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Canopy temperature depression at grain filling correlates to winter wheat yield in the U.S. Southern High Plains

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ABSTRACT

Wheat breeding has improved drought tolerance over the years. However, our knowledge on drought tolerance in relation to the diurnal pattern of canopy temperature (CT) and grain yield is limited. A three-season wheat field study ending 2012, 2015, and 2016 was conducted at Bushland, Texas to investigate the relationship between canopy temperature depression (CTD) and yield during the grain filling period. For each season, 20 elite wheat genotypes were grown under dryland conditions, and CT was measured by Smart Crop wireless IRT sensors every 15 min continuously for 12–15 days during mid-grain filling (~10–25 days after flowering). There was a genotypic variation for CTD regardless of time of the day; however, the variation was more evident during the day time (10:00–18:00 h), with the smallest CTD (i.e., warmer canopy) at 14:00–15:00 h. In a dry season of 2012, TAM 304, TAM 112, Dumas, and Hatcher had greater CTD (i.e., cooler canopy) than other genotypes. In two wet/near normal seasons (2015 and 2016) Duster, TAM 111, TAM 110, TAM 112, and TAM 105 had greater CTD. There was a significant ($P < 0.05$) positive linear relationship between grain yield and day-time CTD. Hence, a cooler plant canopy during the mid-grain filling in winter wheat appears to be an important indicator of greater drought tolerance and yield under dryland condition. This knowledge may help breeders to conduct high-throughput field phenotyping in large breeding populations.

1. Introduction

Drought is the single most important environmental factor causing substantial yield loss in winter wheat (*Triticum aestivum* L.) in the U.S. southern High Plains (SHP). The long-term annual precipitation in the SHP averages about 470 mm. The wheat growing season (Oct.–June) receives an average of about 250 mm precipitation, which is one-third of the evapotranspiration (ET) requirement for wheat (700–800 mm) grown under full irrigation (Musick et al., 1994). In dryland areas, water deficit stress can affect in wheat yield at almost any stage (Eck, 1988; Zhang and Oweis, 1999). However, drought at the critical growth stages of wheat such as tillering, jointing, anthesis, and grain filling can result in significant yield loss (Hanks and Rasmussen, 1982; Eck, 1988; Xue et al., 2006). Therefore, development and adoption of drought-tolerant cultivars, which leave more water available for these critical times, or are able to access more water from the greater soil profile depths is a key strategy for sustainable wheat production in the area (Xue et al., 2014; Thapa et al., 2017a).

Canopy temperature (CT) is one of the many physiological traits that may help identify such drought-tolerant cultivars. Under high solar radiation and drought conditions, stomatal conductance decreases when soil moisture is not adequate to keep up with evaporative demands; and this, in turn increases CT (Jones and Leinonen, 2003; Urban et al., 2007). Plant morphological trait such as canopy architecture also influences CT not only through the angle of leaves to the light source, but also through the degree of mutual-shading in the canopy (Zheng et al., 2008). For example, according to Thapa et al. (2016), compared to conventional evenly spaced planting, growing corn plants in clumps (3 plants clustered) reduced the CT because of mutual-shading. Canopy temperature can provide plant-based information on the water status of the crop (Mahan et al., 2011). Thus CT has been used in drought (Rashid et al., 1999; Lopes et al., 2012) and heat stress experiments (Reynolds et al., 1994; Amani et al., 1996; Ayeneh et al., 2002) as well as for irrigation scheduling (Gontia and Tiwari 2008; Alchanatis et al., 2010). Genotypic differences can be observed in CT, such that CT may be used to characterize genotypic variation in energy balance, stomatal

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conductance, and transpiration (Balota et al., 2008).

Canopy temperature depression (CTD) is expressed as the difference between air temperature and canopy temperature (CTD = $T_{air} - T_{canopy}$) (Jackson et al., 1981; Balota et al., 2007, 2008). When evaporative cooling from transpiration cools the canopy below air temperature, then CTD is positive, conversely, when stomata close and CT rises above air temperature, then CTD is negative. Thus, for example, this value is generally higher, or more positive in well-irrigated plants, but generally lower, or more negative under water deficit conditions (Blum et al., 1989). The CTD can be influenced by a number of biological and environmental factors such as air temperature, soil moisture, wind velocity, evapotranspiration, cloudiness, canopy architecture, leaf adjustment to water deficit, relative humidity, and solar radiation (Bilge et al., 2008). The correlation between CTD and physiological states and processes in plants such as stomatal conductance (Rebetzke et al., 2013), leaf water potential (Cohen et al., 2005), and grain yield (Reynolds et al., 1994; Amani et al., 1996; Rashidet al., 1999; Ayeneh et al., 2002; Balota et al., 2007) under the conditions of limited water supply can be used as a selection criterion for tolerance to drought. The suitability of CTD as an indicator of yield and stress tolerance prediction, however, must be evaluated for every individual environment and, in particular, for every plant species (Blum et al., 1989).

A genotype that has a cooler canopy than another genotypes during the heading and grain filling period in wheat, in the same environment, can be an important indicator of drought stress tolerance (Munjal and Rana, 2003; Bilge et al., 2008). Balota et al. (2007) found genotypic variation in CTD among three closely-related wheat lines. Our previous studies demonstrated that higher grain yield in winter wheat under dryland conditions was closely associated with the effective stem carbon reserve remobilization and the depth and amount of soil water extraction (Xue et al., 2014; Thapa et al., 2017a). We hypothesized that genotypes having a cooler canopy, relative to others, during the hottest part of day produce more grain yield because they probably are more drought tolerant. This study was conducted to compare the CTD among 20 elite wheat cultivars during mid-grain filling and to characterize the relationship between CTD and grain yield under dryland conditions.

