RESEARCH

Evaluation of Grain Yield and Three Physiological Traits in 30 Spring Wheat Genotypes across Three Irrigation Regimes

Ping Li, Jianli Chen,* and Pute Wu

ABSTRACT

Accurate field evaluation of yield-related physiological traits is critical for selecting high yield and drought resistance in wheat (*Triticum aestivum* L.). To characterize grain yield and three physiological traits for 30 spring wheat genotypes, field experiments with three irrigation regimes were conducted in 2009 and 2010 field seasons. Our study suggests that Feekes 11.2 is the optimal stage to evaluate flag leaf senescence (FLS) and canopy temperature (CT) when making selections for high grain yield and drought resistance among wheat genotypes. Flag leaf carbon isotope discrimination (CID) was positively correlated with grain yield, whereas FLS and CT were negatively correlated with grain yield. The three traits together explained 92% of the total phenotypic variation of grain yield. Selected genotypes were classified into four groups based on yield performance across irrigation regimes. High-yield genotypes IDO599, 'Alturas', and IDO702 produced high grain yield across different water conditions; drought-resistant genotypes 'Agawam', 'McNeal', and 'Alpowa' produced higher grain yield under the nonirrigated regime. High yield of those genotypes was contributed by good performance of physiological traits such as late FLS, great CID, or low CT or combinations of these traits. Preliminary results indicate that using physiological traits to estimate yield performance can be effective, and selecting suitable genotypes for different water environments may be crucial for improving yield productivity.

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Abbreviations: CID, carbon isotope discrimination; CT, canopy temperature; CTa, CT evaluated at Feekes 10.5.2 (anthesis); CTc, CT evaluated at Feekes 11.1 (kernels milky ripe); CTd, CT evaluated at Feekes 11.2 (kernels mealy ripe); DR, drought resistant; DS, drought susceptible; DSI, drought susceptibility index; ET, evapotranspiration; FLS, flag leaf senescence; FLSa, FLS evaluated at Feekes 10.5.2 (anthesis); FLSb, FLS evaluated at Feekes 10.5.4 (kernels watery ripe); FLSc, FLS evaluated at Feekes 11.1 (kernels milky ripe); FLSd, FLS evaluated at Feekes 11.2 (kernels mealy ripe); FLSe, FLS evaluated at Feekes 11.3 (kernels hard); HY, high yield; LY, low yield; T2, 50% evapotranspiration irrigated; T3, 100% evapotranspiration irrigated.

Wheat (*Triticum aestivum* L.) is one of the most important food crops in the world. Roughly 230 million ha of land is used for wheat cultivation worldwide and half of this area is routinely afflicted with drought stress (Trethowan and Reynolds, 2007). Development of improved wheat cultivars with drought resistance is critical for sustainable wheat production in these areas. Progress in breeding for drought resistance has required combining measurements of physiological traits associated with yield response determined in controlled environments. Response to drought has been measured using the drought susceptibility index (DSI) and several physiological traits such as flag leaf senescence (FLS), carbon isotope discrimination (CID), and canopy temperature (CT) associated with grain yield (Golestani Araghi

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and Assad, 1998; Merah et al., 2001; Verma et al., 2004; Monneveux et al., 2005). The DSI was derived from the yield difference between stress and nonstress environments. The use of DSI for identifying genotypes with yield stability in moisture limited environments has been reported on numerous occasions (Ahmad et al., 2003; Amiri Fahliani and Assad, 2005).

Carbon isotope discrimination has been used as a physiological tool to evaluate a large number of genotypes for grain yield and water use efficiency under field conditions (Merah et al., 2001; Teulat et al., 2001; Tokatlidis et al., 2004; Monneveux et al., 2005). Association between CID and grain yield under drought was also reported in several cereal crops, including wheat (Sayre et al., 1995; Merah et al., 1999, 2001) and barley (*Hordeum vulgare* L.) (Jiang et al., 2006). However, the reported correlations vary depending on the analyzed organ or tissue, the stage of sampling, and the growth environment (Merah et al., 1999; Jiang et al., 2006; Xu et al., 2007).

When plants grow without water deficit, they transpire and the leaf surfaces become cooler. In contrast, under drought conditions, stomates close to maintain turgor, transpiration is reduced, and leaf surface temperature increases. Therefore, the CT difference across genotypes can be used as a drought tolerance indicator. As a matter of fact, CT has been considered a reliable predictor of yield under drought and a criterion in screening wheat varieties in water limited environments (Pinter et al., 1990; Golestani Araghi and Assad, 1998; Feng et al., 2009).

Association between FLS and tolerance to terminal drought stress has been reported in cereals such as sorghum [*Sorghum bicolor* (L.) Moench] (Borrell et al., 2000), maize (*Zea mays* L.) (Campos et al., 2004), and wheat (Verma et al., 2004). Delayed leaf senescence, particularly of the flag leaf, could help to increase grain yield. Timing of FLS is also an important determinant of yield under both stress and optimal environments (Evans, 1993).

Minimal success has been achieved in breeding for resistance to drought, because of the complex genetic nature of stress-related physiological traits and the unreliability of conventional field-based evaluations. The objectives of the current study were to identify and characterize wheat genotypes with good yield performance across different water conditions and to prioritize the contributions of the three physiological traits to grain yield and their responses to drought stress in controlled irrigation environments.

MATERIALS AND METHODS

Plant Material

Thirty spring wheat genotypes, including 22 cultivars and eight elite breeding lines, were used in this study. The 22 cultivars are well adapted in the Pacific Northwest of the United States. The 30 genotypes comprised 12 hard red, nine soft white, eight hard white, and one durum wheat (Table 1).

Experimental Conditions

Trials were performed in two seasons, 2009 and 2010, in research fields at the University of Idaho Aberdeen Research & Extension Center at Aberdeen, ID (42°57´36″ N, 112°49´12″ W, and elevation 1342 m).

Wheat was planted on a Declo loam (coarse-loamy, mixed, superactive, mesic Xeric Haplocalcids) soil in four-row plots (2009) and seven-row plots (2010) with a plot size 3 m long and 1.5 m wide. Seeds were planted on 22 Apr. 2009 and 14 Apr. 2010. Planting depth was 3.8 cm and seeding rate was 300 seeds m^{-2}. Based on a soil test before planting, 15.8 and 10.6 g m^{-2} of N and P were applied, respectively. Herbicides including Huskie (pyrasulfotole, bromoxynil octanoate, and bromoxynil heptanoate) (Bayer CropScience LP, Research Triangle Park, NC) and Starane (Fluroxypyr-1-methylheptyl ester: ((4-amino-3,5-dichloro-6-fluoro-2-pyridinyl)oxy)acetic acid, 1-methylheptyl ester) (Dow AgroSciences LLC, Indianapolis, IN) were applied at the rates of 0.084 and 0.112 g m^{-2}, respectively, during jointing stage.

In each of the two seasons, the experiment was laid out in a split block design, with three replicates, keeping irrigation treatments in main plots and genotypes in subplots. Genotypes were randomized within each irrigation main plot. Three irrigation regimes, T1 (nonirrigated [severe drought stress]), T2 (50% evapotranspiration [ET] irrigated [moderate drought stress]), and T3 (100% ET irrigated [nonstress]), were applied by above-ground drip irrigation. The drip system included two types of drip tape (DripWorks, 190 Sanhedrin Circle, Willits, CA): T-Tape 515-08-670 for the T3 treatment and T-Tape 515-08-340 for the T2 treatment. Evapotranspiration measurements were determined based on the crop water use information from the Pacific Northwest Cooperative Agricultural Weather Network recommendations (U.S. Bureau of Reclamation, 2010). Irrigation started before heading (Feekes 10.1 [Miller, 1999]), was applied once a week, and ended at maturity (Feekes 11.4). The irrigated plants received irrigation water and rainfall water, while the nonirrigated plants only received rainfall water during the growing season (April to August). During the 2009 growing season, all plots (T1, T2, and T3) received 359 mm of rainfall and irrigated plots T2 and T3 received an additional 173 mm and 345 mm of irrigation water, respectively. During the 2010 growing season, all plots received 102 mm of rainfall and irrigated plots T2 and T3 received an additional 248 mm and 452 mm of irrigation water, respectively.

