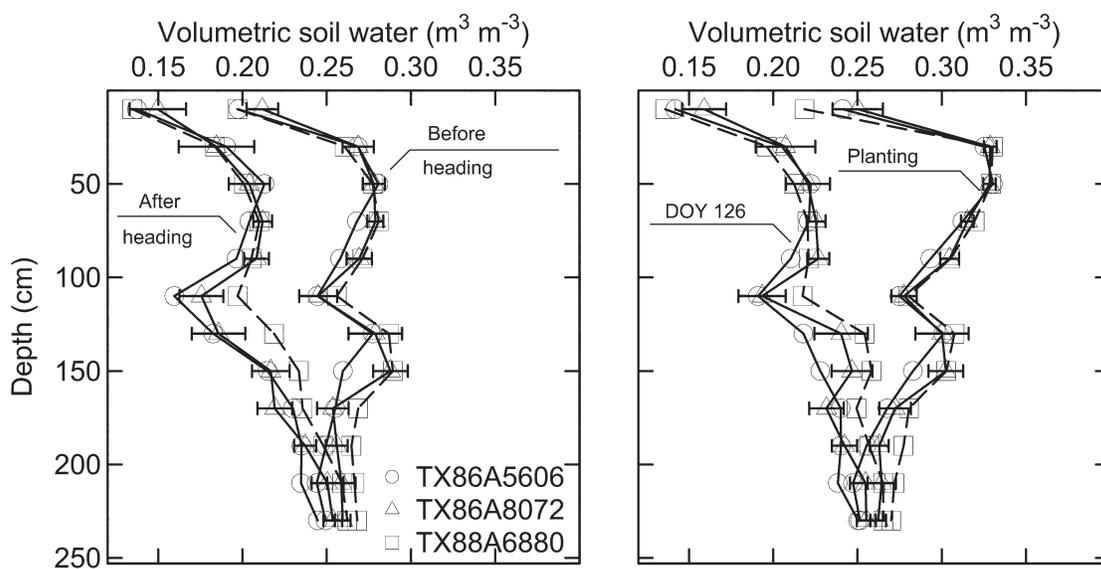


Figure 3. Soil water content of dryland wheat plots in 2002 as affected by genotype at pre-heading and post-heading (left), and at planting and 6 May 2002 (DOY 126) (right). DOY 126 was the closest day of soil moisture readings to DOYs 122 and 128, when noon and pre-dawn gas exchange measurements were taken. Horizontal bars represent ± 1 SE. Because there were no significant differences between genotypes, SE of only TX86A8072 is presented.

intermediate line, TX88A6880, had mean Δ values of 17.6% in dryland and 19.0% under irrigation. In all years when measured, Δ was significantly and positively correlated with CTD in dryland plots (Fig. 6); it was positively correlated with grain yield in dryland plots only in 2001 (Fig. 7). Such correlations have been widely reported in wheat (Condon et al., 1987; Ehdaire et al., 1991; Fischer et al., 1998; Merah et al., 2001; Monneveux et al., 2005; Tokatlidis et al., 2004), especially in more recently developed wheat cultivars (Royo et al., 2002) for which stomatal conductance (g_s) tends to be less sensitive to incipient leaf water stress (Fischer et al., 1998; Ortelli et al., 1996). Carbon-13 isotope discrimination has been positively correlated with A , g_s , and CTD in wheat (Condon et al., 1990; Fischer et al., 1998; Monneveux et al., 2006; Royo et al., 2002), and grain yield and harvest index in barley (Teulat et al., 2001).

Leaf Traits

In irrigated and dryland plots, the drought-tolerant line TX86A8072 had significantly smaller LA (Fig. 8), and smaller leaves in terms of both width and length (Table 4). The line TX86A8072 had the smallest SLA, which is commonly associated with increased leaf thickness (Vile et al., 2005), which in turn has been associated with greater photosynthetic activity, grain yield, and Δ (e.g., Fischer et al., 1998). There were no genotypic differences for SPAD readings (RG) or rate of water loss (RWL) of excised flag leaves (Table 4). The RWL of excised leaf has been extensively used as a selection tool to improve drought tolerance in wheat and other crops; it was

associated with cuticular transpiration and stomatal residual transpiration due to incomplete closure under drought (Balota, 1995; Balota et al., 1996; Clarke, 1983; Clarke and McCaig, 1982a; Clarke and McCaig, 1982b; Clarke and Townley-Smith, 1986; Jaradat and Konzak, 1983; McCaig and Romagosa, 1989; Premachandra and Shimada, 1988a, b; Rao et al., 1998).