2. Materials and methods

2.1. Experimental design

Twenty elite wheat genotypes were used in this study. All 20 genotypes were grown under dryland condition at Bushland, Texas (Lat. 35.19° N, Long. 102.06° W; elevation 1170 m) in the winter wheat seasons ending 2012, 2015, and 2016. Among 20 genotypes, 14 genotypes were grown in all three years, and they were, Billings, Dumas, Duster, Endurance, Hatcher, Jagalene, TAM 105, TAM 110, TAM 111, TAM 112, TAM 113, TAM 304, TX99A0153-1, and Winterhawk. In addition, Bill Brown, Fuller, Jagger, TAM W-101, TX86A5606, and TX86A8072 were grown in the 2012 and 2015 seasons, and AMPSY068, AMPSY588, Iba, PlainsGoldByrd, TAM 114, and TX11Vsyn0101 were grown in the 2016 season. All "TAM" cultivars and experimental lines were developed by Texas A&M AgriLife Research (TAM) at different time periods. The experimental design was a randomized complete block design (RCBD) with three replications. The soil at Bushland is Pullman clay loam, which is a fine, mixed, superactive, thermic Torrertic Paleustoll (Unger and Pringle, 1981). The wheat was seeded on Nov. 03, 2011, Oct. 31, 2014, and Oct. 13, 2015. Each plot had seven rows with row spacing of 0.18 m, and row length of 4.5 m. The seeding rate was 67 kg ha^{-1}.

In each season, fertilizers were applied before planting based on soil tests to meet the dryland wheat yield potential of about 3500 kg ha^{-1}. Pesticides were applied as needed for managing weeds and insects.

2.2. Data collection

The canopy temperature was measured by Smart Crop wireless infrared thermometers (IRTs; Smartfield Inc., Lubbock, TX, www.smartfield.com). In the past, hand-held IRTs and wired IRTs have most commonly been used to monitor CT. The hand-held IRTs, which provide point-in-time values, are more difficult to use for a large number of plots, and also are difficult to use for investigating the relationship of CT with plant growth stage or time of day. Similarly, wired IRTs require substantial time and labor to install the system, and regularly archive the data. In this study, we used continuously recording wireless IRTs that can measure temperature continuously day and night without the hassle of cable management from each sensor, or need to regularly download a data logger. A sensor was installed at the center of each plot (3 reps. in 2012 and 2015, 2 reps. in 2016) at anthesis and a base station unit was established at the edge of the field to collect and transmit data. The IRT sensors were placed in the best part of the plots, where the crops were growing more uniformly with maximum ground cover, and at about 0.15 m above the plant canopy height. The viewing angle was 60° facing downward. Each sensor collected data from a circular field of view with 0.15 m diameter, every minute, auto-averaged to every 15-min., and reported wirelessly to the base station. The CT data collected in the base station were transmitted to a computer system for archiving and subsequent analysis. The base station also recorded ambient temperature every 15 min. The data were continuously collected for 15 days in the 2012 and 2015 seasons and 12 days in the 2016 season at the mid-grain filling. Time period of about 10–25 days after flowering was considered as mid-grain filling.

At first, CTD ($T_{air} - T_{canopy}$) was calculated every 15 min and then, the hourly CTD was calculated as an average of four subsequent 15-min data. The volumetric soil water content (SWC, m^3 m^{-3}) was measured in 12 plots each year at anthesis (AN) and physiological maturity (MA) using a 503 DR1.5 Hydroprobe (CPN, a division of InstroTek, Inc., Raleigh, NC, USA). The probes were previously calibrated *in-situ* at the experimental site using methods described by Evett and Steiner (1995). The access tubes were installed at the center of plots and measurements were taken every 0.2 m, starting at 0.1 m and ending at 2.3 m below the soil surface.

The amount of soil water (SW, mm) in the root zone was calculated as, SW = total soil water content (m^3 m^{-3}) × soil depth (mm) at each layer (Xue et al., 2003; Thapa et al., 2017a). Net soil water extraction (SWE) in the 0.0–2.4 m profile between AN and MA was calculated as, SWE = SW at AN (mm) – SW at MA (mm). However, there was no SWE below 1.4 m in the 2012 and 2015 seasons. Therefore, total soil water content only from the 0.0 to 1.4 m profile was considered for each year for the calculation of evapotranspiration (ET). Evapotranspiration was calculated using the soil water balance method, that is, ET = SWC at AN + precipitation between AN and MA – SWC at MA, assuming that there was no surface runoff. Though there were small variations among the seasons, on average, AN and MA stages corresponded to the day of year (DOY) of 125 and 160, respectively. At maturity, each plot (5.67 m^2) was combine-harvested and yield was determined after air drying. The yields were only available for the 2012 and 2016 seasons because of hail damage in the 2015 season.

2.3. Statistical analysis

Statistical analysis was conducted using SAS 9.4 (SAS Institute Inc, 2013). The PROC MIXED procedure in repeated measure analysis of variance (ANOVA) was used to evaluate the difference in CTD. The ANOVA was also used to evaluate the yield difference among the genotypes. Replication was considered random effect, whereas cultivar was a fixed effect. Means were considered significantly different at least significance difference (LSD) of the 5% level. Since the study was intended to identify more drought tolerant genotypes in relation to CTD and grain yield, regardless of differences in CTD among the days and

Table 1
Mean monthly maximum and minimum temperatures during wheat growing seasons (Oct.–June) at Bushland, TX.
Source: http://www.ncdc.noaa.gov

Seasons	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	Mean
	°C									
Mean maximum										
2011–2012	22.9	16.1	5.5	13.8	11.1	20.9	25.1	28.2	32.7	19.6
2014–2015	23.6	13.6	10.68	6.9	11.4	16.2	22.6	22.3	29.2	17.4
2015–2016	21.8	15.6	11.5	10.1	15.2	19.4	21.1	24.0	31.1	18.9
30-yr mean	22.6	15.7	9.9	10.6	12.4	17.1	21.2	26.4	30.8	18.5
Mean minimum										
2011–2012	5.4	−0.2	−4.9	−5.2	−4.2	2.0	6.6	11.1	16.4	3.0
2014–2015	6.7	−3.5	−4.3	−5.8	−4.5	−0.5	3.2	8.6	16.2	1.8
2015–2016	9.0	−0.2	−3.5	−4.9	−2.5	0.4	4.3	8.1	15.6	2.9
30-yr mean	4.8	−1.7	−6.6	−6.7	−5.3	−1.3	3.2	9.1	14.4	1.1

hours, means were compared for the genotypes only. A linear regression between CTD and grain yield was performed using PROC REG in SAS 9.4. For each year, all 20 genotypes were used to compare and analyze the relationship between CTD and grain yield, however the data trend on the 14 genotypes that were grown in all three years was also taken into consideration.

