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Association of canopy temperature with agronomic traits in spring wheat inbred populations

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Abstract Canopy temperature (CT) is considered a reliable proxy for stomatal conductance. Low CT values of plant canopies under water-limited conditions are associated with high transpiration indicating plants' drought tolerance. Many U.S. Pacific Northwest (PNW) adapted wheat (*Triticum aestivum* L.) cultivars lack stress-adaptive traits resulting in poor performance in drought environments. This study aims to identify the stress-adaptive traits by evaluating the CT in spring wheat populations across different soil moisture conditions in the PNW. An infrared thermometer was used to estimate the CT in two families of recombinant inbred lines, 'Alpowa' × 'Express' (AE population) and 'Hollis' × 'Drysdale' (HD population), in rainfed and irrigated environments of the dryland PNW in 2011 to 2013. Higher reductions in grain yield up to 170%, spike length up to 25%, and spikelets spike^{-1} up to 19% were observed in a rainfed environment compared to the reductions in an irrigated environment. A significant variation in CT was observed in both AE and HD populations. With 1 °C increase in CT at the anthesis stage, grain yield was lowered up to 38 g m^{-2}. Low CT was associated with high grain yield and agronomic traits in both wheat populations ($r = -0.18$ to -0.55, $P \leq 0.05$). The highest association between CT and grain yield was observed at anthesis ($r = -0.47$) and milking ($r = -0.38$) stages ($P \leq 0.001$). Our results show that screening for low CT during terminal wheat growth stage is an effective strategy for improving the selection of new drought-tolerant wheat varieties in the PNW.

Keywords Anthesis · Canopy temperature · Drought · Heading · Inbred · Wheat

Abbreviations

AE population	Alpowa × Express population
CT	Canopy temperature
G× E	Genotype by environment interaction
HD population	Hollis × Drysdale population
PNW	Pacific Northwest
REML	Restricted maximum likelihood
RILs	Recombinant inbred lines
Z	Zadok's growth scale

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Introduction

Due to its broad climatic adaptation, wheat (*Triticum aestivum* L.) is grown across different environments in many parts of the world, ranging from marginal environments to lands with optimal conditions for its growth. Global climate change is predicted to bring warmer and, in many cases, more drought-prone conditions in the future, which will decrease crop yield per unit area of land (Long and Ort 2010) unless genetic advances are made. Therefore, wheat varietal tolerance to drought is important to improve the adaptation of wheat under stressed environments. Drought affects the productivity of wheat to variable degrees, depending on the time of occurrence, duration, and intensity of the stress (Yang et al. 2010). Analysis of physiological measurements that allow studies of traits, e.g., canopy temperature (CT) (Reynolds et al. 2007b), help to identify the mechanism of drought tolerance in a particular stress environment.

Canopy temperature differentiates genotypes' ability to uptake water through roots in stressful environments. Lower CT occurs when plants are actively transpiring, but CT increases when stomata close to conserve water under drought stress (Lopes and Reynolds 2010; Olivares-Villegas et al. 2007). Canopy temperature associated with leaf water potential has been recognized as a good indicator of plant water stress (Cohen et al. 2005; Leinonen et al. 2006). Studies have found the phenotypic traits, including smaller leaves (Balota et al. 2008), leaf rolling (Cal et al. 2019), and the presence of reflective epicuticular wax on the leaf surface (Mohammed et al. 2018), have significant contributions in drought avoidance through lowering the CT.

Assessing drought at the proper growth stage can be important to minimize the risk of crop failure in dryland areas. Drought during the heading to soft-dough stages was critical for wheat production in the great plains of the U.S. (Hanks and Rasmussen 1982). Xue et al. (2006) found that drought significantly reduces wheat yield from jointing to anthesis stages. Under water-limited conditions, an increase in wheat yield was largely related to the plant's ability to extract water from the soil (Thapa et al. 2017). A significant difference in CT was observed among winter wheat genotypes during the anthesis and grain filling stages in dryland wheat production areas (Bhandari et al. 2021). At the heading and grain filling stages, a strong negative association was found between CT and water content in spring wheat genotypes (Babar et al. 2006).

Low CT, an indicator of high leaf transpiration, is an indirect measure of the extent of deep rooting (Saint Pierre et al. 2010), a trait that is very difficult to measure directly under field conditions. The traditional method of root measurements through excavation and sampling with soil cores or augers is destructive and labor-intensive. The canopy temperature, measured with an infrared thermometer, was successfully employed to select breeding materials for heat and drought tolerance by the International Maize and Wheat Improvement Center (CIMMYT), Mexico (Reynolds et al. 2000). Low CT was associated with high yield in optimal and limited soil moisture environments (Pinto et al. 2010; Saint Pierre et al. 2010). Lopes and Reynolds (2010) found that higher allocation of plant assimilates to deeper roots was associated with cooler canopies. Canopy temperature accounted for approximately 60% of the yield variation in a recombinant inbred lines (RIL) population derived from a 'Seri'/'Babax' cross (Olivares-Villegas et al. 2007) when grown under drought conditions.

In the low precipitation region of the Pacific Northwest (PNW), inadequate precipitation during summer has led to dryland wheat farming practices such as growing one wheat crop every other year (Schillinger et al. 2006). Improving the drought tolerance of wheat is an important objective of wheat breeding programs in the low precipitation areas of the PNW. Wheat's ability to extract water through deep rooting has been identified indirectly through CT in diverse PNW adapted spring wheat lines by Li et al. (2012). A wide variation in phenology (e.g., maturity timing) of the diverse wheat lines in these studies could be a limiting factor in establishing significant associations between such traits with yield. This study aimed to examine the association of CT with agronomic traits in two different spring wheat RIL populations with low levels of phenological variation. For the successful indirect selection of secondary traits, identification of simpler traits requiring less cost and labor and having a strong correlation with agronomic traits is important.