The 2009 experiment received more rainfall during the growing season than the 2010 experiment. To some extent, the 2010 experiment was affected by a cool spring as an unexpected factor, which delayed heading by about 10 d compared to the 2009 experiment.

Grain Yield and Drought Susceptibility Index

In both seasons, plots were harvested using a Wintersteiger Classic small plot combine equipped with a Harvest Master weigh system (Wintersteiger Inc., Salt Lake City, UT). Grain yield was determined from the grain weight of each plot of each genotype. The yield value was expressed as 88% dry matter.

Stability in grain yield was estimated for each genotype by the DSI derived from the yield difference between stress

Table 1. Spring wheat cultivars and advanced lines developed by Montana State University (MSU) (Bozeman, MT), University of Idaho (U of I) (Moscow, ID), University of California Davis (UCD) (Davis, CA), Washington State University (WSU) (Pullman, WA), Resource Seeds (RS) (Resource Seeds, Inc., Gilroy, CA), and WestBred (WB) (WestBred, a Unit of Monsanto Company, Bozeman, MT).

No.	Genotype	Height	Class†	Origin	Plant introduction no.	Reference
1	Choteau	Medium	HRS	MSU	PI 633974	Lanning et al., 2004
2	Vida	Tall	HRS	MSU	PI 642366	Lanning et al., 2006
3	McNeal	Tall	HRS	MSU	PI 574642	Lanning et al., 1994
4	Alzada	Medium	Durum	WB	PI 634820	NA‡
5	Agawam	Short	HWS	WB	PI 648027	NA
6	Conan	Medium	HRS	WB	PI 607549	NA
7	Hank	Medium	HRS	WB	PI 613583	NA
8	WB936	Short	HRS	WB	PI 587200	NA
9	Lassik	Short	HRS	UCD	PI 653535	NA
10	UC1600	Short	HRS	UCD	Breeding line	NA
11	Louise	Tall	SWS	WSU	PI 634865	Kidwell et al., 2006
12	Alpowa	Tall	SWS	WSU	PI 566596	Barrett and Kidwell, 1998
13	WA8039	Tall	SWS	WSU	Breeding line	NA
14	UI Winchester	Medium	HRS	U of I	PI 642362	NA
15	Jerome	Medium	HRS	U of I	PI 632712	Souza et al., 2005
16	IDO702	Tall	HRS	U of I	Breeding line	NA
17	Jefferson	Medium	HRS	U of I	PI 603040	Souza et al., 1999
18	Alturas	Medium	SWS	U of I	PI 620631	Souza et al., 2004
19	Cataldo	Medium	SWS	U of I	PI 642361	Chen et al., 2009
20	Lolo	Medium	HWS	U of I	PI 614840	Souza et al., 2003
21	UI Lochsa	Medium	HWS	U of I	PI639952	NA
22	IDO694	Short	HWS	U of I	Breeding line	NA
23	IDO686	Tall	SWS	U of I	Breeding line	NA
24	IDO687	Medium	SWS	U of I	Breeding line	NA
25	IDO599	Short	SWS	U of I	Breeding line	NA
26	IDO644	Medium	SWS	U of I	Breeding line	NA
27	Klasic	Short	HWS	RS	PI 486139	Barrett and Kidwell, 1998
28	Snowcrest	Short	HWS	RS	PI 642376	NA
29	Blanca Grande	Short	HWS	RS	PI 631481	NA
30	Blanca Royale	Short	HWS	RS	PI 655033	NA

†HRS, hard red spring wheat; HWS, hard white spring wheat; SWS, soft white spring wheat.

‡NA, not available.

and nonstress environments. The DSI was determined by the following equation (Fischer and Maurer, 1978):

$$\mathrm{DSI} = [1 - (\bar{\gamma}_D / \bar{\gamma}_P)]/D,$$

where $\bar{\gamma}_D$ and $\bar{\gamma}_P$, are the mean grain yield of each genotype at severe drought stress (T1) and nonstress (T3) conditions, respectively, and $D = 1 - (\bar{Y}_D / \bar{Y}_P)$, where $\bar{Y}_D$ and $\bar{Y}_P$ are the mean grain yield of all the genotypes under drought stress (T1) and nonstress (T3) conditions, respectively.

Agronomic Traits

In both 2009 and 2010 seasons, plant height and days to heading were recorded. Plant height was measured as the distance from the ground to the top of spike excluding the awns at maturity. The 30 genotypes were classified on the basis of plant height under irrigation into three groups: short, medium height, and tall (Table 1). Days to heading was measured as the number of days from planting until 50% of the spikes emerged from the boot in each plot.

Physiological Measurements

Flag leaf senescence was evaluated based on the percentage of flag leaf area that had lost green color by taking an overall visual assessment of all fertile shoots (those with an ear) in situ. An arbitrary scale from 0 to 10 was utilized for scoring senescence (0 being flag leaf completely green and 10 being flag leaf completely brown) (Fig. 1). In the 2009 season, FLS was recorded once at anthesis and two times during grain filling,

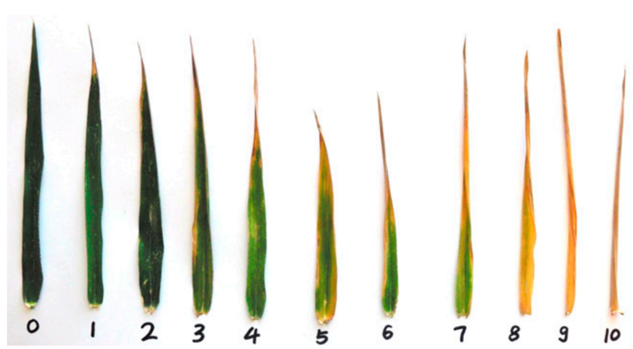


Figure 1. The visual rating scale (0–10) of flag leaf senescence in wheat.

corresponding to the Feekes growth scale (Miller, 1999): Feekes 10.5.2 (anthesis), Feekes 11.1 (kernels milky ripe), and Feekes 11.2 (kernels mealy ripe). In the 2010 season, FLS was recorded once at anthesis and four times during grain filling, corresponding to Feekes 10.5.2 (anthesis), Feekes 10.5.4 (kernels watery ripe), Feekes 11.1 (kernels milky ripe), Feekes 11.2 (kernels mealy ripe), and Feekes 11.3 (kernels hard), which were expressed as FLSa, FLSb, FLSc, FLSd, and FLSe, respectively.

