Agronomic Characteristics and Grain Yield of 30 Spring Wheat Genotypes under Drought Stress and Nonstress Conditions

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ABSTRACT

Drought is an important environmental stress limiting wheat (*Triticum aestivum* L.) productivity in water limited regions. Our aim was to understand the relationships between target agronomic traits and grain yield (GY) responses to drought, and to prioritize genotypes for high yield under different water conditions. Thirty spring wheat genotypes were evaluated over 2009 and 2010 for GY and agronomic traits under T1 (non-irrigated), T2 (50% evapotranspiration [ET] irrigated), and T3 (100% ET irrigated) irrigation regimes. Drought stress caused noticeable fewer days to physiological maturity (PMD), shorter plant height (HT) and exposed peduncle length (EPL), smaller grain volume weight (GVW), higher grain protein content (GPC), smaller kernel weight (KW) and kernel diameter (KD), and less GY. All target traits were significantly correlated with GY except for days to heading (HD) in 2010. Selected traits for 2009 (PMD, HT, GVW) and 2010 (PMD, HT, GPC) together explained 82 and 93% of the total phenotypic variation of GY, respectively. Selected genotypes were classified into four types based on their agronomic and yield performance across three irrigation regimes. High-yield (HY) genotypes IDO599, Alturas, and IDO702 had better agronomic performance and produced high GY across different water conditions; drought-resistance (DR) genotypes Agawam, McNeal, and Alpowa exhibited drought resistance in target traits and produced higher GY than other genotypes under drought. Preliminary results indicate that GY could be estimated on the basis of agronomic performance including PMD, HT, GVW, and GPC, and selecting HY and DR genotypes for water limited environments may be important for improving yield productivity.

Wheat is one of the most important cereal crops in the world, which is grown both in arid and semiarid regions of the world (Akbar et al., 2001; Tunio et al., 2006). Current estimates indicate that 25% of the world's agricultural land is now affected by drought stress. It can be said that drought stress is one of the most devastating environmental stresses that depress wheat yield productivity in many parts of the world. Development of improved wheat cultivars with drought tolerance is critical for sustainable wheat production in these areas. Grain yield is frequently used in wheat as a main criterion for drought tolerance. Selection for drought tolerance typically involves evaluating genotypes for either HY potential or stable performance under varying degrees of water stress (Ahmad et al., 2003).

However, GY actually is a product of several contributing factors and can be estimated on the basis of performance of various components. Therefore, progress has required combining measurements of yield-related traits associated with yield response, and selection based on above yield components would result in yield increases. Agronomic traits such as HD, PMD, and HT with other indices have been used for the estimate of GY and the assessment of drought resistance (Gebeyehou et al., 1982; Bhutta, 2006; Khan et al., 2010). These parameters are the main criteria for selecting other complex traits.

Physiological maturity of grain crops is usually defined as the attainment of maximum seed dry weight. At physiological maturity, the crop has reached maximum possible GY, and kernels, which are no longer growing, merely lose water (Calderini et al., 2000). From there on, the crop is subject to an increasing risk of yield reductions due to damage from different sources (e.g., lodging, preharvest sprouting, hail, biological stresses). Therefore, knowledge of the time of physiological maturity could be critical under some circumstances.

Plant height is a major agronomic metric in wheat breeding because of its association with lodging, seedling growth capacity, and weed control (Donald and Hamblin, 1976). The uppermost internode of wheat plant is the peduncle, which consists of a lower unexposed (i.e., enclosed by the flag leaf sheath and thus heterotrophic part) and an upper exposed autotrophic part. During grain filling, the wheat peduncle acts as a transferable temporary store of water-soluble carbohydrates. It has been estimated that stem carbohydrate content constitutes 10 to 12% of final wheat yield under normal conditions, and more than 40% under drought and heat stress (Davidson and Chevalier, 1992). Therefore, peduncle length is very important for selecting HY under stress.

Other agronomic traits such as GVW, KW, and KD are also good initial indicators of seed quality (Allen et al., 1986;

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Abbreviations: DAP, days after planting; DR, drought resistance; DS, drought susceptibility; EPL, exposed peduncle length; ET, evapotranspiration; GPC, grain protein content; GVW, grain volume weight; GY, grain yield; HD, days to heading; HT, plant height; HY, high yield; KD, kernel diameter; KW, kernel weight; LY, low yield; PMD, days to physiological maturity.

Table 1. Spring wheat cultivars and advanced lines developed by Montana State University (MSU), University of Idaho (U of I), University of California Davis (UCD), Washington State University (WSU), Resource Seeds (RS), and WestBred (WB).

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

† HRS, hard red spring wheat; HWS, hard white spring wheat; SWS, soft white spring wheat.
‡ na, not available.