The relationship of daytime CTD to such leaf characteristics as size, stomatal distribution, thickness, and angle, and to such environmental parameters as irradiance, ambient temperature, and windspeed, have been treated by many authors (e.g., Nobel, 1999; Campbell and Norman, 1998; Smith, 1978). These studies have shown that smaller leaf dimensions such as those of the drought tolerant line, TX86A8072, contribute to greater daytime CTD under dry conditions.

Nighttime CTD

On 2 May and 14 May 2002, flag leaf stomata were not completely closed at pre-dawn, but no significant genotypic differences were observed for g_{lw} of the lines

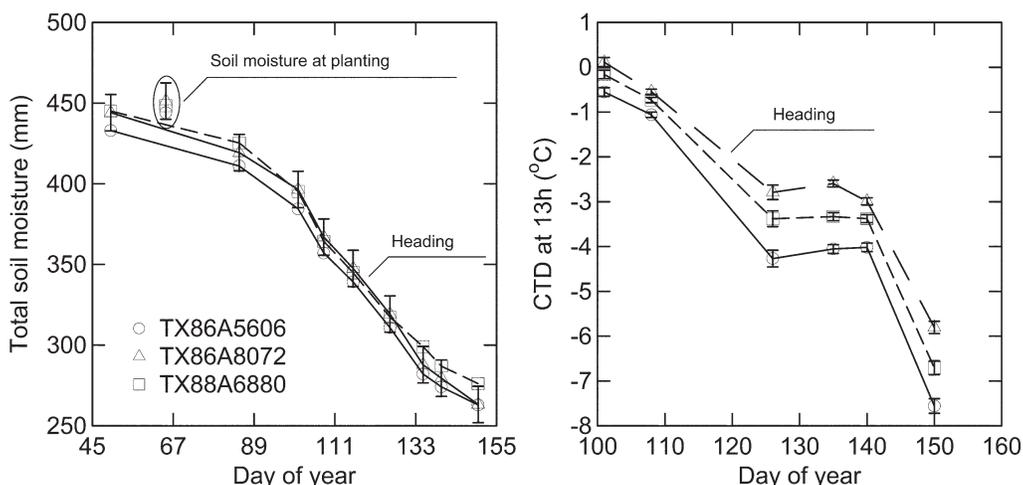


Figure 4. Total soil moisture at 0 to 230 cm depth (left) and canopy temperature depression (CTD) (right) in three closely-related wheat lines in 2002 in dryland plots. Vertical bars are ± 1 SE. Because there were no significant differences between genotypes for total soil moisture SE of only TX86A8072 is included with the figure on the left.

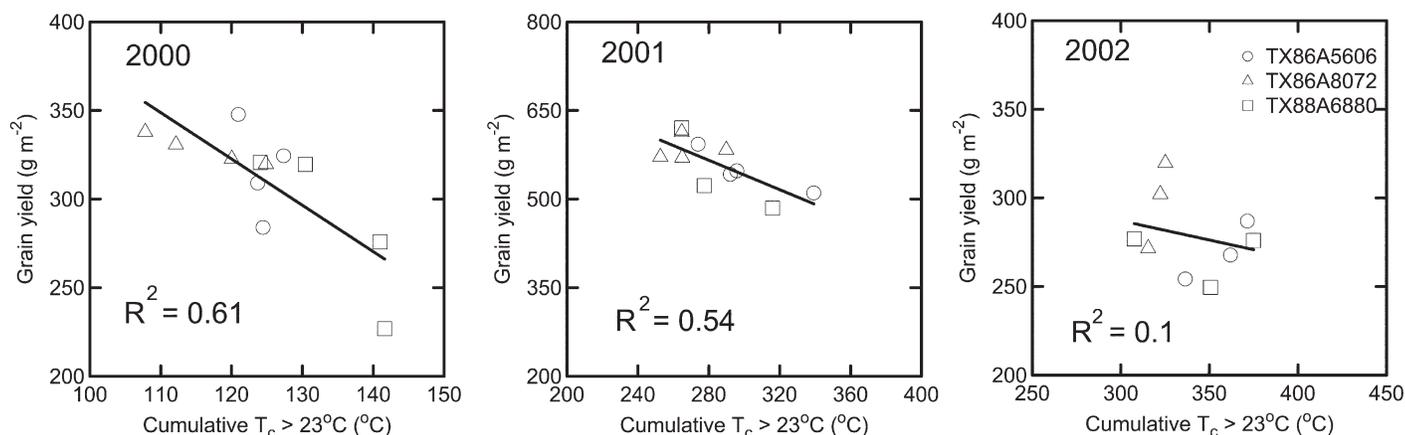


Figure 5. Relation between grain yield and cumulative canopy temperature (T_c) over 23°C in three close-related wheat lines in dryland plots at Bushland, TX.