Materials and methods

Climatic conditions of studied environment

Phenotypic traits were measured at two locations—the Washington State University (WSU) Dryland Research Station at Lind, WA, from 2011 to 2013, and the WSU Spillman Farm at Pullman, WA, in 2012. Lind is located at an elevation of 520 m (N47° 00.358' lat and W118° 33.542' long), and Pullman is located at an elevation of 773 m (N46° 41.711' lat and W117° 08.599' long). The soils at Lind and Pullman are Shano sandy loam (Coarse-silty, mixed, superactive, mesic Xeric Haplocambids) and Palouse silt loam (Fine-silty, mixed, superactive, mesic Pachic Ultic Haploxerolls), respectively. The Shano soil contains 1.5% organic matter, and the Palouse soil contains 4% organic matter in the top 10 cm of undisturbed native soils (Kennedy et al. 2004). The combined effects of tillage and water erosion in cultivated soils have reduced topsoil organic matter from 2 to 1% in the dryer western Palouse and 4.5% to 2% in eastern Palouse (Veseth 1985). Due to low residue production in these areas, increasing the organic matter level is slow.

Based on annual precipitation received, Lind is categorized as a low precipitation region (< 30 cm annual precipitation) and Pullman as a relatively high dryland precipitation region (> 50 cm annual precipitation). The Lind location in 2012 had unusually high precipitation compared to most years, including the 2011 and 2013 seasons (Table 1). Evapotranspiration was also higher in Lind in 2012 compared to the other environments. While wheat-fallow rotations are common in the Lind area, the Lind plots were annually cropped in a wheat-camelina rotation to ensure drought-prone conditions during the study. In Pullman, plots were annually cropped with a spring wheat-spring wheat-winter wheat rotation from 2011 to 2013.

Preplant soil moisture was measured only in the Lind rainfed environments. It was 71, 71, and 97 mm from 0 to 1.2-m soil depth in 2011, 2012, and 2013, respectively. To measure soil moisture content before planting, soil samples were collected from 0.3, 0.6, 0.9, and 1.2 m depths at ten different spots to represent the entire field using a slide hammer (AMS core sampler®, American Falls, Idaho). The soil moisture content was determined as the weight difference of the soil sample before and after drying in an oven at 105 °C for 24 h (Mylavarapu and Zinati 2009). Total moisture, including annual precipitation received during the wheat growing season and the stored soil moisture, in the Lind rainfed environments in 2011, 2012, and 2013 were 142, 210, and 172 mm, respectively. At Lind, two field water regimes were established. One was rainfed (2012), where stress occurred due to low summer rainfall, and the other was irrigated (2011 to 2013), where approximately 250 mm of water was supplemented through drip line irrigation during the growing season (from a month after planting to maturity).

Experimental materials

Two different families/populations of RILs (F5:6) derived through single seed descent from the F2 of the cross of Alpowa × Express (AE) and Hollis × Drysdale (HD) were evaluated in this study. The AE and HD populations consisted of 140 and 165 RILs, respectively. The parents of these populations have different levels of disease resistance, grain quality, and grain yield (Lin and Chen 2007, 2009). Alpowa (PI566596) is soft white spring wheat, and Express (PI573003) is hard-red spring wheat. Alpowa was developed by a modified bulk-pedigree selection from the cross 'Fielder'/'Potam 70'//'Walladay'/3/Walladay/Potam 70. It is semi-dwarf wheat with medium maturity and has a high test weight in low rainfall environments (Konzak et al. 1994). Express was developed from a cross between 'Veery' and 'BH1146'. 'Hollis' (PI632857) is hard-red spring wheat, and 'Drysdale' is hard-white spring wheat. Hollis is adapted to Washington's semi-arid to intermediate rainfall regions (Kidwell et al. 2004). It has high grain protein content and high-test weight. Drysdale is an Australian cultivar widely cultivated in southeast New South Wales (Condon et al. 2004). It is semi-dwarf wheat with early to mid-maturity and has a high yield under drought environments.

Field layout and data collection

All experimental trials were planted in a randomized complete block design with three replications, except the trial located at Pullman, which was planted with two replications. The trials at Lind were planted on 31 Mar. in 2011, 23 Mar. in 2012, and 14 and 15 Mar.

Table 1 Meteorological conditions during spring wheat growing season from March to August 2011, 2012, and 2013 at Lind, WA, and May to September 2012 at Pullman, WA

Month	Lind 2011					Lind 2012				
	Max/Min air temp (°C)[a]	RH (%)[b]	Solar Rad (MJ m^{-2})[c]	Precip. (cm)[d]	ETr A (cm)[e]	Max/Min air temp (°C)	RH (%)	Solar Rad. (MJ m^{-2})	Precip. (cm)	ETr A (cm)
March	17.4/6.7	61.8	17.7	0	0.6	11.3/2.1	74.0	10.9	2.0	2.4
April	12.1/-0.4	58.3	17.4	2.2	12.2	16.4/3.2	63.1	18.4	2.8	13.5
May	18.4/4.4	60.4	21.0	3.7	16.6	20.1/4.6	48.2	23.7	0.4	20.3
June	22.9/7.8	53.9	24.2	0.5	20.9	22.9/9	58.2	23.4	5.2	20.6
July	27.9/10	43.9	27.5	0.7	26.3	31.1/13.5	48.3	26.9	3.4	27.1
August	30.0/11.1	35.6	26.3	0	19.3	31.5/12.4	36.3	24.0	0.1	29.3
Average	21.4/6.6	52.3	22.4	–	–	22.2/7.5	54.7	21.2	–	–
Total				7.1	95.8				13.9	113.2
Month	Pullman 2012					Lind 2013				
	Max/Min air temp (°C)	RH (%)	Solar Rad. (MJ m^{-2})	Precip. (cm)	ETr A (cm)	Max/Min air temp (°C)	RH (%)	Solar Rad. (MJ m^{-2})	Precip. (cm)	ETr A (cm)
March	–	–	–	–	–	13.0/-01.1	61.2	15.9	0.3	6.1
April	–	–	–	–	–	15.5/1.6	56.6	19.3	1.0	14.7
May	18.5/4.9	54.7	23.1	1.0	12.8	21.8/5.6	53.7	22.3	1.2	19.2
June	19.8/8.0	66.8	24.5	4.3	17.0	24.6/9.8	58.1	24.1	2.9	20.6
July	27.8/10.1	61.9	27.5	0	20.8	32.8/13.0	34.6	28.2	0	32.9
August	29.5/6.8	43.3	24.7	0	22.8	30.6/14.1	52.9	21.0	2.0	10.8
September	24.0/2.1	41.0	23.1	0	3.1	–	–	–	–	–
Average	23.9/6.4	53.5	24.6	–	–	23.0/7.2	52.9	21.8	–	–
Total				5.3	76.5				7.5	104.3