Grausgruber et al., 2005; Khan et al., 2010). Wheat seed-storage proteins represent an important source of food and energy, being also involved in the determination of bread-making quality (Cooke and Law, 1998). Genotypes with high GPC tend to exhibit better nutritive value and superior end-use quality (Peltonen, 1993; Nakano et al., 2008). Drought stress during grain filling often decreases starch deposition and increases protein concentration. Drought induces the expression of proteins that are directly or indirectly related to the stress and some functions have been assigned to some of the sequenced proteins (Ozturk et al., 2002). For improvement in yield, study of yield contributing components such as above mentioned agronomic traits as well as their relationships with GY is indispensable.

However, both genotype and the environment affect GY and yield-related agronomic traits. Effective agronomic traits selection and genotype selection across different water environments are obligatory. The objectives of this study were: (i) to evaluate eight target traits (HD, PMD, HT, EPL, GVW, GPC, KW, and KD) and GY across three irrigation regimes in 30 spring wheat genotypes for drought resistance; (ii) to investigate the relationships between target traits with GY and their contributions to GY; and (iii) to prioritize genotypes for good yielding properties across different irrigation regimes.

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 of 12 hard red, 9 soft white, 8 hard white, and 1 durum wheat (Table 1).

Experimental Conditions

Experiments were performed in two seasons of 2009 and 2010 at the research field of University of Idaho Aberdeen Research & Extension Center at Aberdeen, ID (42°57’36” N, 112°49’12” W, and elevation 1342 m). In this area, the annual precipitation is 203 to 279 mm, the mean annual air temperature is 7.2 to 8.3°C, and the frost-free period is 110 to 130 d.

The soil at the experimental site was a Declo loam (coarse-loamy, mixed, superactive, mesic Xeric Haplocalcids) with 0 to 2% slopes and pH of 8.1. Over the growing season, 15.8 and 10.6 g m^{-2} of N and P were applied based on a soil test before planting. Weed control in both seasons was conducted with an application of the herbicides Fluroxypyr ([(4-amino-3,5-dichloro-6-fluoro-2-pyridinyl)oxy]acetic acid) at 29.3 mg a.i. m^{-2}, and Pyrasulfotole ((5-hydroxy-1,3-dimethyl-1H-pyrazol-4-yl)[2-(methylsulfonyl)-4-(trifluoromethyl)phenyl]methanone) plus Bromoxynil octanoate (2,6-dibromo-4-cyanophenyl octanoate) plus Bromoxynil heptanoate (2,6-dibromo-4-cyanophenyl heptanoate) at rates of 2.8, 11.3 and 10.8 mg a.i. m^{-2}, respectively. Seeds were planted on 22 Apr. 2009 and 14 Apr. 2010, respectively. Planting depth was 3.8 cm and seeding rate was 300 seeds per m^2. In two seasons, wheat was planted in four-row plots (2009) and seven-row plots (2010), respectively, with the same plot size of 3.048 m long by 1.524 m wide.

In each one of the two seasons, the experiment was laid out in a split block experimental design, in three replicates, keeping drip irrigation treatments in the fixed main plots and genotypes in subplots. Genotypes were randomized within each irrigation main plot. Three irrigation regimes: T1 (non-irrigated, severe drought), T2 (50% ET irrigated, moderate drought), and T3 (100% ET irrigated, nonstress) were applied by aboveground drip system and determined based on the crop water use information from the Pacific Northwest Cooperative Agricultural Weather Network recommendations (U.S. Bureau of Reclamation, 2009–2010). Irrigation applied once a week, started before heading and during heading for 2009 and 2010 seasons, respectively, and ended at maturity. The amount of water applied per irrigation was determined by the amount of water that plants used and soil surface ET in 1 wk at corresponding growth stages. Irrigated plants received irrigation water and rainfall water, while non-irrigated plants only received rainfall water during the growing season (April–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 and 345 mm of irrigation water, respectively. During the

2010 growing season, all plots received 102 mm of rainfall and the T2 and T3 irrigated plots received an additional 248 and 452 mm of irrigation water, respectively.

The 2009 experiment received more rainfall during the growing season than 2010 experiment. To some extent, the 2010 experiment was affected by a cool spring, which delayed the HD and PMD of genotypes compared with the 2009 experiment.

Grain Yield Measurement

Plots were harvested using a Wintersteiger Classic small plot combine (1998 Wintersteiger Elite, Wintersteiger Seedmech, Salt Lake City, UT) equipped with a Harvest Master weigh system (HM-400, Juniper Systems, Logan, UT). Grain yield was determined from the grain weight with a moisture content of 12% of each plot for each genotype.