TX86A8072 and TX86A5606 (Fig. 9). On 8 May, stomata were closed with values not statistically significantly different from 0. Nonetheless, at the time that flag leaf g_{lw}

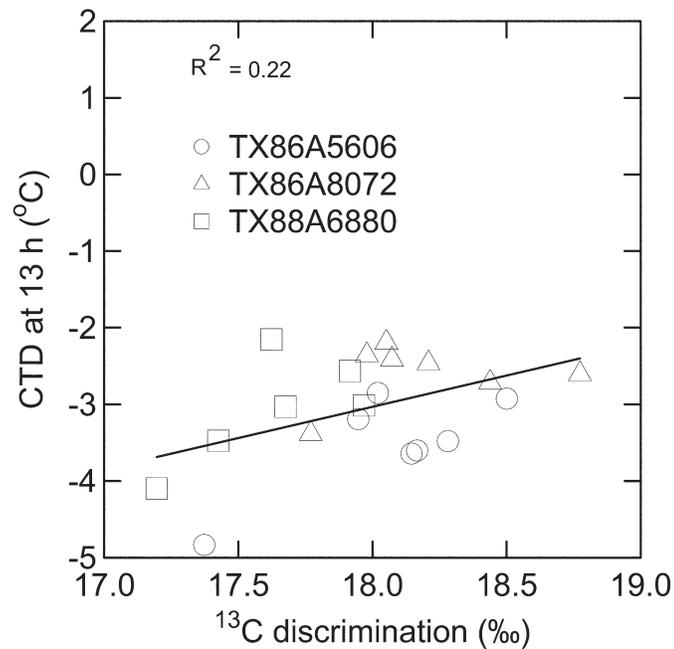


Figure 6. Correlation of seasonal average noon canopy temperature depression (CTD) and carbon 13 isotope discrimination (in ‰) in three close-related wheat lines in dryland at Bushland, TX. Dryland data from 2001 and 2002 were combined. Correlation is significant at $P = 0.014$.

measurements were taken for all 3 d, canopy temperature was cooler for TX86A8072 than for TX86A5606 (Fig. 9). On 2 May, when windspeed was $>2.4 \text{ m s}^{-1}$, both canopies had temperatures very close to T_a , and the temperature of the smaller-leaved canopy of TX86A8072 was closer to T_a

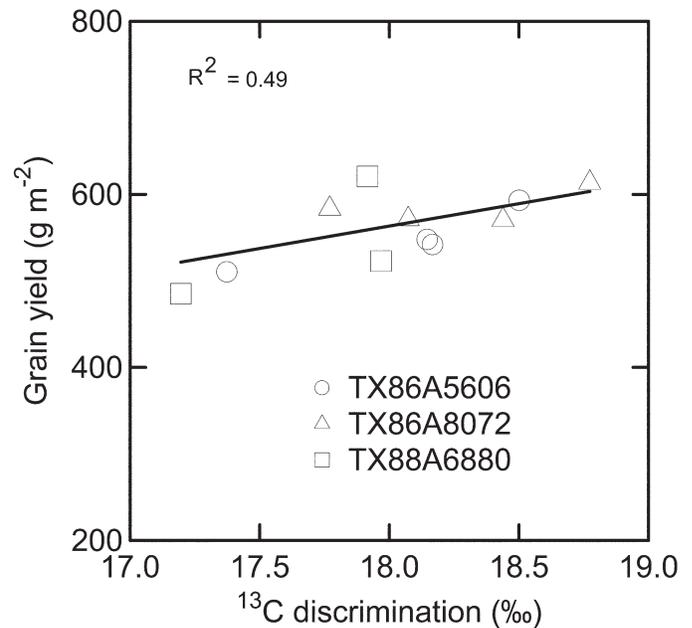


Figure 7. Correlation of grain yield and carbon 13 isotope discrimination (in ‰) in three close-related wheat lines in dryland at Bushland, TX, in 2001. Correlation is significant at $P = 0.016$.