3. Results

3.1. Weather conditions

Table 1 showed that seasonal mean maximum and minimum temperatures were numerically greater in all the experimental years than the 30-yr seasonal averages (18.5 °C max. and 1.1 °C min), except for the mean maximum temperature in the 2015 season (17.4 °C). Among the seasons, mean maximum and minimum temperatures were numerically greater in 2012. The monthly mean maximum temperature during the active growth period of wheat (Mar.–June) was also numerically greater in this season (2012) than the 30-yr average. By contrast, May and June in the 2015 season were cooler than the 30-yr average, mainly due to more precipitation events (Fig. 1).

The precipitation amount varied greatly among years. The seasonal precipitation (Oct.–June) was 231, 531, and 315 mm for the 2012, 2015, and 2016 seasons, respectively, as compared to the 30-yr average of 331 mm. The 2012 season, which followed a historic drought year in the SHP (2011; 60 mm seasonal precipitation), was also very dry itself, and wheat plots experienced extreme drought stress. In contrast, 2015 was the wettest season with significant precipitation, of which more than half (298 mm) occurred during the grain filling period. The 2016 season was a favorable season for wheat growth and development with better distributed rainfall during the growing season. This season also benefitted from excess water stored in the soil profile from the end of the 2015 season.

3.2. Soil water extraction (SWE) and evapotranspiration (ET)

Fig. 2 showed the SWC at anthesis and physiological maturity within the 0.0–2.4 m soil profile for the three growing seasons ending 2012, 2015, and 2016. The amount of net SWE was closely associated with the amount of precipitation. For example, the soil water content at anthesis in the 2015 season was more than that in the other seasons (Fig. 2B). Further, this season received 298 mm of rainfall during AN – MA. So, water extracted by plants was replaced by the water from precipitation events. As a result, there was no net soil water depletion or extraction between AN and MA in 2015. The 2012 season received only 45 mm of rainwater during AN – MA, SWE did not occur during this period (Fig. 2A). This was probably because there was a very low amount of plant available water in the soil profile, which eventually reflected as a poor grain yield. The 2016 season benefitted from the previous as well as current season precipitation. Weather in this season was near-normal and the early crop establishment was very good. This season received 80 mm of precipitation during AN – MA, and 6.0 mm of SWE occurred, especially from the lower soil profile (Fig. 2C). Evapotranspiration essentially followed the same trend as that of precipitation. On average, the ET between AN and MA was significantly ($P < 0.05$) greater in 2015 (292 mm) than in 2012 (39 mm) and 2016 (86 mm; data not shown).

3.3. Canopy temperature depression (CTD)

Canopy temperature depression in 20 wheat genotypes averaged across the entire measurement period is presented in Fig. 3. Due to the large number of genotypes, Fig. 3 is generally useful to understand the diurnal pattern of decrease or increase in CTD for different seasons, while CTD values for all genotypes in each year are compared in Table 3. There was a genotypic variation for CTD at any time for all three seasons, but the difference was more evident during the day, and especially at about 14:00–15:00 h, Central Standard Time (CST) in the

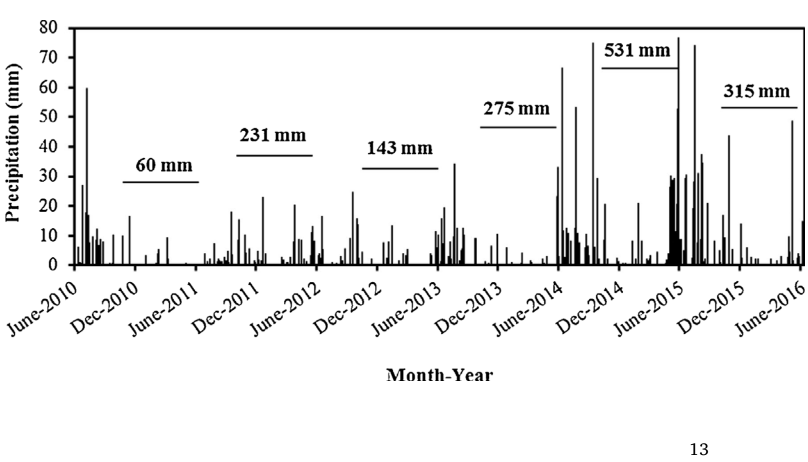

Fig. 1. Daily precipitation from June 2010 to June 2016 at Bushland, TX. Numbers above bars represent precipitation during the winter wheat growing season (Oct.–June).
Data Source: http://www.ncdc.noaa.gov

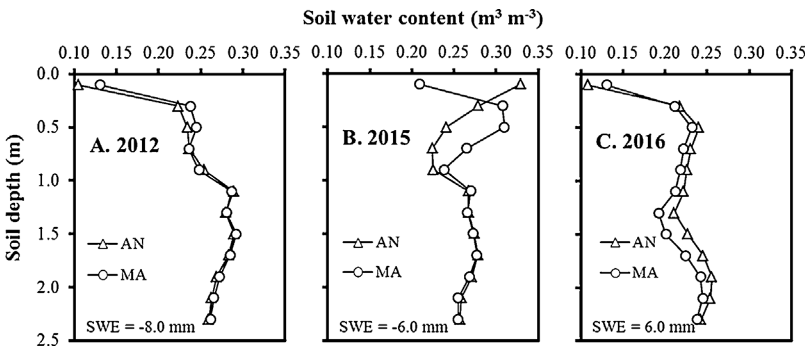

Fig. 2. Soil water content (SWC) in 0.0–2.4 m soil profile at anthesis (AN) and maturity (MA) for growing seasons ending 2012, 2015, and 2016. SWE = soil water extraction.

afternoon when CTD was at its minimum value (Fig. 3). Therefore, at first, data for all hours (00:00–24:00 h) was analyzed, and then were separated into two parts, day time (10:00–18:00 h) and night time (19:00–9:00 h; including early morning) for further evaluation.