'– ', data not presented. Weather data obtained from http://weather.wsu.edu;

[a]Maximum and Minimum air temperature; [b]Relative Humidity; [c]Solar Radiation; [d]Precipitation, and [e]Evapo-transpiration in alfa-alfa

in 2013, respectively. In Pullman, the experiment was planted on 10 May in 2012. In 2011, 25 g of seeds were sown in each plot (1.52 m×2.44 m) using a seven-row plot planter (Wintersteiger, Salt Lake City, UT) with double disc openers spaced at 18 cm. The seed sowing density was increased by 5 g in 2012 and 2013 to facilitate the measurement of CT with minimal soil exposure. Plots were harvested on 22 Aug. in 2011, 31 Aug. in 2012, and 14 and 15 Aug. in 2013, respectively, at Lind, and on 05 Sep. in 2012 in Pullman using a plot combine harvester (Wintersteiger Inc., Salt Lake City, UT).

Several plots were evaluated for the emergence of the head from the boot. When more than 50% of the plants in each of these referenced plots had half of the ear emerge, the heading was measured in Zadok's (Z) scale (Zadoks et al. 1974) on all the plots on the same day. The measurements were taken on 14 and 16 June 2011, 07 and 08 June 2012, and 07 June 2013 in the Lind rainfed and Lind irrigated environments; and 19 July 2012 in the Pullman rainfed environment. Plant height was measured in cm at the dough development period from the base of the plant to the tip of the tallest head, excluding awns. Five to ten plants were measured per plot for plant height measurements. Spike length (cm) and the number of spikelets spike^{-1} were measured after maturity. The spike length was measured on 3 to 5 plants per plot, and the number of spikelets spike^{-1} was measured by counting the spikelet numbers on five heads. Grain yield and test weight were recorded after harvest.

The CT was measured in °C using a portable Fluke 561 infrared thermometer (Cole-Parmer, Illinois, USA) on standing wheat with a slight modification to the method described by Reynolds et al. (2007a). The measurements were performed between 11:00 and 14:00 h PST on clear, sunny days with low wind velocity (<8 km hr^{-1}). The CT was taken by standing at the edge of each plot (15 cm away from the plot), keeping the thermometer inclined at an angle of 45°, and holding one meter above the crop canopy. Two CT readings were taken in each plot along the central two rows of the seven-row plots. The CT was measured at different growth stages, including heading, anthesis, and milking stages, to identify the stage at which the trait is fully expressed in the PNW environmental conditions. Efforts were made to take CT readings at similar physiological stages in the different environments as weather conditions permitted. In the AE population, CT was measured at various growth stages in four environments, including Lind irrigated in 2011, Lind rainfed in 2012, Lind irrigated in 2012, and Pullman rainfed in 2012. The CT was measured at the heading stage (Z57-59) in the Lind irrigated environment in 2011. In 2012, the measurements were taken at the anthesis stage (Z60-69) in the Lind rainfed environment and at heading and anthesis stages in the Lind irrigated environment. The CT was measured at heading, anthesis, and milking (Z73-75) stages at Pullman in 2012. In the HD population, CT was measured in two environments, including Lind irrigated in 2012 and 2013. The CT was measured at heading and anthesis stages in the Lind irrigated environment in 2012, and at heading, anthesis, and milking stages in the Lind irrigated environment in 2013.

Agronomic management

Before sowing, seeds were treated with a mixture of Raxil® MD (Tebuconazole and Metalaxyl), Allegiance® (Metalaxyl), Gaucho® 600 Flowable (Imidacloprid) (Bayer CropScience LP, St. Louis, MO), and water (1 ml per 100 g seed) to reduce the influence of pests and pathogens at the seedling stage. Plots were amended with 50.44, 11.21, and 6.73 kg ha^{-1} N, P_2O_5, and Sulphur prior to planting, and an additional 5.60 kg N ha^{-1} was applied when Huskie® (Bayer CropScience LP, St. Louis, MO) was sprayed on plots (at booting to pre-flag leaf initiation stage). The plots received 1.68 kg ha^{-1} Glyphosate (Bayer CropScience LP, St. Louis, MO) two weeks before planting. In the late spring or early summer (May or June), postemergence herbicides of Huskie® (0.91 to 0.98 kg ha^{-1}), Brox®-M (0.84 to 1.40 kg ha^{-1}) (Albaugh LLC, Ankeny, IA), and Buctril (1.75 L ha^{-1}) (Bayer CropScience LP, St. Louis, MO) were applied. To control fungal infestations, plots were sprayed with 0.28 kg ha^{-1} Bumper® 41.8 EC (Adama US, Raleigh, NC) in June 2011 and 2012, and 0.56 kg ha^{-1} Tebustar® (a.i. Tebuconazole) (Albaugh LLC, Ankeny, IA) in June 2013.

Statistical analyses

The data were analyzed using a random-effects model in JMP Pro 15 (SAS Institute Inc., Cary, North Carolina, USA), where genotypes, locations, and replications were considered random effects.