Table 3. Mean carbon assimilation rate (A), total leaf conductance to water vapor (g_{lw}) at noon and at pre-dawn, transpiration rate (E), internal CO_2 ($[\text{CO}_2]_i$), apparent mesophyll conductance ($A:[\text{CO}_2]_i$), and their correlation with CTD measured during the same days and hours in two wheat lines in 2002. Days of measurement were 2 May (195 DAS[§]), 8 May (201 DAS) and 14 May 2002 (207 DAS) from 1100 to 1500 h, except pre-dawn g_s which was measured from 0600 to 0700 h.

Genotype	Noon					Pre-dawn
	A	g_{lw}	E	$[\text{CO}_2]_i$	$A:[\text{CO}_2]_i$	g_{lw}
	$\mu\text{mol m}^{-2} \text{ s}^{-1}$	$\text{mol m}^{-2} \text{ s}^{-1}$	$\text{mmol m}^{-2} \text{ s}^{-1}$	μmol	$\text{mol m}^{-2} \text{ s}^{-1}$	$\text{mol m}^{-2} \text{ s}^{-1}$
Dryland						
TX86A5606	12.49	0.140	7.89	226	61.8	0.022
TX86A8072	13.55	0.151	8.44	216	67.1	0.026
SE	0.245	0.004	0.265	3.58	2.21	0.006
Genotype effect (P)	0.004	0.002	0.077	0.037	0.100	NS
Day effect (P)	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
Genotype × day (P)	NS	NS	NS	NS	NS	NS
Irrigation						
TX86A5606	16.73	0.196	10.67	217	83.6	0.025
TX86A8072	17.71	0.231	11.66	121	88.0	0.010
SE	0.226	0.008	0.234	3.69	2.47	0.001
Genotype effect (P)	0.003	0.001	0.004	NS	NS	0.007
Day effect (P)	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
Genotype × day (P)	0.01	0.030	0.042	0.002	0.021	NS
Correlation with CTD	0.73*	0.80**	0.79*			NS

*Correlation coefficient significant at the 0.10 probability level.

**Correlation coefficient significant at the 0.05 probability level.

[§]Days after sowing.

than the temperature of the larger-leaved canopy of TX86A5606, consistent with theory (Leuning, 1989). As windspeed decreased below 2 m s^{-1} , on 8 May and 14 May, CTD was much larger and both canopies were much cooler than the air. However, TX86A8072's canopy was still cooler than that of TX86A5606.

Leuning (1988) developed a theory of nighttime leaf temperature under different assumptions of convection (free, mixed, and forced), and demonstrated that non-transpiring leaves can be cooler than air during nighttime due to radiational cooling. However, larger leaves should be cooler than small ones during clear nights because of a smaller exchange coefficient for sensible heat transfer from the warmer air. Therefore, the cooler nighttime temperatures of the drought-tolerant line, TX86A8072, are inconsistent with its smaller leaves if stomata were closed and no transpiration was taking place.

But it has been increasingly documented that nighttime T occurs in wheat and other plant species (Howard and Donovan, 2007; Caird et al., 2005, 2006), especially in low humidity environments (Richards et al., 2002; Snyder et al., 2003; Tolk et al., 2006). Although the benefits of nighttime T are not clear, it is known to differ among and within plant species, and that it can be independently regulated by such environmental variables as water, nutrient availability, and salinity (Caird et al., 2006). In Australia, Rawson and Clarke (1988) observed that wheat stomata began to open "some hours" before dawn, and that nighttime T differed significantly among genotypes both in amount and in response to VPD. They stated that "The most profligate genotype transpired at $50 \text{ g m}^{-2} \text{ leaf h}^{-1}$ at a VPD of 30 mbar, which was twice the rate of the most thrifty genotype," and concluded that transpiration could exceed 0.05 mm h^{-1} at nighttime in unstressed crops.

Table 4. Flag-1 and flag leaf area (LA), width, length, specific leaf area (SLA), relative greenness (RG), and rate of excised-leaf water loss (RWL) of three wheat related lines. Leaf width and length were measured only in 2002 at 206 and 214 d after sowing (DAS); LA in 2001 at 202 DAS and in 2002 at 174, 206, and 214 DAS; RWL in 2001 at 203 DAS; all other traits were measured in 2000, 2001, and 2002 (see Table 1 for details).