In all three seasons, daytime CT was generally higher than the air temperature, resulting in negative CTD values. Though CTD followed the same general diurnal pattern of decrease or increase in all seasons, CTD in 2012 was lowest at 15:00 h, while it was lowest at 14:00 h in the 2015 and 2016. In the 2012 and 2016 seasons, the negative CTDs dropped down to about −8 °C, while the lowest CTD was about −4 °C in the 2015 season. This was mainly because of more precipitation (both frequency and amount) in the 2015 season (Fig. 1) resulting in a

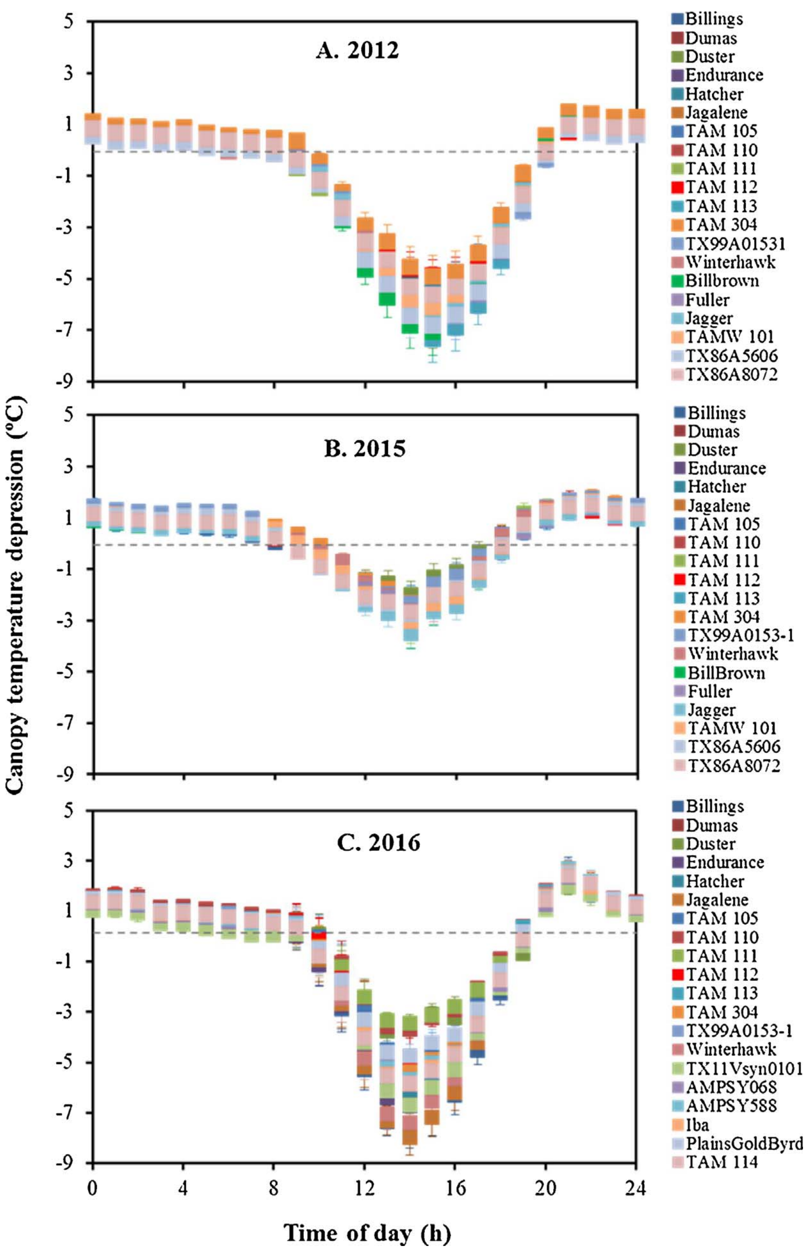

Fig. 3. Canopy temperature depression (CTD) for 20 winter wheat genotypes recorded every 15 min (converted to an hourly basis) continuously for 15 days (2012 and 2015) and 12 days (2016) at the mid-grain filling (~10–25 days after flowering).

Table 2
Repeated measure ANOVA (P-values) of canopy temperature depression (CTD) for the 20 winter wheat genotypes as affected by genotype, day, and hour (time of day) and their interactions.

Effect	2012			2015			2016		
	01–24 h	10–18 h	19 – 09 h	01–24 h	10–18 h	19 – 09 h	01–24 h	10–18 h	19 – 09 h
Genotype (G)	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Day (D)	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Hour (H)	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
G × D	1.0000	1.0000	0.9988	< 0.0001	< 0.0001	< 0.0001	1.0000	1.0000	0.9998
G × H	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
D × H	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
G × D × H	1.0000	1.0000	0.9999	< 0.0001	< 0.0001	0.4396	1.0000	1.0000	0.8786

small difference between air temperate and canopy temperature. For all seasons, CTD was greatest at 21:00–22:00 h.

During both day and night hours, there was a significant ($P < 0.05$) difference in CTD among the genotypes in all seasons (Table 2). Further, CTD was significantly ($P < 0.05$) influenced by the main effects of hours and day and all two-way interactions (except genotype × day in 2012 and 2016) and a three-way interaction in 2015 (except for night time). In the dry season of 2012, cultivar TAM 304 had the highest day time CTD (−3.03 °C) (Table 3), TAM 304 was followed by TAM 112 (−3.41 °C), Dumas (−3.59 °C), and Hatcher (−3.71 °C). In this season, TAM 113 had the lowest day time CTD (−4.97 °C). In the 2016 season, Duster (−1.82 °C) had the highest day time CTD followed by TAM 111 (−2.21 °C), TAM 110 (−2.52 °C), TAM 112 (−2.54 °C), and TAM 105 (−2.88 °C). In this season, Billings (−4.95 °C) and Jagalene (−4.84 °C) had the lowest day time CTD. The CTD trend in the 2015 season was close to that of the 2016 season, but the genotypic variation in day time CTD was smaller than in the 2012 and 2016 seasons. Among the 14 genotypes that were grown in all years, TAM 113, Fuller, and Bill Brown generally had smaller day time CTD, whereas, TAM 304, TAM 110, TAM 111, and TAM 112 had greater. Overall, the night time CTD followed a similar trend as that of the day time CTD. For instance, TAM 304 (0.99 °C) in the 2012 season and Duster (1.24 °C) in the 2015 season had higher night time CTD than the other genotypes. Further, TX86A5606 (0.07 °C) in the 2012 season and Billings (0.49 °C) in the 2015 season had the lowest night time CTD. The night time CTD in the 2016 season ranged from 0.65 °C (Bill Brown) to 1.23 °C (TAM 110). Overall, the mean CTD across the 20 genotypes was greater in the 2015 season followed by the 2016 and 2012 seasons, but mean values among the years were not compared statistically due to some different genotypes in the 2016 season (Table 3).