Restricted maximum likelihood (REML) was used to obtain an unbiased estimation of variance components. Least-square means were computed for each location and year. Two-way ANOVA was used to determine genotype (G) by environment (E) interaction (G × E) for agronomic and phenological traits of AE and HD populations, in which both locations and years effects were combined. Four environments for AE (Lind irrigated 2011, Lind rainfed 2012, Lind irrigated 2012, and Pullman rainfed 2012) and two environments for HD (Lind irrigated 2012 and Lind irrigated 2013) populations were used for the G × E analysis. In the RIL population, broad-sense heritability closely estimates the narrow-sense heritability (h^2) and was calculated for the CT using the method described by Cullis et al. (2006) and Piepho et al. (2008):

$$h^2 = 1 - \frac{(avesed)^2}{2V_g}$$

where *avesed* is the average standard error of the difference between best linear unbiased predictors (BLUPs), and V_g is the REML variance component estimate for the genotypes. The relationships of CT with agronomic and phenological traits were evaluated using Pearson Correlation Coefficient (r) and linear regression (R^2). The least-square means calculated from one- and two-way ANOVA were used for deriving the relationships (using r and R^2) between CT and growth traits.

Results

Evaluation of agronomic and phenological traits in spring wheat inbred populations

Two-way ANOVA was used to determine the G × E effect across the moisture environments (rainfed and irrigated) and years (AE population: 2011 and 2012; HD population: 2012 and 2013) (Table 2). A significant G × E effect was found in the AE population for agronomic and phenological (except the spike length) traits across the locations and years (Table 2). The genotype effect was significant for most traits, except for the yield of the AE population. As expected, the AE wheat genotypes generally performed better in Lind irrigated or the Pullman environments than in the dryer Lind rainfed environments (Table 3). Wheat yield was 170% higher in Lind irrigated than in the Lind rainfed environment and 25% higher in Pullman rainfed than in Lind irrigated environment. In the HD population, the G × E effect was observed on test weight, plant height, and heading ($P \leq 0.05$) (Table 2). The genotype effect was significant for all traits. The average values of all the studied traits were higher in 2012 than in 2013, except for yield (Table 3). The yield was 16% higher in Lind irrigated environment in 2013 than in the same environment in 2012.

Table 2 Sources of variance of agronomic, phenological, and canopy temperature (CT) traits of Alpowa × Express (AE) and Hollis × Drysdale (HD) populations across the environments

Sources of variance	Yield	Test weight	Plant height	Spike length	Spikelets spike^{-1}	Heading[a]	CT$_{Head}$[b]	CT$_{Anth}$[c]
AE population								
Genotype (G)	77.89	83.97***	38.48***	0.03**	0.08**	2.97***	0.09	0.03
Environment (E)	9557.61	161.11	88.3	1.36	4.04	16.39	14.7	15.9
G × E	351.48***	94.03***	9.29**	0.02	0.13**	2.02***	0.12	0.19*
HD population								
G	791.52***	32.76**	30.91***	0.25***	1.03***	0.08***	0.13	0.10*
E	911.62	275.67	126.03	0.004	6.59	0.23	17.04	4.97
G × E	42.93	48.83***	8.94**	0.05	0.09	0.07***	0.01	0.001

Four environments for AE population, Lind irrigated 2011, Lind rainfed 2012, Lind irrigated 2012, and Pullman rainfed in 2012; Two environments for HD population, Lind irrigated 2012 and 2013;

[a]Heading in Zadok's scale; [b]CT$_{Head}$: canopy temperature at heading; [c]CT$_{Anth}$: canopy temperature at anthesis

*, **, and ***: Significant at $P \leq 0.05, \leq 0.01$, and ≤ 0.001, respectively

Table 3 Mean, maximum, minimum, and standard error of agronomic, phenological, and canopy temperature traits of Alpowa × Express and Hollis × Drysdale (AE and HD) populations studied in Lind rainfed (LR), Lind irrigated (LI), and Pullman rainfed (PR) environments

Trait	Parameters	AE population				HD population	
		LI-2011	LR-2012	LI-2012	PR-2012	LI-2012	LI-2013
Yield (g m^{-2})	Mean	290.3	95.1***	223.1**	320.1***	275.7	319.5***
	Maximum	553.6	176.8	377.8	487.3	427.6	584.0
	Minimum	116.8	28.7	118.4	159.5	101.5	104.4
	Standard error	4.1	1.2	2.1	3.6	2.5	3.4
Test weight (kg m^{-3})	Mean	950	925***	924***	923***	931***	908***
	Maximum	984	991	976	991	968	935
	Minimum	890	828	850	839	820	880
	Standard error	0.8	1.2	1.0	1.7	1.0	0.5
Plant height (cm)	Mean	66.6	48.5*	60.4***	70.2***	87.0***	71.4***
	Maximum	98.0	89.7	93.1	100.1	105.8	99.7
	Minimum	35.6	22.9	29.6	35.3	63.9	47.3
	Standard error	0.5	0.6	0.6	0.8	0.5	0.4
Spike length (cm)	Mean	7.0	4.9	5.2	7.1***	6.7***	6.6***
	Maximum	8.8	7.6	8.5	8.9	9.3	9.8
	Minimum	4.5	3.0	3.0	5.3	4.2	3.1
	Standard error	0.04	0.04	0.04	0.03	0.04	0.1
Spikelets $spike^{-1}$	Mean	14.3	11.4**	12.8***	16.1***	14.7***	11.1***
	Maximum	17.8	14.6	15.8	19.4	17.4	16.2
	Minimum	10.6	8.6	9.0	12.2	11.4	5.8
	Standard error	0.1	0.1	0.05	0.1	0.1	0.1
Heading (Zadok's scale)	Mean	54.6	58.7***	58.4***	64.5***	58.7***	51.9***
	Maximum	59.0	69.0	69.0	69.0	69.0	59.0
	Minimum	41.0	49.0	49.0	59.0	49.0	40.0
	Standard error	0.2	0.2	0.1	0.2	0.01	0.03
Canopy temperature (°C) [a]	Mean	–	–	29.3	28.4**	25.2	30.80**
	Maximum	–	–	34.3	31.2	27.7	34.5
	Minimum	–	–	22.8	25.5	22.1	27.8
	Standard error	–	–	0.1	0.1	0.05	0.05

[a] Canopy temperature measurement was mean across heading and anthesis stages in Lind irrigated 2012, mean across heading, anthesis, and milking stages in Pullman rainfed 2012, and mean across heading, anthesis, and milking stages in Lind irrigated 2013. The data values used for the analysis were least square means derived from the one-way ANOVA in which genotypes and replications were considered random effects