Genotype	LA	Width	Length	SLA	RG [§]	RWL
	cm ²	cm	cm	cm ² g ⁻¹		g g ⁻¹ h ⁻¹
Dryland						
TX86A5606	10.2	1.1	12.0	141.5	54.23	0.207
TX86A8072	9.7	1.0	11.2	130.4	54.66	0.198
TX88A6880	10.1	1.1	12.0	137.5	54.34	0.187
SE	0.176	0.010	0.147	3.08	1.127	0.008
Genotype effect (P)	0.050	0.040	0.0001	0.010	NS	NS
Year effect (P)	0.0001			0.0001	0.0001	
Genotype×year (P)	NS			NS	NS	
Irrigation						
TX86A5606	14.8	1.3	15.6	168.0	52.24	0.237
TX86A8072	12.2	1.2	14.3	160.3	51.85	0.245
TX88A6880	14.1	1.3	16.4	162.4	54.04	0.243
SE	0.248	0.032	0.244	4.47	0.921	0.006
Genotype effect (P)	0.0001	0.0001	0.0001	NS	NS	NS
Year effect (P)	0.0001			0.0001	0.0001	
Genotype×year (P)	NS			NS	NS	

[§]Arbitrary units of the Minolta SPAD meter.

The larger nighttime CTD (cooler canopy) values of TX86A8072, measured on several non-flag leaves by the IRT at the same time that flag leaf g_{lw} was measured by the LI-COR 6200 (Fig. 9), suggest that the drought tolerant line had slightly larger nighttime T rates than the drought-sensitive line.

Energy Balance and Nighttime CTD

Many classic leaf energy balance models assume stomatal closure at night, despite a growing body of evidence that this is often incorrect, and therefore cannot be used to

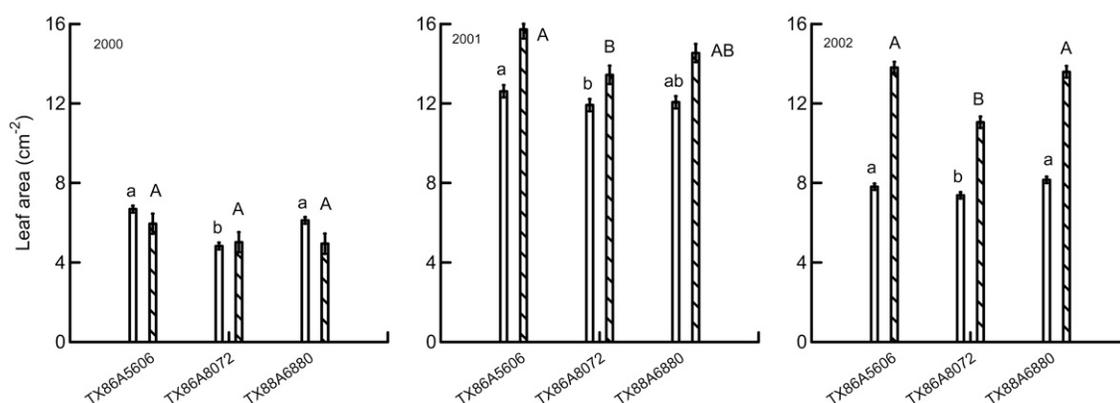


Figure 8. Leaf area of three wheat sister lines with contrasting canopy temperature depression measured in 3 yr, two water regimes, and at different vegetative stages. Leaves were the eighth fully developed leaf in 2000, flag leaf in 2001, and flag-1 and flag leaves in 2002. For vegetative stages see Table 1. Open bars represent dryland and dashed ones irrigated leaves. Vertical bars are ± 1 SE. Means with different letters are significantly different using LSD test $P < 0.05$. Comparisons were made within each environment, i.e., dryland and irrigated plots.

better understand nighttime CTD. Zweifel et al. (2007), for example, measured significant nighttime T in Scots pine (*Pinus sylvestris* L.), but their model could not simulate it, despite good agreement with daytime T . Leuning (1988) laid out several theoretical considerations, but he was concerned with temperatures near freezing and non-transpiring leaves.