The actual CT for a particular day in each season when the CTD was at its lowest value is presented in Fig. 4. The CTD was as low as about −7.5 °C (May 23, 2012), −3.5 °C (May 18, 2015), and −8.0 °C (May 24, 2016) at the hottest part of day (2:00–3:00 pm). The CT on the corresponding day and time was as high as 46.5 °C, 29.0 °C, and 43.0 °C, respectively. Due to the frequent rain events and cloudy weather during the measurement period (mid-grain filling), the maximum ambient temperature was limited to about 26 °C in the 2015 season, while it was maximum of about 39 °C in the 2012 and 35.5 °C in the 2016 season. The difference in CT between the genotypes having highest and lowest CT at the same day and time was about 5 °C in the 2012 and 2016 seasons, but was only about 3 °C in the 2015 season (Fig. 4).

3.4. Grain yield

The effect of genotype on grain yield was marginal ($P = 0.1205$) in

Table 3
Mean canopy temperature depression (CTD) for the 20 winter wheat genotypes for the seasons ending 2012, 2015, and 2016. STD = standard deviation; LSD = least significance difference.

Genotypes	2012; CTD (°C)			2015; CTD (°C)			Genotypes	2016; CTD (°C)		
	00–24 h	10–18 h	19–09 h	00–24 h	10–18 h	19–09 h		00–24 h	10–18 h	19–09 h
Billings	−1.59	−4.49	0.14	−0.13	−1.17	0.49	Billings	−1.19	−4.95	1.05
Dumas	−1.04	−3.59	0.48	0.00	−1.46	0.87	Dumas	−0.97	−3.48	1.09
Duster	−1.55	−4.26	0.25	0.39	−0.86	1.24	Duster	0.03	−1.82	1.15
Endurance	−1.45	−4.26	0.23	0.00	−1.57	0.93	Endurance	−1.01	−4.31	0.96
Hatcher	−1.14	−3.71	0.44	0.03	−1.42	0.91	Hatcher	−0.75	−3.86	1.11
Jagalene	−1.38	−4.11	0.27	0.21	−1.27	1.09	Jagalene	−1.13	−4.84	1.08
TAM 105	−1.63	−4.42	0.19	0.25	−1.20	1.13	TAM 105	−0.48	−2.88	0.95
TAM 110	−1.52	−4.12	0.17	0.11	−1.35	0.98	TAM 110	−0.17	−2.52	1.23
TAM 111	−1.48	−3.95	0.21	−0.05	−1.59	0.99	TAM 111	−0.24	−2.21	0.93
TAM 112	−1.24	−3.41	0.52	−0.10	−1.49	0.94	TAM 112	−0.81	−2.54	1.06
TAM 113	−1.81	−4.97	0.17	−0.06	−1.66	0.90	TAM 113	−0.54	−3.46	1.21
TAM 304	−0.59	−3.03	0.99	0.34	−1.09	1.19	TAM 304	−0.57	−3.38	1.11
Winterhawk	−1.33	−3.95	0.25	0.08	−1.30	0.91	Winterhawk	−1.07	−4.48	0.97
TX99A0153-1	−1.58	−4.42	0.11	0.31	−1.16	1.19	TX99A0153-1	−0.68	−3.61	1.06
Bill Brown	−1.64	−4.79	0.26	−0.25	−2.07	0.68	TX11Vsyn0101	−1.13	−4.11	0.65
Fuller	−1.56	−4.52	0.22	−0.13	−1.56	0.72	AMPSY068	−0.75	−3.64	0.98
Jagger	−1.37	−4.01	0.26	−0.08	−1.70	0.89	AMPSY588	−0.62	−3.52	1.11
TAM W-101	−1.43	−4.00	0.24	−0.02	−1.63	1.02	Iba	−0.86	−3.62	1.08
TX86A5606	−1.73	−4.72	0.07	0.00	−1.61	0.98	PlainsGoldByrd	−0.41	−3.02	1.16
TX86A8072	−1.25	−3.94	0.36	−0.06	−1.59	0.85	TAM 114	−0.74	−3.74	1.05
Mean	−1.41	−4.13	0.29	0.04	−1.43	0.94	Mean	−0.70	−3.74	1.04
STD	0.26	0.46	0.19	0.16	0.26	0.17	STD	0.32	0.81	0.12
LSD (P = 0.05)	0.42	0.67	0.18	0.26	0.43	0.18	LSD (P = 0.05)	0.50	0.76	0.25

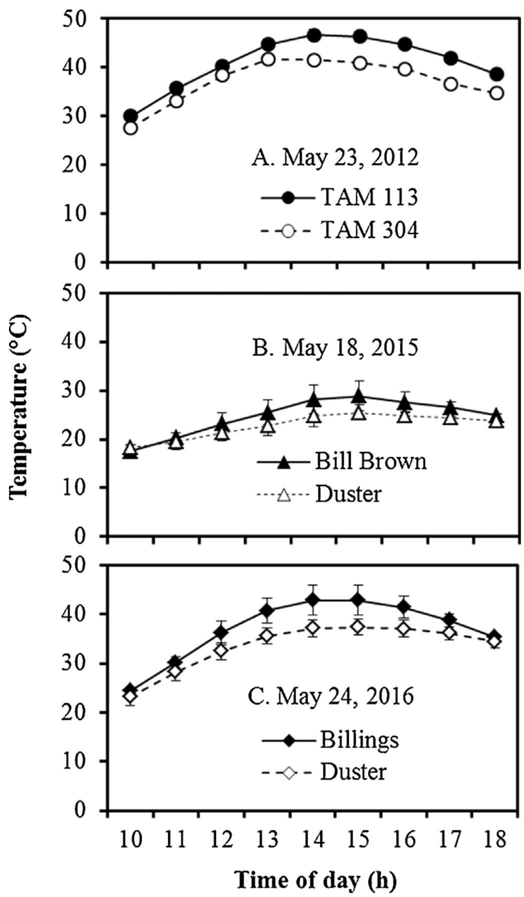

Fig. 4. Actual canopy temperature (CT) for the particular days in different seasons when the canopy temperature depression (CTD) was in its lowest value. In each graph, upper solid line indicates the genotype with the highest CT and lower dotted line indicates the genotype with the lowest CT on the same day and time.