'- ' Canopy temperature data for locations LI-2011 and LR-2012 are shown in Table 4

*, **, and ***: Significant at $P \leq 0.05, \leq 0.01$, and ≤ 0.001, respectively

Evaluation of canopy temperature in spring wheat inbred populations

A significant G × E effect was found for CT (at the anthesis stage) across the locations and years in the AE population (Table 2). Due to the significant G × E effect in the AE population, h^2 was estimated only for the CT at the anthesis stage. The estimate of h^2 for the trait (CT at anthesis) was 0.54. The CT was 9.2 °C lower in high moisture (Lind irrigated and Pullman) environments than in low moisture (Lind rainfed) environments (Tables 3 and 4). The CT varied considerably with the growth stage (Table 4). The CT at anthesis was 7.8 higher than at the heading stage in the AE population (Table 4). In the HD population, the genotype effect for CT (at the anthesis stage) was

Table 4 Mean, maximum (Max), minimum (Min), and standard error of canopy temperature (CT in °C) at different growth stages in Alpowa × Express and Hollis × Drysdale (AE and HD) populations at each and across the locations

Population/location	Growth Stage[a]	Mean	Max	Min	Standard error
AE population					
Lind irrigated 2011	CT_{Head}	29.4	36.2	24.3	0.10
Lind rainfed 2012	CT_{Anth}	37.6*	45.0	33.5	0.10
Lind irrigated 2012	CT_{Head}	25.9	32.6	20.0	0.13
	CT_{Anth}	33.0	37.0	30.5	0.06
Pullman rainfed 2012	CT_{Head}	21.7*	25.3	17.9	0.08
	CT_{Anth}	29.7	33.2	26.5	0.06
	CT_{Milk}	33.8*	38.8	29.9	0.09
	$CT_{Anth+Milk}$	31.7**	35.0	28.9	0.07
Across the locations	CT_{Head}	26.1***	36.2	17.9	0.11
	CT_{Anth}	33.9***	45.0	26.5	0.10
HD population					
Lind irrigated 2012	CT_{Head}	23.8	27.5	18.5	0.08
	CT_{Anth}	26.6	31.5	22.3	0.08
Lind irrigated 2013	CT_{Head}	29.8	35.7	24.6	0.10
	CT_{Anth}	29.7**	33.9	27.3	0.05
	CT_{Milk}	32.8*	37.3	29.6	0.06
	$CT_{Anth+Milk}$	31.3**	35.0	28.7	0.05
Across the locations	CT_{Head}	27.2***	35.7	18.5	0.12
	CT_{Anth}	28.4***	33.9	22.3	0.07

[a] CT_{Head}: canopy temperature at heading; CT_{Anth}: canopy temperature at anthesis; CT_{Milk}: canopy temperature at milking; $CT_{Anth+Milk}$: canopy temperature across anthesis and milking stages. The data values used for the analysis were least square means derived from the one-way ANOVA in which genotypes and replications were considered random effects

*, **, and ***: Significant at $P \leq 0.05, \leq 0.01,$ and ≤ 0.001, respectively

significant; the h^2 was estimated only for the CT at the anthesis stage. The estimate of h^2 for the trait (CT at anthesis) was 0.64. The CT was 5.6 °C lower in Lind irrigated in 2012 than in 2013 (Table 3). The CT at anthesis was 1.2 °C higher than at the heading stage in the HD population (Table 4).

Association of canopy temperature with agronomic and phenological traits

In the RIL populations, low CT was associated with high yield, high test weight, tall plants, long spike length, more spikelets spike^{-1}, and early heading ($P \leq 0.05$) (Table 5). In both the AE and HD populations, the associations between CT and yield depended somewhat on the stage at which CT was determined. In the AE population, the best significant negative correlation between CT and yield was observed at the anthesis stage than at the heading and milking stages ($r = -0.47$) (Table 5). In the HD population, higher correlation between CT and yield was observed in the combined anthesis and milking stages than in other growth stages. The evaluation for CT at the milking stage was undertaken in a single environment in both AE and HD populations.

The CT at anthesis measured at Lind rainfed (2012) and the CT at heading measured at Pullman rainfed (2012) environments in the AE population and Lind irrigated (2013) in the HD population were significant (Table 4). Therefore, we used the CT at anthesis of Lind rainfed and the CT at heading of Pullman rainfed environments for AE population, and Lind irrigated (2013) environment in the HD population to derive the relation with agronomic and phenological traits across the locations and years (Figs. 1, 2, and 3). The total moisture available to plants at Lind was 34.9 cm (Lind rainfed 2012) and 49.7 cm (Lind irrigated 2013), respectively. The R^2 shows that CT was a weak predictor of agronomic traits in the studied wheat genotypes ($R^2 = 0.03$ to 0.30, $P \leq 0.05$) (Figs. 1, 2, and 3). However, low CT was significantly associated with higher grain yield and agronomic performances. With a 1 °C increase in CT at the anthesis stage, wheat grain yield was significantly

Table 5 Correlation of canopy temperature (CT) with growth traits in Alpowa × Express (AE) and Hollis × Drysdale (HD) populations at Pullman rainfed 2012 (PR 2012), Lind irrigated 2013 (LI 2013), and across the locations

Population/ growth stages	Location	Yield	Test weight	Plant height	Spike length	Spikelets spike^{-1}	Heading
AE population [a]							
CT_{Head}	Across	−0.39***	−0.19*	−0.35***	−0.27***	−0.27***	0.18*
CT_{Anth}	Across	−0.47***	−0.25**	−0.47***	−0.27**	−0.25**	0.27**
CT_{Milk}	PR 2012	−0.39***	−0.22**	−0.51***	−0.18*	−0.05	0.19*
$CT_{Anth+Milk}$	PR 2012	−0.36***	−0.20*	−0.46***	−0.19*	−0.05	0.22**
HD population [b]							
CT_{Head}	Across	−0.19*	0.01	−0.27***	−0.33***	−0.13	0.35***
CT_{Anth}	Across	−0.29***	0.04	−0.55***	−0.49***	−0.45***	0.39***
CT_{Milk}	LI 2013	−0.38***	0.14	−0.24**	−0.40***	−0.41***	0.34***
$CT_{Anth+Milk}$	LI 2013	−0.46***	0.14	−0.38***	−0.55***	−0.51***	0.46***