Ignoring contributions of long wave radiation from the soil surface, the leaf's energy balance at any time can be represented from the equation:

$$0 = R_{s_{in}} - R_{s_{out}} + Rl_{in} - Rl_{out} + L + H \quad [1]$$

where $R_{s_{in}}$ is shortwave radiation from the sun to the leaf, Rl_{in} is the longwave energy radiation from the sky to the leaf, $R_{s_{out}}$ is shortwave radiation reflected from the leaf, Rl_{out} is longwave energy radiated and reflected from the leaf, L is the latent heat of transpiration due to evaporating water, and H is the energy transferred between the leaf surface and flux units are in $W\ m^{-2}$.

At night we assume that $R_{s_{in}}$ and $R_{s_{out}}$ are zero. The sum, Rl_{out} , of reflected incoming longwave radiation and emitted longwave radiation from the leaf is:

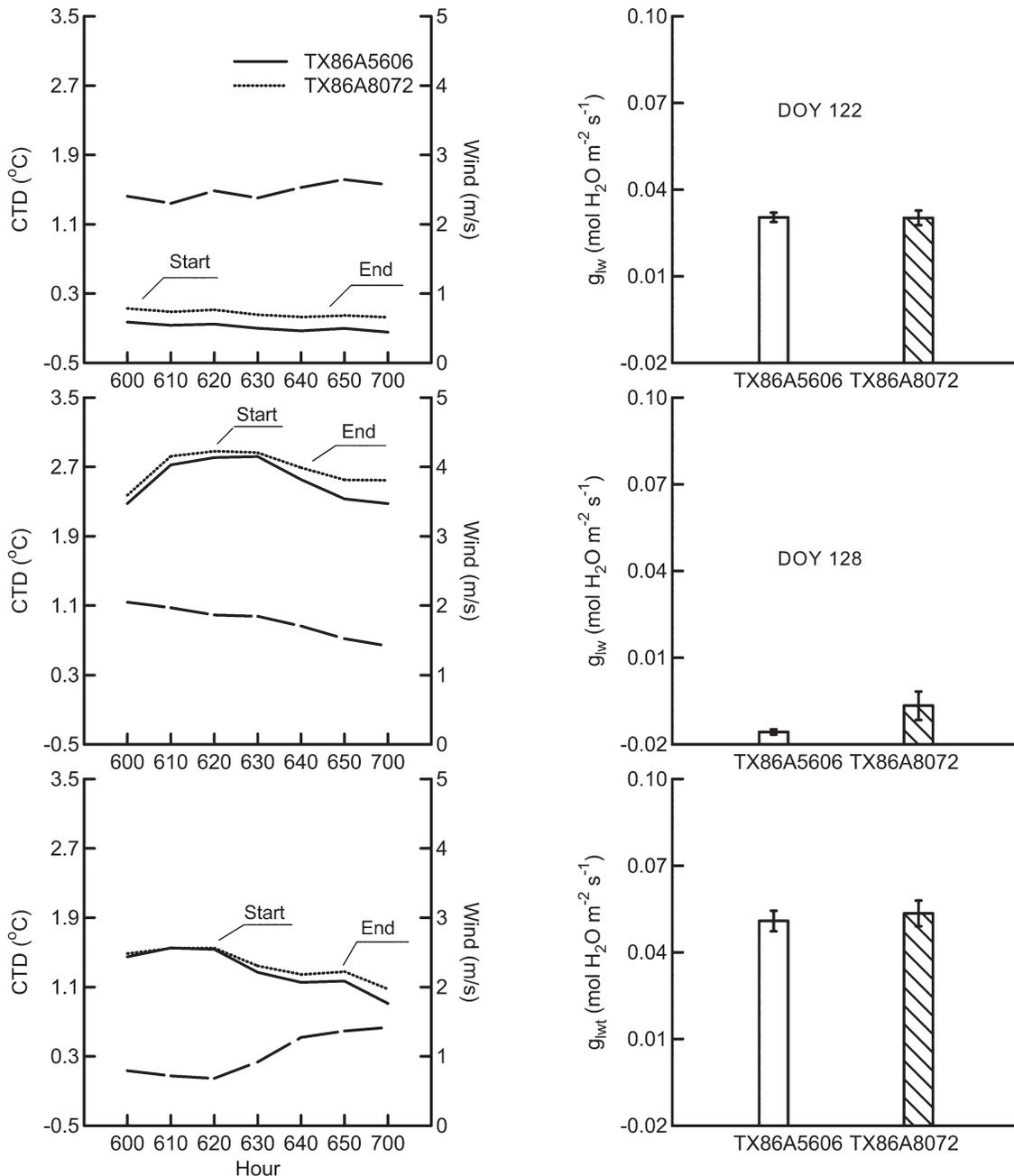


Figure 9. Canopy temperature depression (CTD) (left) and windspeed (left, dashed line), and flag leaf total conductance to water vapor (g_w) (right) measured at pre-dawn in dryland plots in 2002. Start and end of g_w measurements are indicated on the CTD graphs. Vertical bars are ± 1 SE for the genotypic effect on g_w . The upper graphs represent measurements on day of year (DOY) 122, the middle ones DOY 128, and the lower ones DOY 134. Heading DOY was 118. For all days, g_w was NS among genotypes according to LSD test $P < 0.05$.

$$Rl_{out} = \alpha \times Rl_{in} + 2 \times \epsilon_1 \times \sigma \times T_l^4 \quad [2]$$

where α is the albedo, ϵ_1 is the emissivity of the leaf (unitless), T_l is the leaf temperature in $^{\circ}\text{K}$, and σ is the Stefan-Boltzman constant ($5.67 \times 10^{-8} \text{ W m}^{-2} \text{ }^{\circ}\text{K}^{-4}$). The coefficient of 2 is to account for energy loss from both sides of the leaf. The value of Rl_{in} can be estimated from:

$$Rl_{in} = \epsilon_a \sigma (T_a)^4 \quad [3]$$

where T_a is the air temperature in $^{\circ}\text{K}$ and ϵ_a is the emissivity of the sky, which for Bushland conditions can best be estimated from the vapor pressure (e_a) and temperature (T_a , $^{\circ}\text{C}$) of the air by Idso's (1981) equation (Howell et al., 1993):