Table 4
Mean grain yields for the 20 winter wheat genotypes in the 2012 and 2016 seasons. Grain yield for the 2015 season was not available due to the hail damage. STD = standard deviation; LSD = least significance difference; ns = not significant.

2012		2016	
Genotype	Yield (kg ha^{-1})	Genotype	Yield (kg ha^{-1})
Billings	958	Billings	2152
Dumas	774	Dumas	2684
Duster	967	Duster	3283
Endurance	1001	Endurance	2045
Hatcher	861	Hatcher	3128
Jagalene	999	Jagalene	2671
TAM 105	862	TAM 105	3544
TAM 110	864	TAM 110	3451
TAM 111	875	TAM 111	3650
TAM 112	1049	TAM 112	3173
TAM 113	777	TAM 113	3432
TAM 304	784	TAM 304	2843
TX99A0153-1	1038	TX99A0153-1	2381
Winterhawk	979	Winterhawk	3256
Billbrown	780	TX11Vsyn0101	2339
Fuller	909	AMPSY068	2507
Jagger	1011	AMPSY588	2779
TAM W-101	662	Iba	3308
TX86A5606	834	PlainsGoldByrd	3928
TX86A8072	788	TAM 114	1939
Mean	889	Mean	2874
STD	105	STD	558
LSD (P = 0.05)	ns	LSD (P = 0.05)	1089

2012, but was significant in 2016 ($P < 0.05$). In the dry season of 2012, TAM 112 (1049 kg ha^{-1}) and TX99A0153-1 (1038 kg ha^{-1}) had highest yields, whereas, Dumas (774 kg ha^{-1}) and TAM W-101 (662 kg ha^{-1}) had the lowest (Table 4). In the more favorable (near-normal) season of 2016, PlainsGoldByrd (3928 kg ha^{-1}), TAM 111 (3650 kg ha^{-1}), and TAM 105 (3544 kg ha^{-1}) produced highest yields, whereas, Endurance (2,045.6 kg ha^{-1}) and TAM 114 (1939 kg ha^{-1}) produced the lowest. Among the 14 common genotypes, Duster, Winterhawk, TAM 105, TAM 110, TAM 111, and TAM 112 generally performed better in both years. Averaged across all 20 genotypes, the mean grain yield in 2012 and 2016 seasons were 889 kg ha^{-1} and 2874 kg ha^{-1}, respectively (Table 4).

3.5. Relationship between CTD and grain yield

In the 2012 season, the night time and early morning (19:00 − 09:00 h) CTD for all 20 genotypes had no relationship with grain yield (Fig. 5A). For the day time (10:00–18:00 h) too, CTD did not show relationship with grain yield (Fig. 5B). However, Fig. 5B clearly showed that there were three cultivars (TAM W-101, Dumas, and TAM 304; left to right, respectively in the box), which had relatively higher CTDs, but the grain yield did not increase as like in other genotypes. When these three cultivars were removed from the regression analysis, grain yield showed a significant linear increase with increasing CTD ($R^2 = 0.42$, $P = 0.0053$, $N = 17$; Fig. 5D). In contrast, with the removal of these cultivars too, the relationship between night time CTD and grain yield did not improve (Fig. 5C).

In the 2016 season, there was no relationship between night time and early morning (19:00 − 9:00 h) CTD and grain yield (Fig. 6A), but day time (10:00–18:00 h) CTD showed a significant linear relationship ($R^2 = 0.37$, $P = 0.0046$, $N = 20$) with grain yield (Fig. 6B). The outlier cultivars in the 2012 season (Dumas and TAM 304; TAM W-101 was not grown in 2016), remained below the regression line in the 2016 season too, but they did not affect the overall outcome of the association between CTD and grain yield.

Correlation between grain yield and CTD at different times of day in the severely drought year (2012) showed that 13:00 to 15:00 h are the best time for CTD measurement at mid-grain filling, though the relationship between CTD and grain yield were significant anytime between 11:00 and 17:00 h. The relationship between CTD and grain yield was significant at all hours in the afternoon in the 2016 season (Table 5).

4. Discussion

4.1. SWE, ET, and CTD

Soil water extraction and use during grain filling are important for the expression of wheat yield potential. However, in drylands, a considerable amount of soil water can be lost by evaporation as well as high rate of transpiration. This results for the plants usually run out of soil water during the later growth stages such as reproductive and grain filling, and this is the main reason for dryland crops having lower harvest index compared to the irrigated crops (Thapa et al., 2017b). In all seasons of our study, there was no or very minimum net SWE between AN and MA. It probably was because either all the water extracted by plants was replaced by the water from precipitation (most likely in the 2015 season) or there was a very low amount of soil water available for plants to extract (most likely in the 2012 season). This explanation seems reflected in the ET (AN − MA), which had a trend of 292 mm (2015) > 86 mm (2016) > 39 mm (2012). Since increased plant transpiration causes a decrease in the plant surface temperature (Maes and Steppe, 2012), more rain events in the 2015 season helped plants to extract more soil water and keep CT close to the ambient temperature, so the day time CTD was greater in this season compared to the 2012 and 2016 seasons (Fig. 3, Table 3). In this study, the CT was