[a] CT_{Head}: canopy temperature at heading across Lind irrigated in 2011, Lind irrigated in 2012, and Pullman rainfed in 2012; CT_{Anth}: canopy temperature at anthesis across Lind rainfed, Lind irrigated, and Pullman rainfed in 2012; CT_{Milk}: canopy temperature at milking in Pulman rainfed in 2012; $CT_{Anth+Milk}$: canopy temperature at anthesis and milking in Pullman rainfed in 2012; [b] CT_{Head}: canopy temperature at heading across Lind irrigated in 2012 and 2013; CT_{Anth}: canopy temperature at anthesis across Lind irrigated in 2012 and 2013; CT_{Milk}: canopy temperature at milking in Lind irrigated in 2013; $CT_{Anth+Milk}$: canopy temperature at anthesis and milking in Lind irrigated in 2013. The data values used for the analysis were least squares means (LS Means) derived from one- and two-way ANOVA. For CT_{Head} and CT_{Anth}, the LS Means were derived from two-way ANOVA for both AE and HD populations; for $CT_{Anth+Milk}$, the LS Means were derived from a single environment analysis (PR 2012 for AE population and LI 2013 for HD population); for agronomic and phenological traits, the LS Means were derived from the two-way ANOVA analyzed across Lind irrigated 2011, Lind rainfed 2012, Lind irrigated 2012, and Pullman rainfed 2012 environments for AE population and across Lind irrigated in 2012 and 2013 for HD population

*,**, and ***: Significant at $P \leq 0.05$, ≤ 0.01, and ≤ 0.001, respectively

lowered by 5 and 38 g m^{-2} in AE and HD populations (Figs. 1 and 3). Yield reduction associated with the increase in CT (at the anthesis stage) was 111% higher in the HD population than in the AE population (Figs. 1 and 3). An increase in CT by 1 °C at the anthesis stage reduces plant height up to 9 cm, lowers spike length < 1 cm, and decreases spikelets spike^{-1} up to 2, in AE and HD populations (Figs. 1 and 3). Test weight was lowered up to 8 kg m^{-3} with the 1 °C increase in CT at heading and anthesis stages in the AE population (Figs. 1 and 2).

Discussion

Genotype was the most important in determining agronomic and phenological traits of the factors included in this study. A significant G × E effect was observed for all traits in the AE population, resulting from the differences in the precipitation over the years during the growing season. Genotype × environment interaction effects in agronomic traits have been documented in wheat by other studies (Eltaher et al. 2021; Otteson et al. 2007). The differences in soil moisture availability to plants could make the G × E effect significant. Low yield, small spike length, low numbers of spikelets spike^{-1}, and reduced plant height resulted from drought, as observed by others (Gupta et al. 2001). Another factor contributing to the significant G × E effect was likely attributed to the use of different seed rates in plantings in 2011. A significant interaction effect of the seeding rate and the environment was also reported in spring wheat genotypes (Otteson et al. 2007). Such interaction has a confounding impact on determining yield stability and the pattern of genotypes response across environments affecting the reliability of selection (Romagosa and Fox 1993). Significant differences in grain yield occurred across all environments in the HD population. In 2012 and 2013, when uniform seed rates for plantings were used, the G × E effect was observed only in a few traits in the HD population.

Drought tolerance in the studied wheat genotypes may be regulated through water harvesting mechanisms like root systems, which can access deep soil moisture to fulfill the transpiration demand of the

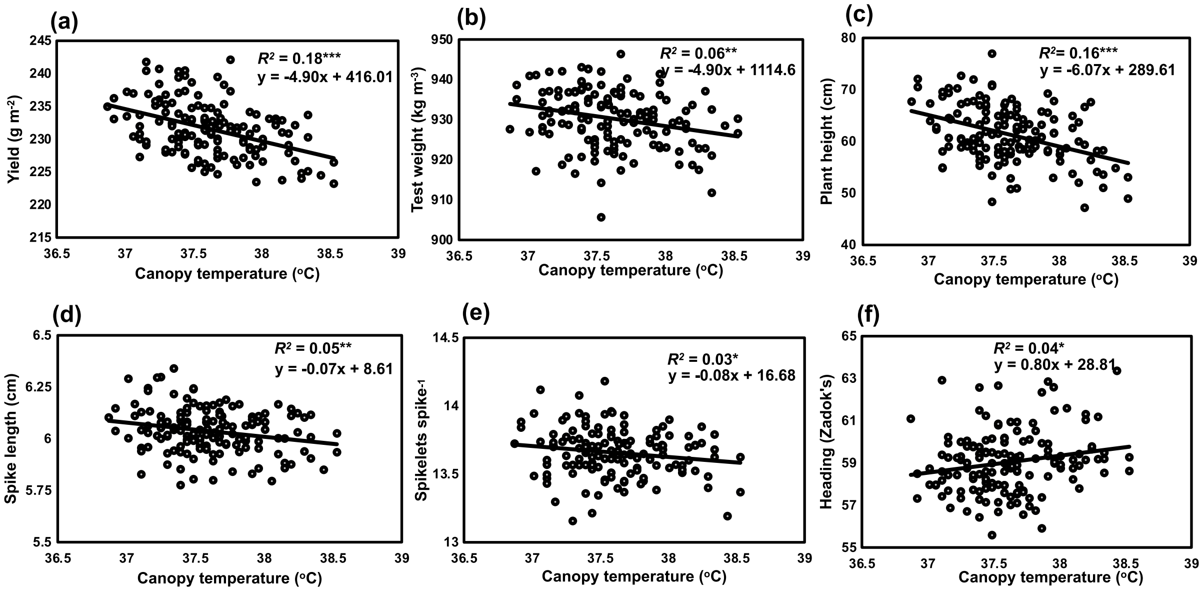

Fig. 1 The relationship of canopy temperature at anthesis (at Lind rainfed 2012) with agronomic and phenological traits (averaged across Lind irrigated 2011, Lind rainfed 2012, Lind irrigated 2012, and Pullman rainfed 2012 environments) of Alpowa × Express population (a to f). The data values used for the analysis were least squares means (LS Means) derived from one- and two-way ANOVA. For canopy temperature at anthesis, the LS Means were derived from a single environment (Lind rainfed 2012); for agronomic and phenological traits, the LS Means were derived from two-way ANOVA analyzed across Lind irrigated 2011, Lind rainfed 2012, Lind irrigated 2012, and Pullman rainfed 2012 environments. *, **, and ***: Significant at $P \leq 0.05$, and $P \leq 0.01$, and $P \leq 0.001$, respectively