$$\epsilon_a = 0.70 + 5.95 \times 10^{-4} e_a \exp\left(\frac{1500}{T_a + 273.16}\right) \quad [4]$$

Assuming a depth of water transpired (D_T , mm d^{-1}) and density of water being 1 Mg m^{-3} , latent heat loss (L) is calculated from:

$$L = \lambda \frac{10^6}{8640} \left(\frac{D_T}{\text{LAI}}\right) \quad [5]$$

where λ is the latent heat of evaporation (assumed to be 2.45 MJ kg^{-1}) and LAI is the leaf area index in $\text{m}^2 \text{ m}^{-2}$.

The sensible heat flux, H , is calculated from (Parlange and Waggoner, 1972):

$$H = 2 \times 0.453 \beta k P_r^{1/3} (\nu X / U)^{-0.5} \times (T_l - T_a) \quad [6]$$

where the coefficient of 2 is for both sides of the leaf, β is a coefficient found to be 2.5 for a leaf in turbulent air (Parlange and Waggoner, 1972), k is the thermal conductivity of dry air ($0.0243 \text{ W m}^{-1} \text{ }^{\circ}\text{C}^{-1}$), P_r is the Prandtl number (taken to be 0.72), ν is the kinematic viscosity of air ($1.6 \times 10^{-5} \text{ m}^2 \text{ s}^{-1}$), X is the leaf width (m), U is the wind speed (m s^{-1}), and T_a is the temperature of the air in $^{\circ}\text{K}$. The model must be solved iteratively since both H and Rl_{out} are dependent on leaf temperature.

Ancillary data for our pre-dawn measurements illustrated in Fig. 9 show that nighttime wind speeds ranged from 1 to 3 m s^{-1} and relative humidity averaged 54%. Assuming an albedo of 0.23 (Evelt, 2002), leaf emissivity of 0.98 (Evelt, 2002), wind speed of 3 m s^{-1} , and LAI of 3 (full cover conditions), the CTD estimated from the model for a leaf with width of 0.010 m ranged from 2.19 to 2.63°C for transpiration rates ranging from 0 to 0.042 mm h^{-1} , respectively (Fig. 10). Decreasing the assumed wind speed to 1 m s^{-1} caused CTD values to increase by $\sim 1.5^{\circ}\text{C}$ for both leaf width values, indicating less sensible heat transfer from the air to the leaf, which is in accordance with the theory in Eq. [1–6]. This phenomenon is illustrated well in Fig. 9. For a wider leaf (0.011 m) and a wind speed of 3 m s^{-1} , modeled CTD values indicate a slightly cooler leaf, ranging from 2.30 to 2.76°C over the same range of transpiration. These CTD values are somewhat