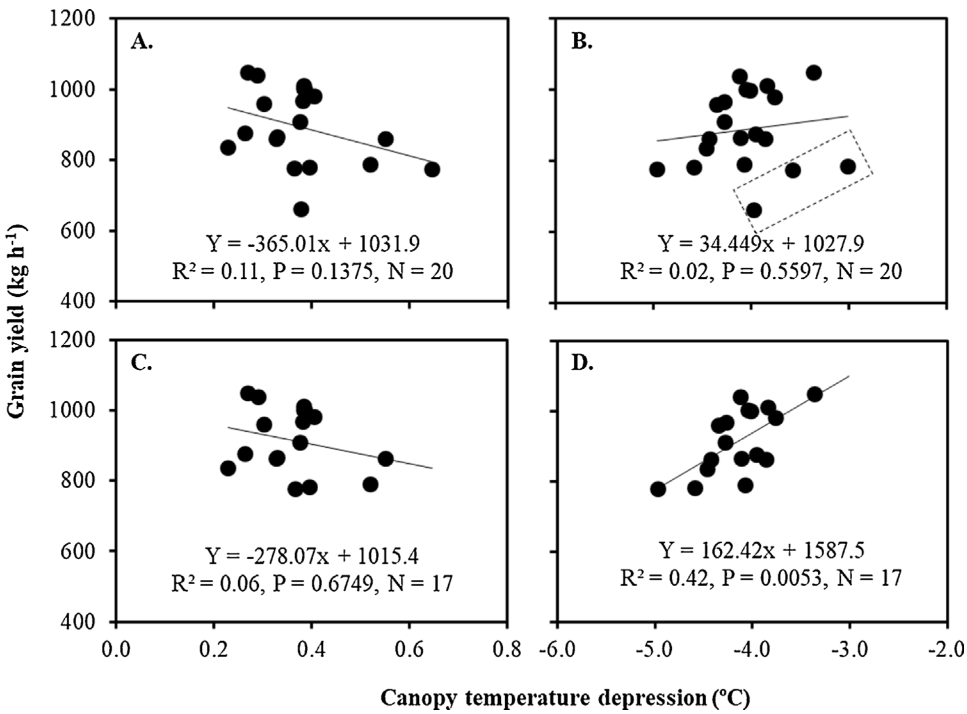

Fig. 5. The relationship between grain yield and canopy temperature depression (CTD) in the 2012 season for 19.00 to 9.0 h (A) and 10.00–18.00 h (B). A and B show regression curves and values for all 20 genotypes, and C and D show regression curves and values excluding TAM W-101, Dumas, and TAM 304 (left to right, respectively in the box). Canopy temperature was measured and grain yield was determined from all three replications for each genotype. So, each data point is the average of three replications.

found to reach a maximum of about 8 °C warmer than the air temperature. Balota et al. (2007, 2008) used wired IRTs in their wheat study in the same location (Bushland, TX) and found that CT was as high as 10 °C than the air temperature during the months of May and June. A similar difference, i.e. CT higher by 8.8 °C than the air temperature, was also found in chickpea in India which was measured by an infrared camera (Purushothaman et al., 2015). High temperature stress during the grain filling can reduce photosynthesis and CO_2 assimilation, but can increase photorespiration (Farooq et al., 2011). Temperature stress also accelerates the rate of grain filling which shortens the grain filling period (Dias and Lidon, 2009). These are some of the reasons for crops having lower yields under semi-arid climate compared to other climates.

Generally, in semi-arid climates when soil moisture is limited, as daytime air temperatures rise, stomatal conductance decreases, which subsequently increase CT and decrease CTD (Yoshida and Shioya, 1976; Urban et al., 2007). This was found true in our study, where regardless of the weather conditions in three seasons, CTD decreased and reached a minimum at the hottest part of the day (14:00–15:00 h). Though CTDs for 00.00–24:00 h, day time (10:00–18:00 h) and night time (19:00 − 09:00 h) are presented in Table 3, discussions are focused on the day time CTD, which was significantly correlated with the grain yield (Figs. Figure 5D and Figure 6B).

Table 5
Pearson's correlation coefficient (r) between grain yield (kg ha^{-1}) and canopy temperature depression (°C) for 20 genotypes at different times of day during mid-grain filling. Cultivars TAM W-101, Dumas, and TAM 304 were not included in this analysis in 2012. So, N = 17 in 2012 and N = 20 in 2016.

Time of day (h)	2012		2016	
	r	P-value	r	P-value
10	0.45	0.0776	0.68	0.0011
11	0.65	0.0079	0.70	0.0005
12	0.60	0.0137	0.65	0.0021
13	0.71	0.0064	0.62	0.0034
14	0.69	0.0111	0.60	0.0049
15	0.72	0.0001	0.65	0.0020
16	0.62	0.0119	0.67	0.0013
17	0.60	0.0125	0.60	0.0056
18	0.56	0.0645	0.68	0.0010

We found a significant genotypic variation in wheat CTD, which was reported previously either on the bases of point-in-time or season long measurements (Blum et al., 1989; Rashid et al., 1999; Royo et al., 2002; Balota et al., 2007). Cultivars TAM 304, TAM 112, Dumas, and Hatcher had greater day time CTD (i.e., cooler canopy) during the dry season of 2012. Similarly, cultivars Duster, TAM 111, TAM 110, TAM 112, and

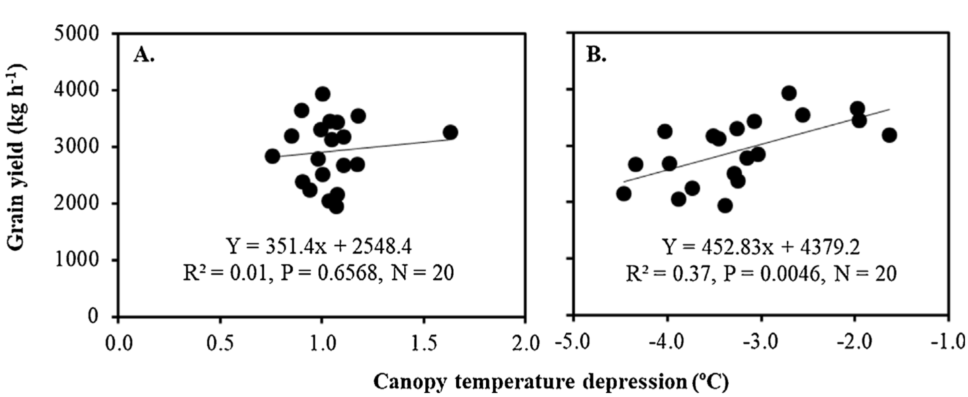

Fig. 6. The relationship between grain yield and canopy temperature depression (CTD) for all 20 genotypes in the 2016 season for 19.00 to 9.00 h (A) and 10.00–18.00 h (B). Canopy temperature was measured and grain yield was determined from two replications for each genotype. So, each data point is the average of two replications.