Carbon isotope discrimination was analyzed using flag leaf samples collected during the grain filling stage, corresponding to Feekes 11.1 (kernels milky ripe) (Miller, 1999), for both the 2009 and 2010 seasons. Flag leaves of 10 randomly selected plants from each plot were excised, dried at 80°C for 48 h, and then ground to pass a 0.5-mm sieve. Ground samples were analyzed for $^{13}C:^{12}C$ using an isotope rationing mass spectrometer at Augustana College, Sioux Falls, SD. Carbon isotope composition was expressed as $\delta^{13}C$ values (Farquhar et al., 1989), where $\delta^{13}C$ (‰) = [R(sample)/R(standard) – 1] × 1000, R = $^{13}C/^{12}C$ ratio, where R(sample) and R(standard) are the $^{13}C:^{12}C$ ratios of the sample and standard, respectively. The standard is Pee Dee Belemnite carbonate. Precision of the $\delta^{13}C$ measurements was ±0.1‰. The CID value was calculated according to the formula (Farquhar et al., 1989) CID = $(\delta_a - \delta_p)/(1 + \delta_p)$, where δ_a and δ_p refer to air and plant sample, respectively. The value for the isotopic composition of atmospheric CO_2 (δ_a) was assumed to be –8‰ (Brugnoli and Farquhar, 2000). Due to the high cost of isotope analysis, CID was only measured once during each growing season. In 2009, samples from the two irrigation regimes (T1 and T3) were evaluated, whereas in 2010, samples from all three irrigation regimes (T1, T2, and T3) were evaluated.

Canopy temperature was measured using a hand-held infrared thermometer (IRtec MicroRay HVAC, Langhorne, PA) between 1300 and 1500 h during the day. The time chosen to measure CT was determined based on a preliminary study (data not shown) when stable air temperature was achieved. Four measurements were taken for each plot. In 2009, CT was measured at anthesis and grain filling, corresponding to Feekes 10.5.2 (anthesis) and Feekes 11.2 (kernels mealy ripe) (Miller, 1999). In 2010, CT was recorded at anthesis and two times during grain filling, corresponding to Feekes 10.5.2 (anthesis), Feekes 11.1 (kernels milky ripe), and Feekes 11.2 (kernels mealy ripe), which were expressed as CTa, CTc, and CTd.

Statistical Analysis

Data were analyzed using SAS Version 9.1 (SAS Institute, 2001) and SPSS 17.0 (SPSS Inc., 2007) statistical software. Pearsons' correlations were conducted between grain yield and other evaluated traits within each irrigation regime and over three irrigation regimes. The regression analyses including single variable regression and principal components analysis (extraction criteria: eigenvalues cumulative >90%, two components were retained) were conducted among evaluated traits over three irrigation regimes. Analysis of variance for grain yield, FLS, CID, CT, days to heading, and plant height were performed using the Proc GLM procedure of SAS (genotype subplots and main plots were fixed effects and replications were random effects). The effect of year between 2009 and 2010 was also tested. Significant differences among genotypes and irrigation regimes were determined using Fisher's protected LSD at $p = 0.05$.

RESULTS

Analysis of Variance

Analysis of variance of the 30 genotypes revealed significant differences ($p < 0.05$) in grain yield, FLS, CID, and CT within each and between the three irrigation regimes (Table 2). No genotype × irrigation treatment interaction occurred for most evaluated traits. However, genotype × irrigation treatment interaction for plant height and CID were significant ($p < 0.05$) in both seasons. Slight to moderate year effects were observed for most traits except for FLS measured at Feekes 11.2 (FLSd) (Miller, 1999) and plant height.

Grain Yield Responses to Drought

Drought stress caused a reduction in grain yield in both seasons. In 2009, the mean grain yield of all genotypes was 181.2, 319.5, and 429.1 g m^{-2}; in 2010, the mean grain yield of all genotypes was 198.7, 570.4, and 739.0 g m^{-2} for T1, T2, and T3, respectively. The seven-row plots for the irrigated regimes (T2 and T3) in 2010 produced greater grain yield than the four-row plots in 2009, while for the nonirrigated regime (T1), the grain yield did not increase much with the increased number of plot rows in the same plot area. Within each of the three irrigation regimes, the grain yield among the 30 genotypes was significantly different. Variation in DSI values among genotypes ranged from 0.4 to 1.3 for 2009 and from 0.8 to 1.2 for 2010 (Table 3).

Seven genotypes ('Agawam', 'Alpowa', 'McNeal', IDO694, 'Louise', 'Jefferson', and 'Blanca Royale') had smaller DSI values (DSI ≤ 1) in both seasons, indicating that these genotypes possessed better yield stability across different irrigation regimes. Four genotypes ('Choteau', 'Cataldo', 'Lolo', and IDO686) had greater DSI values (DSI > 1), and two of those genotypes (Choteau and Cataldo) produced less grain yield for all three irrigation regimes. Greater DSI value was confirmed to be an adverse factor for drought resistance. The DSI only indicates yield stability and not absolute yield potential; therefore, absolute yield level should be considered along with DSI.

Combining the performance of grain yield including absolute yield level and yield stability of each genotype under three irrigation regimes in 2009 and 2010, 13 selected genotypes were classified into four groups (high yield, drought resistant, drought susceptible, and low yield). Among the 13 selected genotypes, nine had medium height, three were tall, and one was short.

The high-yield (HY) group included three genotypes, IDO599, 'Alturas', and IDO702, that produced greater grain yield under all irrigation regimes and intermediate DSI for both 2009 and 2010 seasons and could be recommended for both water limited and water sufficient environments. The drought-resistant (DR) group contained three genotypes, Agawam, McNeal, and Alpowa, that produced higher grain yield under the nonirrigated regime and intermediate grain yield under irrigated regimes. The DR genotypes

Table 2. Analyses of variance for grain yield (GY), flag leaf senescence (FLS), carbon isotope discrimination (CID), canopy temperature (CT), days to heading (DTH), and plant height (HT) in 30 spring wheat genotypes.

Trait	Source of variation	2009			2010		
		df	Mean square	*F* value	df	Mean square	*F* value
GY, g m^{-2}	Genotype (G)	29	9820.1	2.2**	29	17520.9	3***
	Irrigation treatment (I)	2	926266.9	205.8***	2	6876019.3	1189.6***
	G × I	58	5884.5	1.3 NS†	58	11785.9	2**
FLSa‡	Genotype	29	1.1	7.5***	29	1	4.9***
	Irrigation treatment	2	0.4	2.6*	2	13.4	62.8***
	G × I	58	0.1	0.8 NS	58	0.3	1.4 NS
FLSb	Genotype	NA§	NA	NA	29	1.9	3.3***
	Irrigation treatment	NA	NA	NA	2	75.6	129.2***
	G × I	NA	NA	NA	58	0.9	1.5 NS
FLSc	Genotype	29	0.8	1.7***	29	1.9	1.9**
	Irrigation treatment	2	12.6	74.8***	2	469.6	492.9***
	G × I	58	1	1.4 NS	58	1.3	1.4 NS
FLSd	Genotype	29	17.2	2.9***	29	2	4.3***
	Irrigation treatment	2	579.9	97.8***	2	1019.5	2195.5***
	G × I	58	5.8	1 NS	58	0.6	1.4 NS
FLSe	Genotype	NA	NA	NA	29	2.6	5.9***
	Irrigation treatment	NA	NA	NA	2	875.1	1974.6***
	G × I	NA	NA	NA	58	1.6	3.5***
CID, ‰	Genotype	29	0.6	3.3***	29	0.5	0.8***
	Irrigation treatment	1	36	203.9***	2	39.3	198.8***
	G × I	29	0.7	5.4*	58	0.6	1*
CTa‡, °C	Genotype	29	2.2	1.6*	29	6.6	1.2 NS
	Irrigation treatment	2	101.7	93***	2	446.5	78.4***
	G × I	58	3	2.9 NS	58	6.4	1.1 NS
CTc, °C	Genotype	NA	NA	NA	29	3.5	1.1 NS
	Irrigation treatment	NA	NA	NA	2	4502.2	1377.8***
	G × I	NA	NA	NA	58	3.6	1.1 NS
CTd, °C	Genotype	29	9.9	1.7**	29	2.9	1*
	Irrigation treatment	2	2694.7	460.5***	2	2116.9	728.1***
	G × I	58	6.4	1.1 NS	58	3.6	1.3 NS
DTH, DAP¶	Genotype	29	45.2	85.8***	29	23.1	40.5***
	Irrigation treatment	2	33.2	63***	2	13.1	23***
	G × I	58	0.7	1.4 NS	58	0.9	1.7*
HT, cm	Genotype	29	241.9	19.4***	29	278.5	12.2***
	Irrigation treatment	2	1392.7	111.5***	2	9198.5	403.5***
	G × I	58	25.2	2*	58	49.4	2.2**

*Significant at the 0.05 probability level.