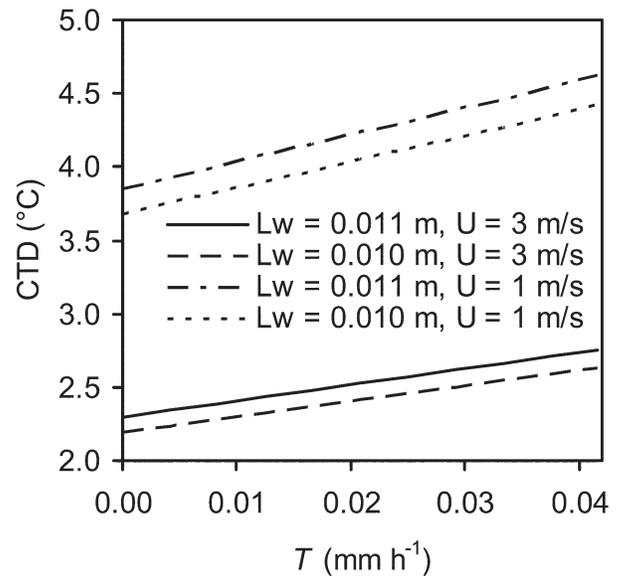


Figure 10. Modeled canopy temperature depression as a function of transpiration rate (T) at night for leaf widths (L_w) of 0.010 m and 0.011 m, and for wind speeds (U) of 1 and 3 m s^{-1} .

larger than those shown in Fig. 2, but are close to those for DOY 128, 2002 in Fig. 9. Contrary to the measured data for TX86A8072, the smaller leaf is estimated to be warmer (smaller CTD) during the night. This is consistent with Leuning's (1988) model, conceived for much colder conditions. If this model of CTD is correct, then transpiration from TX86A8072 must be larger than that of TX86A5606 at nighttime in order for it to reach a lower temperature. The nighttime T rate of TX86A8072 would have to be $>0.013 \text{ mm h}^{-1}$ greater than that of TX86A5606 in order for evaporative cooling to cause CTD to be greater for TX86A8072 than for TX86A5606.

The uniformly greater nighttime total leaf conductance to water vapor measured for TX86A8072, along with mounting evidence from the literature, indicates that increased nighttime T is indeed possible. While nighttime T is generally not associated with carbon fixation in C_3 plants, it has been linked to improved supply of water-soluble nutrients carried in the transpiration stream (Caird et al., 2005), especially nitrate (McDonald et al., 2002; Conroy and Hocking, 1993). However, in glass-house experiments with *Helianthus* species, Howard and Donovan (2007) found that nighttime T did not increase with induced nitrate deficiency, but it did decrease with induced water stress. Similarly, Zweifel et al. (2007) found that nighttime T of Scots pine (*Pinus silvestris* L.) in Switzerland was reduced by drought conditions. Daley and Phillips (2006) concluded that nighttime T of paper birch (*Betula papyrifera* L.) was responsible for over 10% of the total daily sap flux during the growing season. They speculated nighttime T might be a mechanism for delivering oxygen to respiring cells, and could be an ecological adaptation to maximize photosynthesis and growth.

Summarizing existing studies on nighttime T , Caird et al. (2006) pointed out that strong correlations exist for nighttime and daytime gas exchange patterns. Although we cannot rule out the possibility that increased nighttime T serves as a mechanism of drought tolerance in TX86A8072, on the basis of the scant evidence available in the literature, it would appear to be instead a reflection of its overall better water status relative to the other lines, which is consistent with superior yield, CTD, and gas exchange data.

CONCLUSIONS

Overall, our results for greater daytime CTD of the drought tolerant line TX86A8072 are consistent with its smaller, thicker leaves. Data showed that the smaller- and thicker-leaved line had higher A , $A:[CO_2]_i$, and grain yield than the larger-leaved TX86A5606 under similar conditions of plant water availability. Gas exchange and carbon-13 data suggest that smaller leaves also lead to greater CTD during the day. The cooler nighttime temperatures of the drought-tolerant line, however, cannot be explained by its smaller leaf dimensions, and are probably caused by greater nighttime T . Whether greater nighttime T plays an adaptive role under dryland conditions is unknown and deserves further study, but it may simply be a reflection of better water status and daytime gas-exchange patterns.

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