plants and maintain a low CT. However, the G×E effect could have reduced the association between the phenotypic and genotypic values and led to bias in the accurate estimation and prediction of the CT. In the future, using the field with uniform moisture distribution, the genotypes with uniform phenology, and taking the measurements at the same growth stage may improve the accuracy of measuring the CT across the environments and make it a more viable tool for identifying drought-tolerant germplasm.

The low CT was associated with high yield in RIL populations across the environments examined in this study. The lower CT and higher grain yield association have also been reported in other low rainfall dryland environments (Lopes and Reynolds 2010), irrigated environments (Fischer et al. 1998), and both types of environments (Saint Pierre et al. 2010). Through the screening of a hard spring wheat population for water use efficiency by using carbon isotope discrimination (Δ), Shrestha et al. (2020) found that high Δ values (high transpiration) were associated with a higher grain yield in an irrigated environment at Lind. Low CT and high yield in annual cropping systems in our study area were observed in the irrigated environment (Lind), where higher soil moisture availability could have resulted in higher transpiration and low CT. Pinter et al. (1990) found that wheat cultivars with high CT under well-watered conditions used less water and had lower stomatal conductance than cultivars with low CT. Drysdale, which was used as a male parent for developing HD population, was primarily bred for high WUE (low transpiration through low stomatal conductance). During the study period, plants received more precipitation in 2012 than in 2013. The HD population's CT was lower in 2012 than in 2013; however, carbon assimilation rate could be limited due to the small stomatal aperture size that could have adversely affected grain yield in the HD population in 2012.

The growth stage in which CT was measured affects how well it is associated with grain yield production. Drought during the terminal growth stage, including anthesis and grain filling stages, reduces grain size and subsequently decreases grain yield (Lu et al. 2020). The CT was generally higher at the anthesis and milking stages (July at Lind, WA;

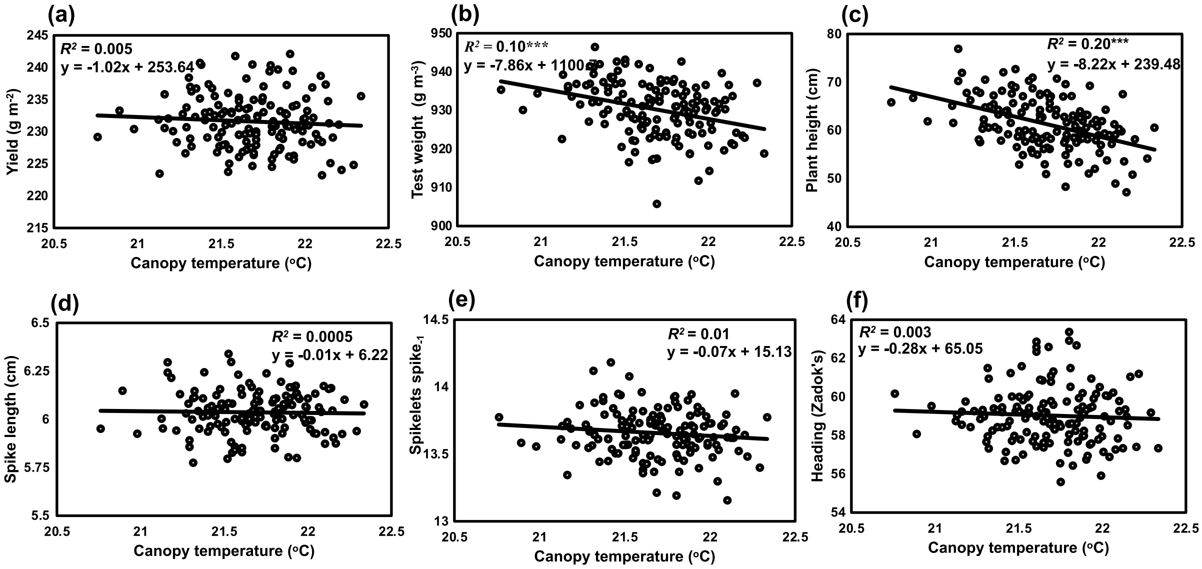

Fig. 2 The relationship of canopy temperature at heading (at Pullman rainfed 2012) with agronomic and phenological traits (averaged across Lind irrigated 2011, Lind rainfed 2012, Lind irrigated 2012, and Pullman rainfed 2012 environments) of Alpowa × Express population (a to f). The data values used for the analysis were least squares means (LS Means) derived from one- and two-way ANOVA. For canopy temperature at heading, the LS Means were derived from a single environment (Pullman rainfed 2012); for agronomic and phenological traits, the LS Means were derived from two-way ANOVA analyzed across Lind irrigated 2011, Lind rainfed 2012, Lind irrigated 2012, and Pullman rainfed 2012 environments. ***: Significant at $P \leq 0.001$