**Significant at the 0.01 probability level.

***Significant at the 0.001 probability level.

†NS, nonsignificant at the 0.05 probability level.

‡a through e stand for traits assessed at Feekes 10.5.2 (anthesis), Feekes 10.5.4 (kernels watery ripe), Feekes 11.1 (kernels milky ripe), Feekes 11.2 (kernels mealy ripe), and Feekes 11.3 (kernels hard) (Miller, 1999), respectively.

§NA, not available.

¶DAP, days after planting.

can be recommended for water deficit environments. The drought-susceptible (DS) group included two genotypes, IDO686 and Lolo, that produced less grain yield under the nonirrigated regime and greater grain yield under the irrigated regimes in both growing seasons. The DSI values were high for these genotypes as well. Therefore, the DS genotypes would be recommended only for moist environments. The low-yield (LY) group contained five genotypes ('Klasic', Choteau, UC1600, 'Snowcrest', and Cataldo) that produced less grain yield than other genotypes under all irrigation regimes. Among the LY genotypes, Choteau and Cataldo showed higher DSI values and should be replaced by superior genotypes in the future. Comparison of the mean grain yield of genotypes in each group and the mean grain yield of all 30 genotypes under each of three irrigation regimes is reported in Fig. 2.

Table 3. The mean grain yield (GY, g m^{-2}) and drought susceptibility index (DSI), carbon isotope discrimination (CID, ‰), flag leaf senescence evaluated at Feekes 11.2 (kernels mealy ripe) (FLSd, 0–10), and canopy temperature evaluated at Feekes 11.2 (kernels mealy ripe) (CTd, °C) at grain filling (Feekes 11.2 [Miller, 1999]) in 2009 and 2010 under three irrigation regimes, T1 (non-irrigated), T2 (50% evapotranspiration [ET] irrigated), and T3 (100% ET irrigated), for 30 spring wheat genotypes.

		GY				FLSd		CID		CTd	
No.	Genotype	T1	T2	T3	DSI	T1	T3	T1	T3	T1	T3
1	Choteau	154.79	341.53	539.58	1.1	8.0	2.8	19.3	20.8	38.8	30.2
2	Vida	182.98	480.42	636.34	1.1	9.0	2.5	19.0	20.7	37.4	29.1
3	McNeal	199.68	458.76	534.94	1.0	7.5	2.8	18.8	19.7	40.7	30.5
4	Alzada	181.58	419.95	560.39	1.1	8.8	2.3	19.1	20.1	42.3	30.5
5	Agawam	245.06	483.12	473.23	0.7	7.5	3.5	19.4	20.7	40.8	33.1
6	Conan	217.59	429.52	558.37	1.0	8.5	2.7	19.3	20.6	40.4	30.0
7	Hank	209.90	421.85	618.85	1.0	9.2	2.5	19.7	21.1	39.0	29.2
8	WB936	183.44	401.57	581.54	1.0	8.5	3.8	19.9	20.9	39.7	28.9
9	Lassik	207.71	488.73	634.43	1.1	8.7	4.7	19.1	20.5	41.7	28.9
10	UC1600	149.30	406.17	503.37	1.1	9.2	4.2	19.3	19.9	40.8	30.7
11	Louise	193.04	465.33	574.94	0.9	8.8	4.0	19.0	20.1	39.3	32.8
12	Alpowa	237.43	415.19	572.07	0.8	8.0	4.7	19.8	20.5	39.9	32.1
13	WA8039	257.52	477.03	636.59	0.8	7.7	5.7	19.6	20.8	39.8	31.3
14	UI Winchester	203.05	432.46	648.38	1.1	9.0	3.2	19.3	21.3	41.2	30.5
15	Jerome	166.34	440.99	576.06	1.0	8.8	2.8	19.2	20.8	39.1	32.8
16	IDO702	216.82	487.40	657.89	1.1	9.5	2.5	19.4	20.2	38.9	31.9
17	Jefferson	191.72	476.34	545.52	0.9	8.5	4.7	19.1	21.0	40.3	32.1
18	Alturas	191.59	465.81	659.74	1.1	8.8	2.7	19.6	20.5	40.9	29.3
19	Cataldo	118.44	375.22	578.33	1.2	10.0	3.7	19.1	20.5	40.2	29.9
20	Lolo	145.71	458.65	608.43	1.2	9.5	3.0	19.1	19.8	38.4	29.5
21	UI Lochsa	204.46	412.68	589.17	1.1	9.3	2.0	19.4	21.1	41.2	29.4
22	IDO694	218.84	472.16	564.27	0.9	9.8	3.5	19.2	20.6	39.4	32.1
23	IDO686	132.82	492.07	644.81	1.3	8.5	2.0	19.0	20.9	41.5	29.9
24	IDO687	191.24	444.54	576.99	1.0	9.3	4.0	19.3	20.3	42.3	29.7
25	IDO599	240.58	448.67	742.65	1.0	8.7	2.3	19.5	20.8	41.2	30.1
26	IDO644	174.72	461.50	645.93	1.0	7.3	2.8	19.4	20.5	39.5	31.9
27	Klasic	134.42	349.44	467.61	1.1	9.5	4.2	19.0	20.2	41.9	32.0
28	Snowcrest	176.89	400.01	472.23	1.0	9.8	4.5	19.0	20.5	42.1	33.5
29	Blanca Grande	184.43	505.57	583.48	1.1	9.7	2.8	19.5	20.4	43.0	30.9
30	Blanca Royale	186.34	535.08	535.39	1.0	9.8	4.8	19.5	20.1	41.1	32.6
Mean		189.95	444.93	584.05	1.00	9.1	3.5	19.3	20.5	40.4	30.8
SD		33.95	44.84	62.41	0.12	1.04	1.11	0.44	0.47	1.74	1.61
$LSD_{0.05}$		73.90	73.90	73.90		0.95	0.95	0.95	0.95	2.25	2.25

Effect of Flag Leaf Senescence on Grain Yield Response to Drought

Variation in FLS occurred across irrigation regimes at all evaluated stages except for anthesis in 2009; the differences tended to be greater with more advanced developmental stage (Fig. 3). Drought stress accelerated FLS for all genotypes. The extent of acceleration was different among the genotypes. Under T1, T2, and T3, the mean FLS score of all genotypes at Feekes 11.2 (Miller, 1999) was 9, 6, and 4 and 9, 4, and 3, respectively, for 2009 and 2010. The mean FLSd of 2009 and 2010 for genotypes under T1 and T3 are presented in Table 3.

Among the 30 genotypes, IDO 686, 'UI Lochsa', IDO644, and McNeal had later FLS with intermediate grain yield concurrently across irrigation regimes for both seasons, while Blanca Royale, Snowcrest, Klasic, and Cataldo had earlier FLS, and three genotypes (Snowcrest, Klasic, and Cataldo) produced low grain yield across irrigation regimes in both seasons. Our results suggest that earlier FLS tends to result in lower grain yield and that delayed FLS may result in intermediate rather than higher grain yield.