TAM 105 were cooler than other genotypes during the wet/near-normal seasons of 2015 and 2016. Our recent study showed that compared to the older cultivar TAM 105, more recent cultivars such as TAM 112, TAM 110, and TAM 111 were able to extract more water from the deeper soil profile during the dry seasons, including 2012 (Thapa et al., 2017a). This difference was consistent in case of CTD as well. For example, in the 2012 and 2016 seasons, there was a clear trend that TAM 105 had lower day time CTD than TAM 110, TAM 111, and TAM 112 (Table 3). Further study on comparing CTD between the large number of older and newer wheat cultivars is recommended.

Cultivar TAM 113 in the 2012 and 2015 seasons and cultivars Jagalene and Billings in the 2016 season had lower day time CTD compared to other genotypes. Genotypes having lower CTD probably used more soil water during the early developmental stage leaving less water available for grain filling or were unable to extract soil water from the deeper soil profile due to the poor shoot and root growth. Lopes and Reynolds (2010) suggested that CT was often associated with the plant's ability to extract deep water. According to Manschadi et al. (2006), the drought-tolerant wheat cultivar SeriM82 had a more compact, uniform, and deep root architecture as compared to drought-susceptible cultivars. Lopes and Reynolds (2010) reported that genotypes with a cooler canopy were able to develop 40% more root mass at 0.60–1.20 m deep in the soil profile and 30% higher yields. Further studies on root architecture would be helpful to understand the different cooling behaviors of wheat genotypes under drought conditions.

4.2. CTD and grain yield

Compared to 2012 and 2016 seasons, the 2015 season had lower air temperature, more precipitation, and greater CTD during grain filling. The reduced stress probably would have resulted in much higher yields for all the genotypes in this (2015) season; however, the crop was lost due to the hail storm. In the 2012 and 2016 seasons, the relationship between grain yield and daytime CTD for all 20 genotypes was significant (except three genotypes in 2012). Overall, grain yield increased as the day time CTD during the mid-grain filling increased.

In the 2012 season, cultivars TAM W-101, TAM 304, and Dumas did not fit well in the regression model because they had relatively greater CTD but lower grain yield than the other genotypes. This indicated that these cultivars probably had different physiological and/or morphological mechanisms for keeping a canopy cooler during the hottest part of a day. TAM W-101 is an older cultivar (released in 1971) and has been used as a historical check. According to Rudd et al. (2015), TAM 304 has an excellent grain yield potential particularly in the adequate rainfall or high input irrigated production systems. Bean and Rudd (2009) reported that Dumas was a very good cultivar under full irrigation. This suggests that these cultivars are more suitable to irrigated environments, but under dryland conditions, they were unable to translate their cooler canopy trait to increased gain yield. Though Cultivar TAM 113 was well adapted to the High Plains of Texas and similar areas (Rudd et al., 2011), because of its lower day time CTD (-4.97 °C) and lower grain yield (777 kg ha^{-1}) in the dry season in 2012 (Tables 3 and 4), it may not be suitable for extreme drought conditions. Similarly, in the 2016 season, Jagalene, Billings, and TX99A053-1 had lower day time CTD than other genotypes during the mid-grain filling and all of them ended up with poor grain yield, so they may not be recommended for dryland environments. In contrast, genotypes TAM 112, Hatcher, and Winterhawk in the 2012 season and Duster, TAM 105, TAM 110, TAM 111, and TAM 112 in the 2016 season showed or proved their adaptation under dryland conditions with moderate to high CTD as well as grain yield. A previous study also reported that the yield benefits from two cultivars, TAM 111 and TAM 112 were particularly evident in the U.S. Southern High Plains in the dry seasons of 2011 and 2012 (Xue et al., 2014), and our results further help explain why they remain the leading cultivars planted in Texas, accounting for 17.6% and 6.9% of the state's 2016 planted wheat acres, respectively (USDA-NASS, 2016).

Similar to our results, Amani et al. (1996), Fischer et al. (1998) and Lopes and Reynolds (2010) also found a significant positive correlation of CTD with grain yield in spring wheat. Under drought condition, closure of stomata is the main determinant for decreased photosynthesis. So, wheat plants with cooler canopies (higher stomatal conductance) probably achieved higher net photosynthesis rates, leading to higher grain yield. Our study also showed a genotypic variation in CTD during the night time (19:00 − 09:00 h, including early morning), but the regression analysis revealed no relationship between the night time CTD and grain yield. The night time CTDs were always positive indicating no sign of water stress, which was reported by Arnon (1975). Studying five genotypes used in this study, Pradhan et al. (2014) also found that pre-dawn (00:00–08:00 h) and night time (21:00–23:00 h) temperatures were not related to the grain yield under the severe drought. Therefore, despite some variation in CTD during the night time too, this study suggested that nighttime and early morning CTDs are not useful for differentiating genotypes for grain yield under dryland conditions.

5. Conclusions

Canopy temperature has often been measured using hand-held IRTs that provide point-in-time values and wired IRTs that require more time to install and more field maintenance. In this study, we used continuously recording wireless IRTs to investigate whether CTD is useful in screening winter wheat genotypes; and how CTD at mid-grain filling affects grain yield. Though more data is needed, this study depicted distinct differences of the stress response among the winter wheat genotypes with respect to CTD. More clearly, there was a genotypic variation for CTD, regardless of time of the day, but only day time (10:00–18:00 h) CTD showed significant association with grain yield. The positive and significant association between continuously determined CTD (day time) during grain filling and grain yield further contributed to the literature by confirming the correlation between CTD and grain yield. And, in conjunction with our recent associated findings of soil water extraction (Thapa et al., 2017a), this paper further suggested that newer cultivars that had cooler canopy probably achieved this by extracting more water from deeper soil profile. Hence, CTD appears to be one of the effective selection criterions for tolerance to drought stress and high yielding genotypes in winter wheat.

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