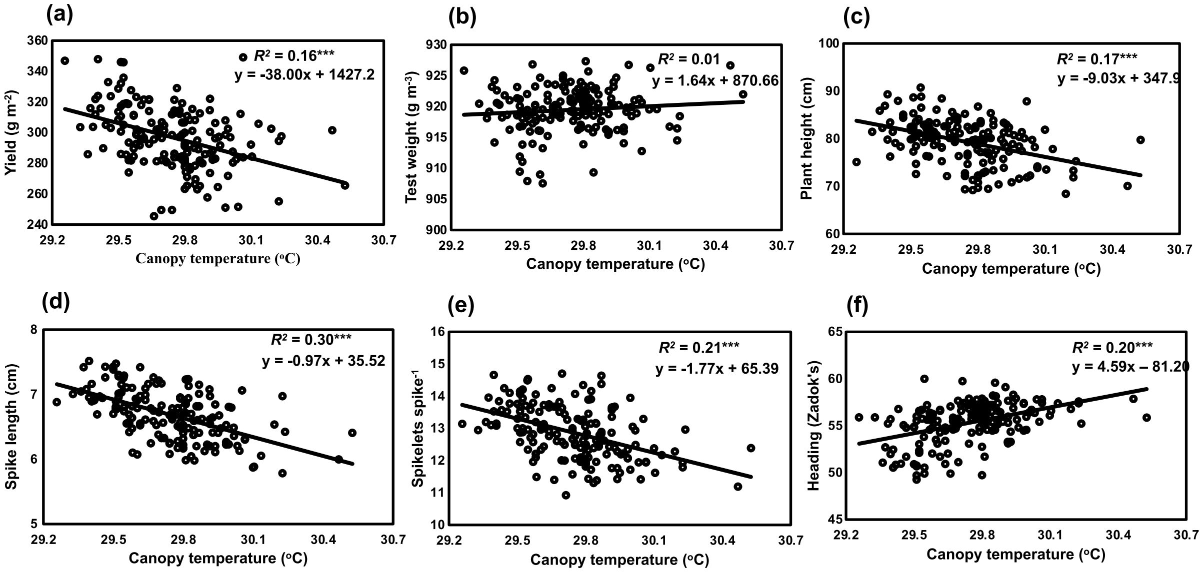

Fig. 3 The relationship of canopy temperature at anthesis (at Lind irrigated 2013) with agronomic and phenological traits (averaged across Lind irrigated in 2012 and 2013 environments) of Hollis × Drysdale population (a to f). The data values used for the analysis were least squares means (LS Means) values derived from one- and two-way ANOVA. For canopy temperature at anthesis, the LS Means were derived from a single environment (Lind irrigated 2012); for agronomic and phenological traits, the LS Means were derived from two-way ANOVA analyzed across Lind irrigated 2012 and 2013 environments. ***: Significant at $P \leq 0.001$

and July–August at Pullman, WA) than at the heading stage in our study. We observed that increase in CT during the anthesis stage by 1 °C lowers grain yield up to 38 g m^{-2} in the wheat populations. Other performance traits, including test weight, spike length, spikelets $spike^{-1}$, and plant height, were also reduced due to an increase in the CT. Brdar et al. (2008) reported that 1 °C increase in temperature by than optimum during the grain filling period would decrease the grain yield by 2.8 mg. Another study (Ottman et al. 2012) has found a reduction in grain yield by 91 g m^{-2} per 1 °C increase in temperature above the optimal temperature (13.3 °C).

The best negative linear correlation between CT and yield was observed at the anthesis stage compared to the heading stage in most environments. The results indicated that the genetic variation in grain yield might be attributed to the ability of plants to withdraw deeper soil moisture during the terminal growth stage, resulting in cooler canopies. Babar et al. (2006) found a strong relation between CT and biomass yield at the later growth stages. Low CT could be an advantageous for such genotypes when transpiration demand is high. Canopies with higher water content could fix more carbon through greater stomatal conductance (as determined by low CT) compared to the canopies with poor water content, resulting in a higher yield (Pinter et al. 1990). In the current wheat-fallow cropping systems practiced in the PNW, soil moisture is depleted through the growing season. In such a case, more extensive or efficient roots could access conserved soil moisture to fulfill the transpiration demand of the plants and maintain a low CT. Furthermore, due to terminal drought prevailed in the studied locations, the differences in rooting behavior of the plants at the later stage of the growth could be more important.

Low CT was advantageous for early heading genotypes to escape through post-anthesis drought in our study. Rebetzke et al. (2013) found that early heading genotypes have cooler canopies than later heading ones. In the early vigor genotypes with greater leaf area and shoot biomass, lower evapotranspiration during stem elongation and anthesis reduced water loss through soil evaporation (Fang et al. 2017). Developing a vigorous root system during the early growth stage is advantageous in capturing more water and nutrients and facilitating root and shoot growth (Gregory 2006). Both AE and HD populations evaluated in this study have early and early-medium maturity. The early establishment of roots to uptake deep soil moisture and the development of physiological mechanisms to cope with the environmental factors in the early heading genotypes could have improved the performance of these genotypes. In addition, our study observed a moderate negative correlation between CT and plant height in both AE and HD populations. This is in line with previous studies in other wheat populations in which a significant negative correlation between CT and plant height was also observed (Olivares-Villegas et al. 2007; Rebetzke et al. 2013). Friedli et al. (2019) found that rooting depth increased with increasing plant height. Ekanayake et al. (1985) found a positive association between deep roots and plant height of rice in drought conditions. Deeper roots facilitate root water uptake to fulfill the transpiration demand of plants.

Conclusions

The results demonstrated that higher yield was associated with low CT in environments with different moisture levels. It highlights the potential of selecting higher-yielding wheat cultivars in drought environments through agronomic traits, which can be indirectly assessed through low CT at the terminal growth stage. Water uptake ability (as determined through low CT) that best described the yield in the studied populations is important to incorporate into the trait introgression program and breeding of better cultivars in low moisture environments.

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Author contributions All authors have important contributions on project design, performing the experiments and preparing the manuscript. SLS carried out research activities and SHH helped supervise the project. SLS wrote the manuscript with input from all authors. KAG-C contributed in developing research methodologies and statistical analysis, CMS aided in physiological trait screening, WLP assisted on technical details, and SHH directed the overall project. All authors discussed the results and contributed to the final manuscript. All authors provided critical feedback and helped shape the research, analysis, and manuscript.

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Data availability The datasets generated and analyzed in this study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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