Among the seven genotypes that showed better yield stability (DSI ≤ 1), McNeal, Agawam, Alpowa, Jefferson, and Louise showed delayed FLS than other genotypes under the nonirrigated regime (T1); IDO694 and Blanca Royale showed earlier FLS under both nonirrigated and irrigated regimes.

At Feekes 11.2 (Miller, 1999), the FLS of HY genotypes was obviously later than that of LY genotypes. Drought-resistant genotypes showed delayed FLS compared to DS genotypes under T1 and earlier FLS than DS genotypes under T3 (Fig. 4). Our results indicate that selecting genotypes with late FLS would improve yield production.

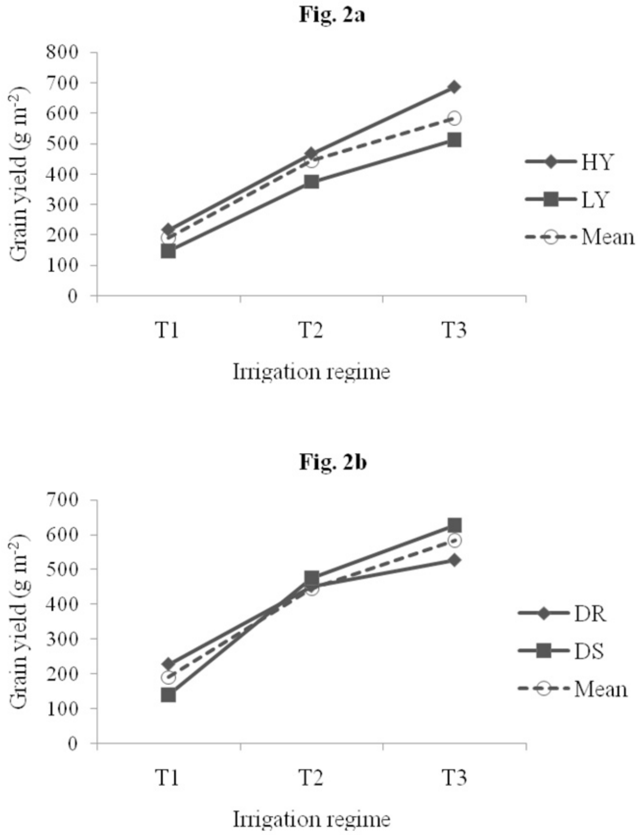


Figure 2. Comparison of the mean grain yield of 30 spring wheat genotypes (Mean) and the mean grain yield of genotypes in each group for (a) high-yield (HY) and low-yield (LY) genotypes and for (b) drought-resistant (DR) and drought-susceptible (DS) genotypes under three irrigation regimes, T1 (nonirrigated), T2 (50% evapotranspiration [ET] irrigated), and T3 (100% ET irrigated), based on data from 2009 and 2010.

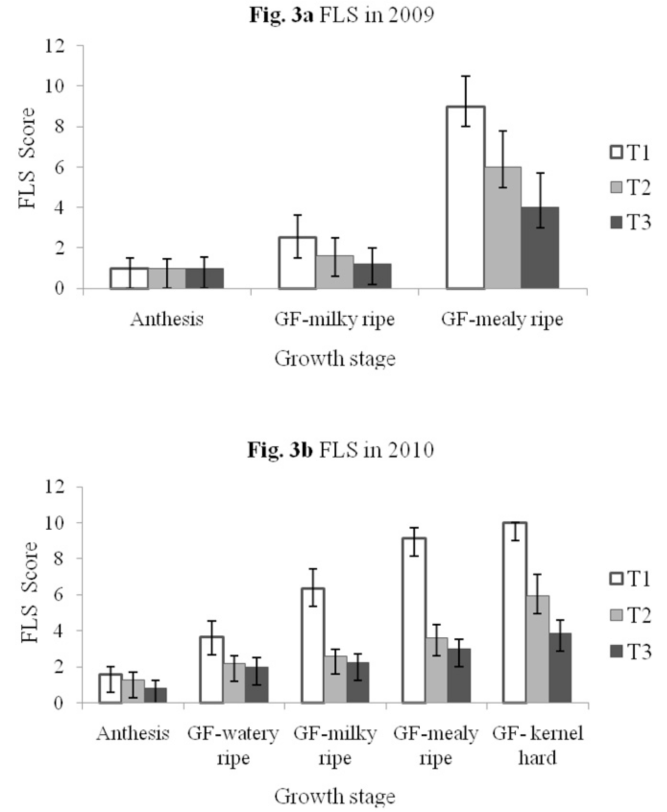


Figure 3. The mean flag leaf senescence (FLS) score (0–10) ± SD of 30 spring wheat genotypes under three irrigation regimes, T1 (nonirrigated), T2 (50% evapotranspiration [ET] irrigated), and T3 (100% ET irrigated), at anthesis and grain filling (GF) stages in (a) 2009 and (b) 2010.

Effect of Carbon Isotope Discrimination on Grain Yield Response to Drought

Drought stress caused an obvious decrease in flag leaf CID sampled at grain filling (Feekes 11.1 [kernels milky ripe] [Miller, 1999]) across all 30 wheat genotypes. In 2009, the mean CID of the 30 genotypes under T1 and T3 was 19.7 and 20.8‰, respectively. In 2010, the mean CID of 30 genotypes under T1, T2, and T3 was 18.9, 19.9, and 20.2‰, respectively. Differences among the 30 genotypes for CID were also observed in 2009 and 2010 (Table 3).

Under all irrigation regimes, IDO599, 'WB936', and 'Hank' had greater CID and high or intermediate grain yield, while McNeal, 'Alzada', and Lolo had lower CID and intermediate or low grain yield. Among the seven genotypes that showed better yield stability (DSI ≤ 1), Jefferson, Louise, and Blanca Royale had relatively high CID under the nonirrigated regime.

Comparison of the mean CID of genotypes in each group and the mean CID of all 30 genotypes under each irrigation regime over 2 yr is reported in Fig. 5. High-yield genotypes had greater CID than LY genotypes under treatments T1 and T3. Drought-resistant genotypes had greater CID than DS genotypes under T1 but lower CID than DS genotypes under T3, indicating that under two contrasting irrigation regimes (nonirrigated and well watered), high grain yield was, to some extent, associated with greater CID. However, different results were observed for T2; that is, CID of LY genotypes was greater than HY genotypes suggesting that further studies are needed.

Effect of Canopy Temperature on Grain Yield Response to Drought

Drought stress increased CT at both anthesis and grain filling, especially at Feekes 11.2 (Miller, 1999) (Fig. 6). Plants that suffered greater drought stress tended to have warmer CT at midday. The extent that CT increased due to drought stress for the 30 wheat genotypes was different. The mean CT increase of all genotypes was 9.6°C over T1 and T3; the mean CTd of the 2009 and 2010 seasons for the 30 genotypes under T1 and T3 are summarized in Table 3.

Among the 30 genotypes, 'Vida' and 'Conan' had lower CT whereas Snowcrest and 'Blanca Grande' had greater CT across irrigation regimes at anthesis and grain filling. Among those seven genotypes that showed better

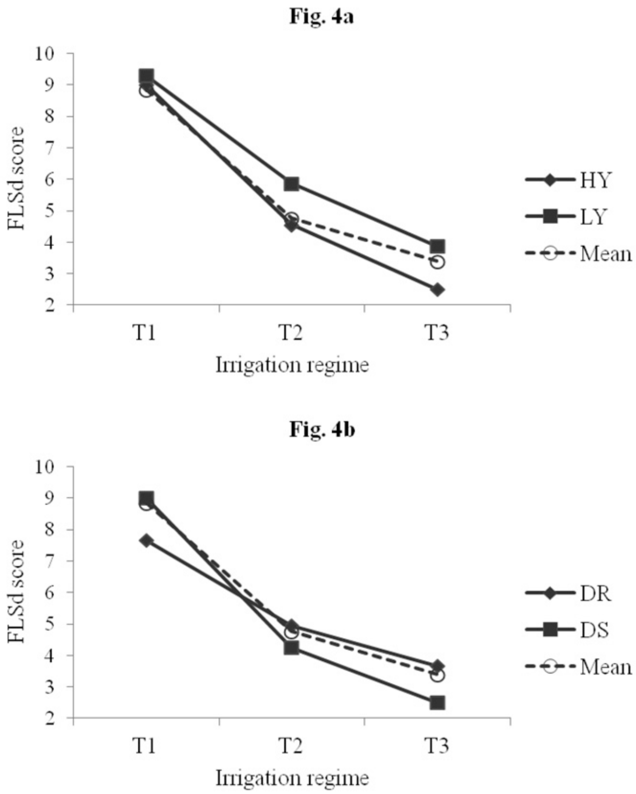


Figure 4. Comparison of the mean flag leaf senescence evaluated at Feekes 11.2 (kernels mealy ripe) (Miller, 1999) (FLSd, 0–10) of 30 spring wheat genotypes (Mean) and the mean FLSd of (a) high-yield (HY) and low-yield (LY) genotypes and (b) drought-resistant (DR) and drought-susceptible (DS) genotypes under three irrigation regimes, T1 (nonirrigated), T2 (50% evapotranspiration [ET] irrigated), and T3 (100% ET irrigated), based on data from 2009 and 2010.

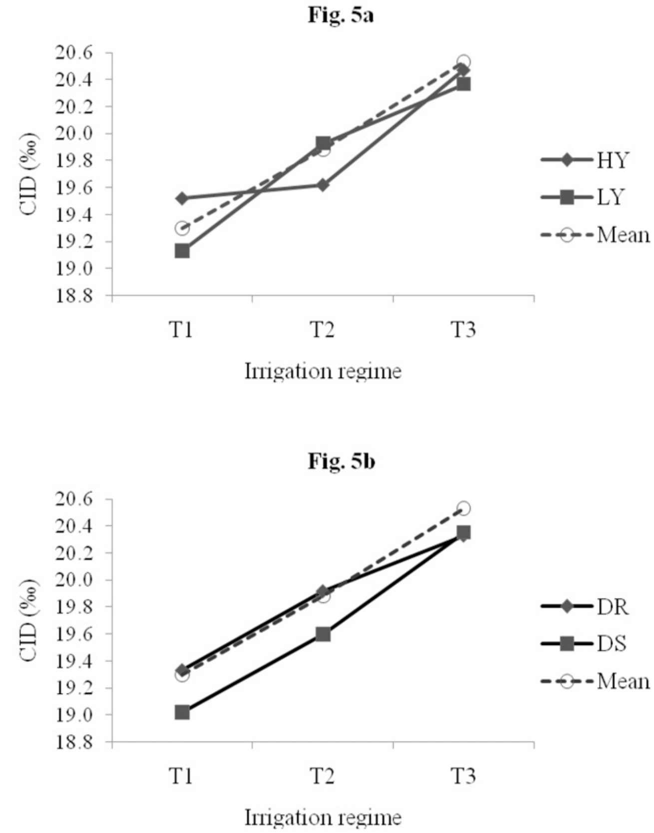


Figure 5. Comparison of the mean flag leaf carbon isotope discrimination (CID) of 30 spring wheat genotypes (Mean) and the mean CID of genotypes in each group for (a) high-yield (HY) and low-yield (LY) genotypes and for (b) drought-resistant (DR) and drought-susceptible (DS) genotypes under three irrigation regimes, T1 (nonirrigated), T2 (50% evapotranspiration [ET] irrigated), and T3 (100% ET irrigated), based on data from 2009 and 2010.

yield stability (DSI ≤ 1), IDO694, Louise, and Alpowa had lower CT under T1 in 2009 and 2010.

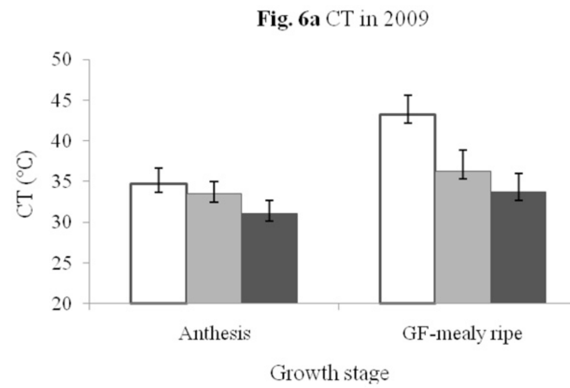
The comparison of the mean CTd of genotypes in each of the four groups under the T3 regime was converse with comparison of grain yield, which indicated the negative association between CT and grain yield in the well-watered environment. For stress conditions (T1 and T2), the CTd of those genotypes that produced greater grain yield was similar or even greater than that of genotypes that produced lower grain yield (Fig. 7). This suggests that using CTd as an indicator to select high grain yield in moist environments may be more reliable than in drought conditions.

Correlations and Regression

Within each of the three irrigation regimes, FLSd was negatively correlated with grain yield. The correlation between FLSd and grain yield was more significant with less irrigation—T1 ($p < 0.001$), T2 ($p < 0.001$ and $p < 0.01$), and T3 ($p < 0.01$ and $p < 0.05$)—for both seasons. Similarly, CID was positively and significantly correlated with grain yield especially under the nonirrigated regime (T1). For CT, though, CTa and CTd were both negatively correlated with grain yield within each irrigation regime. However, CTa had greater correlations with grain yield under the drought stressed regimes (T1 and T2), while CTd had greater correlations with grain yield under the irrigated regimes (T2 and T3) (Table 4).

All physiological traits evaluated across the three irrigation regimes, except FLSa in 2009, were all correlated with grain yield ($r > 0.5$, $p < 0.001$) (Tables 5 and 6). The correlations between grain yield and FLS were negative and significant at grain filling (FLSb, FLSc, FLSd, and FLSe) for both seasons. Flag leaf senescence evaluated at Feekes 11.2 (kernels mealy hard) (Miller, 1999) was greatly associated with grain yield, with coefficients of −0.859 and −0.931 ($p < 0.001$) for 2009 and 2010, respectively. For FLSe, though, the genotype × irrigation treatment interaction was significant, which suggests that FLS at Feekes 11.3 (Miller, 1999) cannot be evaluated without the effect of water regimes. Results from each irrigation regime and over three regimes indicate that Feekes 11.2 would be the best and latest stage for assessing FLS in spring wheat genotypes.

Over the three irrigation regimes, positive correlations occurred between grain yield and flag leaf CID in 2009 ($r = 0.869$, $p < 0.001$) and in 2010 ($r = 0.763$, $p < 0.001$). There were negative correlations between grain



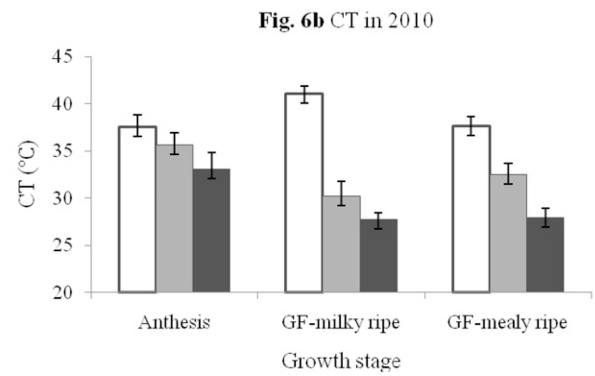
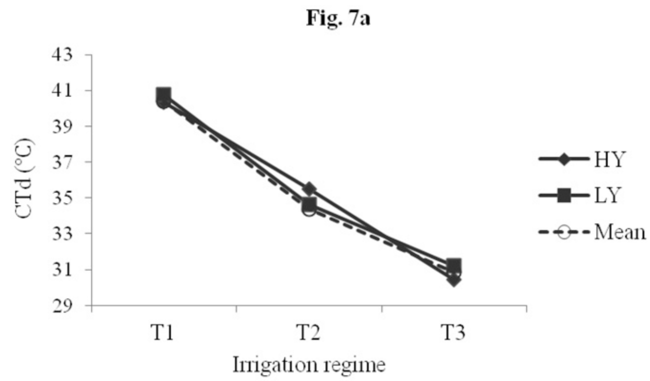


Figure 6. The mean canopy temperature (CT) ± SD of 30 spring wheat genotypes under three irrigation regimes, T1 (nonirrigated), T2 (50% evapotranspiration [ET] irrigated), and T3 (100% ET irrigated), at anthesis and grain filling (GF) stages in (a) 2009 and (b) 2010.



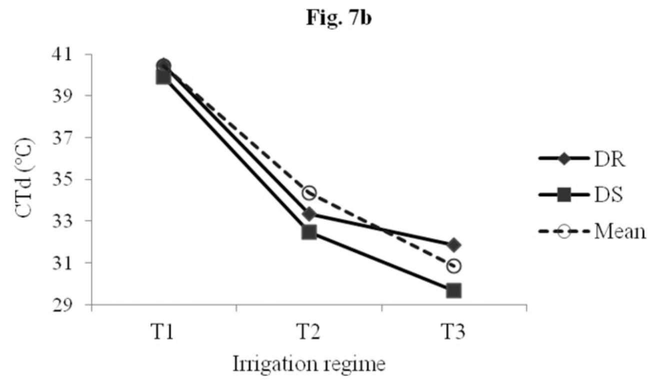


Figure 7. Comparison of the mean canopy temperature evaluated at Feekes 11.2 (kernels mealy ripe) (Miller, 1999) (CTd) of 30 spring wheat genotypes (Mean) and the mean CTd of genotypes in (a) the high-yield (HY) and low-yield (LY) groups and (b) the drought-resistant (DR) and drought-susceptible (DS) groups under three irrigation regimes, T1 (nonirrigated), T2 (50% evapotranspiration [ET] irrigated), and T3 (100% ET irrigated), based on data from 2009 and 2010.

yield and CT at both anthesis and grain filling stages, with coefficients of −0.837 and −0.926 ($p < 0.001$) for late grain filling (Feekes 11.2 [Miller, 1999]) of 2009 and 2010, respectively (Tables 5 and 6). Results suggest that Feekes 11.2 (kernels mealy ripe) would be an optimal stage for CT measurement compared with the earlier stages of Feekes 10.5.2 (anthesis) and Feekes 11.1 (kernels milky ripe).

Plant height was correlated with grain yield and evaluated physiological traits, whereas correlations between days to heading and other traits were low. This suggests that under conditions of this study, the influence of plant height on grain yield and physiological traits should be considered; however, to some extent, the effects of days to heading on the target traits might be ignored.

Linear regressions of grain yield on FLSd, CID, and CTd across three irrigation regimes were all highly significant ($p < 0.0001$). Flag leaf senescence evaluated at Feekes 11.2 (kernels mealy ripe) explained 79 and 87%, CID explained 76 and 58%, and CTd explained 81 and 86% of the total phenotypic variation of grain yield in 2009 and 2010, respectively. The principal components analysis identified that the three physiological traits together explained 91 and 92% of the total phenotypic variation of grain yield for 2009 and 2010, respectively (Table 7).

DISCUSSION

Exposure of plants to drought led to a noticeable decrease in grain yield, acceleration of FLS, decrease in flag leaf CID, and increase in CT. The extent of drought effects on grain yield and the three target physiological traits were different among the 30 genotypes over three irrigation regimes. Our results indicate that wheat genotypes respond to drought stress using various physiological processes. The physiological changes observed in our study could be the response of various defense mechanisms adapted by the plant.

Significant correlations were observed between grain yield and all three physiological traits within each regime and over the three regimes. This infers that selection of late FLS, low CT, and high CID may benefit high grain yield selection. For FLS and CT, the absolute correlation coefficients in later growth stages were always higher than those in early stages. Therefore, selection of the two physiological traits at later grain filling (Feekes 11.2 [Miller, 1999]) would be more effective than at the earlier stages (Feekes 10.5.2 and Feekes 11.1). In addition, FLSd would be a more reliable predictor for grain yield under drought stress environments.

Merah et al. (1999) reported that the flag leaf CID at anthesis correlated with grain yield only under strong water limitation conditions in durum wheat. Jiang et al. (2006)

Table 4. Pearsons' correlation coefficients between grain yield (GY, g m^{-2}) and other evaluated traits (days to heading [DTH, height [HT], flag leaf senescence [FLS, 0–10], carbon isotope discrimination [CID, ‰], and canopy temperature [CT, °C]) in 30 spring wheat genotypes within each of the three irrigation regimes, T1 (nonirrigated), T2 (50% evapotranspiration [ET] irrigated), and T3 (100% ET irrigated), in 2009 and 2010.

	2009			2010		
Trait	T1	T2	T3	T1	T2	T3
FLSa†	NS‡	NS	NS	NS	NS	–0.391*
FLSc	–0.375*	–0.523**	–0.382*	–0.365*	NS	–0.386*
FLSd	–0.660***	–0.633***	–0.540**	–0.474***	–0.415**	–0.384*
CID	0.718***	NA§	0.513**	0.491**	0.380**	NS
CTa†	–0.572**	–0.527**	–0.410*	–0.561**	–0.606**	NS
CTd	NS	–0.481**	–0.578***	–0.408*	–0.490**	–0.480**
DTH	0.410*	NS	0.544*	–0.368*	NS	NS
HT	0.476**	0.381*	0.694**	0.534**	NS	0.398*

*Significant at the 0.05 probability level.

**Significant at the 0.01 probability level.

***Significant at the 0.001 probability level.

†a, c, and d stand for traits assessed at Feekes 10.5.2 (anthesis), Feekes 11.1 (kernels milky ripe), and Feekes 11.2 (kernels mealy ripe) (Miller, 1999), respectively.

‡NS, nonsignificant at the 0.05 probability level.

§NA, not available.

indicated that CID was not a reliable predictor for barley yield under severe water stress. More recently, Xu et al. (2007) found that there was no correlation between grain yield and CID in leaves at anthesis under optimal irrigation in spring wheat. In the current study, positive and significant correlation was found between flag leaf CID at grain filling and grain yield across different water conditions, but the correlation was greater under the nonirrigated regime (T1) than other regimes, suggesting that CID would be a more reliable predictor for grain yield under severe drought stress.

Canopy temperature is a potential indicator of the capacity of the roots to supply water under high evaporative demand. In drought environments, genotypes with cooler CT at grain filling had higher grain yield. The current study confirmed that cooler CT at grain filling is significantly associated with higher grain yield across different water conditions. Amiri Fahliani and Assad (2005) reported that CT of cultivars during anthesis, under nonstress conditions, could help discriminate between resistant and susceptible cultivars better than at other stages. However, our results show that CT of genotypes at both anthesis and grain filling could help predict yield, but CT evaluated at anthesis (CTa) would be more reliable for drought stressed conditions while CT evaluated at grain filling (CTd) would be more reliable for well-watered conditions.

Accurate field evaluation of yield-related physiological traits is critical for understanding the genetic mechanism controlling grain yield. Our study suggests that the Feekes 11.2 (kernels mealy ripe) (Miller, 1999) stage of grain filling is the optimal time for FLS and CT measurements. In 2009 and 2010, the linear regressions of grain yield on FLSd, CID, and CTd were all highly significant ($p < 0.0001$) and together explained 91 and 92% of the total phenotypic variation of grain yield, respectively, indicating that the three physiological traits can be used to predict yield performance across different water environments.

These findings can be used to identify likely high yielding and drought resistant advanced lines while discarding those that are clearly low yielding and drought susceptible and be applied to a controlled selection experiment. Although these physiological traits are considered useful tools for screening wheat genotypes, their combination with other methods may provide a more accurate assessment of yield performance and drought resistance.

In the two growing seasons, genotype IDO694 showed different responses to drought stress for grain yield. In 2009, IDO694 produced relatively lower grain yield than other genotypes under all irrigation regimes, while in 2010, it produced relatively higher grain yield than other genotypes under all irrigation regimes.

Among the 30 wheat genotypes, HY genotypes IDO599, Alturas, and IDO702 produced consistent high grain yield across different water conditions and appeared

Table 5. Pearsons' correlation coefficients between grain yield (GY), days to heading (DTH), height (HT), flag leaf senescence (FLS), carbon isotope discrimination (CID), and canopy temperature (CT) evaluated at different growth stages in 30 genotypes across three irrigation regimes, T1 (nonirrigated), T2 (50% evapotranspiration [ET] irrigated), and T3 (100% ET irrigated), in 2009.

	GY	FLSd†	FLSc	CID	CTd†	CTa	DTH
FLSa†	NS‡						
FLSd	–0.859***						
FLSc	–0.602***	0.523***					
CID	0.869***	–0.723***	–0.531***				
CTd†	–0.837***	0.748***	0.557***	–0.769***			
CTa	–0.688***	0.699***	0.328**	–0.659***	0.605***		
DTH	0.391***	–0.300**	NS	0.484***	–0.267*	NS	
HT	0.664***	–0.536***	–0.413***	0.643***	–0.585***	–0.349**	0.658***

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

*** Significant at the 0.001 probability level.

†a, c, and d stand for traits assessed at Feekes 10.5.2 (anthesis), Feekes 11.1 (kernels milky ripe), and Feekes 11.2 (Miller, 1999), respectively.

‡NS, nonsignificant at the 0.05 probability level.

Table 6. Pearsons' correlation coefficients between grain yield (GY), days to heading (DTH), height (HT), flag leaf senescence (FLS), carbon isotope discrimination (CID), and canopy temperature (CT) evaluated at different growth stages in 30 genotypes across three irrigation regimes, T1 (nonirrigated), T2 (50% evapotranspiration [ET] irrigated), and T3 (100% ET irrigated), in 2010.

	GY	CTa†	CTc†	CTd†	FLSa†	FLSb†	FLSc†	FLSd†	FLSe†	CID	DTH
CTa†	−0.795***										
CTc†	−0.958***	0.755***									
CTd†	−0.926***	0.815***	0.929***								
FLSa†	−0.590***	0.543***	0.551***	0.629***							
FLSb†	−0.750***	0.580***	0.762***	0.705***	0.637***						
FLSc†	−0.895***	0.679***	0.924***	0.847***	0.580***	0.883***					
FLSd†	−0.931***	0.697***	0.970***	0.884***	0.559***	0.825***	0.964***				
FLSe†	−0.949***	0.772***	0.949***	0.936***	0.569***	0.745***	0.885***	0.941***			
CID	0.763***	−0.603***	−0.754***	−0.712***	−0.368***	−0.523***	−0.677***	−0.728***	−0.685***		
DTH	NS‡	NS	NS	−0.213*	−0.361***	−0.278**	NS	NS	−0.278**	−0.209*	
HT	0.829***	−0.757***	−0.786***	−0.809***	−0.625***	−0.666***	−0.742***	−0.774***	−0.807***	0.640***	0.208*

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

*** Significant at the 0.001 probability level.

†a through e stand for traits assessed at Feekes 10.5.2 (anthesis), Feekes 10.5.4 (kernels watery ripe), Feekes 11.1 (kernels milky ripe), Feekes 11.2 (kernels mealy ripe), and Feekes 11.3 (kernels hard) (Miller, 1999), respectively.

‡NS, nonsignificant at the 0.05 probability level.

to be promising parents for wheat breeding programs. Drought-resistant genotypes Agawam, McNeal, and Alpowa produced greater grain yield under the nonirrigated regime and intermediate grain yield under the irrigated regimes indicating their adaptation to drought conditions. Later FLS, greater CID, or lower CT or combinations of these traits contributed to the high yield of these selected genotypes under corresponding water conditions. The results indicate that if water for irrigation is scarce, planting the HY and DR genotypes would greatly reduce the risk of significant grain yield reduction. Drought-resistant genotypes are more stable in yield production over the range of drought stresses applied and would be useful as parents to combine their stability with the higher yield potential of HY genotypes.

Drought-susceptible genotypes IDO686 and Lolo produced greater grain yield under the irrigated regimes but less grain yield under the nonirrigated regime in both years. The DS genotypes had higher DSI values concurrently, which would be only recommended for moist environments. Low-yield genotypes Choteau and Cataldo showed lower grain yield with a concurrent higher DSI across different water conditions for both seasons and may not be preferable wheat genotypes. Our study put forward the concepts of yield performance classification across different water conditions, and proposed the possible application to the selection of wheat genotypes. Progeny of a cross between HY and DR genotypes would be expected to segregate significantly in yield performance and drought resistance and provide great opportunity to obtain elite wheat genotypes. Therefore, the classification of wheat genotypes with different yield performance across water environments could be introduced in assessing procedures of wheat genotype improvement, particularly facilitating the breeding of wheat genotypes for drought resistance.

Acknowledgments

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Table 7. Single variable regression and principal components analyses between grain yield (GY) and flag leaf senescence evaluated at Feekes 11.2 (kernels mealy ripe) (FLSd), carbon isotope discrimination (CID) and canopy temperature evaluated at Feekes 11.2 (kernels mealy ripe) (CTd) at grain filling stage, Feekes 11.2 (Miller, 1999), across three irrigation regimes, T1 (nonirrigated), T2 (50% evapotranspiration [ET] irrigated), and T3 (100% ET irrigated), in 2009 and 2010.

Year	Trait	Regression equation	R^2	Probability
2009	FLSd	GY = −42.722 FLSd + 568.591	0.793	<0.0001
	CID	GY = 169.772 CID − 3136.826	0.755	<0.0001
	CTd	GY = −23.399 CTd + 1204.958	0.807	<0.0001
	FLSd, CID, and CTd	GY = −7.832 FLSd + 56.797 CID − 23.382 CTd + 2397.95	0.914	<0.0001
2010	FLSd	GY = −77.853 FLSd + 911.561	0.866	<0.0001
	CID	GY = 240.074 CID − 4218.286	0.583	<0.0001
	CTd	GY = −53.158 X_3 + 2240.639	0.857	<0.0001
	FLSd, CID, and CTd	GY = −16.36 FLSd + 70.089 CID − 53.287 CTd + 952.491	0.921	<0.0001

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