Evaluation of Agronomic Traits

Data was recorded for all plots included HD, PMD, HT, GVW, and GPC for 2009 and 2010 seasons. In 2010 season, EPL, KW, and KD were also recorded.

Days to heading was determined as the number of days from planting to the date when 50% of the heads in the plot were completely emerged. Days to physiological maturity was assessed as the number of days from planting to the date when 50% of the peduncles turned yellow. Plant height was measured at maturity in the middle rows, at two positions for each plot. Plant height was the average of two measurements made from the soil surface to the top of the spikes, excluding awns. Exposed peduncle length was the upper exposed autotrophic part of peduncle length and recorded as the average EPL of 10 randomly selected main stems at maturity.

Grain volume weight, that is, test weight was measured from a sample of cleaned grain by using a one-pint (5.5×10^{-4} m^3) container. Grain protein content was obtained on whole grain samples using a grain analyzer (Inframatic 9100; Perten Instruments Inc., Springfield, IL). Single kernel weight and KD were measured from a sample of cleaned grain with the single-kernel characteristics system (SKCS 4100; Perten Instruments Inc., Springfield, IL).

In this study, drought resistance was defined as the relative stable performance of evaluated traits across different irrigation regimes. Drought susceptibility was defined as the greatly-affected performance of evaluated traits across different irrigation regimes. Combining the GY and agronomic performance of each genotype under three irrigation regimes in 2009 and 2010 seasons, selected genotypes were classified into four types: HY, DR, drought susceptibility (DS), and low yield (LY). Selected DR genotypes were not affected or slightly affected by drought stress on target traits compared with other genotypes.

Statistical Analyses

Data were analyzed using SAS Version 9.1 (SAS Institute, Cary, NC) and SPSS 17.0 statistical software. Pearsons' correlation, single variable regression and stepwise regression (criteria: probability-of-F-to-enter $\leq$0.05, probability-of-F-to-remove $\geq$0.10) were conducted among evaluated traits. Analysis of variance for GY, HD, PMD, HT, EPL, GVW, GPC, KW, and KD were performed using the Proc GLM procedure (genotype subplots 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 treatments were determined using Fisher's protected LSD at probability = 0.05.

RESULTS

In both seasons, genotype × irrigation (G×I) interaction effects ($P < 0.01$) for HT, GVW and GPC were observed (Table 2). The G × I interaction effects ($P < 0.01$) were also observed for GY, HD, and KW in 2010 season. Differences ($P < 0.0001$) among the three irrigation regimes (T1, T2, and T3) in PMD were found for both seasons. In 2009 season, changes in GY and HD caused by irrigation regimes were also significant ($P < 0.0001$). In 2010 season, EPL and KD were greatly affected by irrigation regimes ($P < 0.0001$). In addition, differences ($P < 0.0001$) among wheat genotypes were observed for PMD in both seasons. Analysis of the variance of the 30 genotypes revealed differences among genotypes in GY ($P < 0.001$) and HD ($P < 0.0001$) for 2009 season, and in EPL ($P < 0.0001$) and KD ($P < 0.0001$) for 2010 season. There were year effects for GY, HD, PMD, GVW, and GPC, but no year effect for HT.

Table 2. The ANOVA for grain yield (GY), days to heading (HD), days to physiological maturity (PMD), plant height (HT), exposed peduncle length (EPL), grain volume weight (GVW), grain protein content (GPC), kernel weight (KW), and kernel diameter (KD) for 30 spring wheat genotypes.

Year	Traits	Degree of freedom	Mean square	F value	R^2	Interaction (G × I)†	Irrigation effect	Genotype effect	Year effect
2009	GY, g m^{-2}	92	27951.24	6.21***	0.87	ns‡	***	**	**
	HD, DAP§	92	16.03	30.43***	0.97	ns	***	***	**
	PMD, DAP	92	21.97	3.70***	0.8	ns	***	***	**
	HT, cm	92	123.08	9.85***	0.91	*	***	***	ns
	GVW, kg m^{-3}	92	2425.39	10.26***	0.85	**	***	***	*
	GPC, %	92	7.05	22.37***	0.92	**	***	***	*
2010	GY, g m^{-2}	95	161871.18	28.01***	0.94	**	***	***	
	HD, DAP	95	8.51	14.89***	0.89	*	***	***	
	PMD, DAP	95	108.65	42.58***	0.96	ns	***	***	
	HT, cm	95	324.94	14.25***	0.89	**	***	***	
	EPL, cm	95	71.81	10.30***	0.85	ns	***	***	
	KW, mg	95	180.07	30.86***	0.94	*	***	***	
	KD, mm	95	0.37	28.63***	0.94	ns	***	***	
	GVW, kg m^{-3}	95	1426.68	23.39***	0.93	**	***	***	
	GPC, %	95	13.21	27.62***	0.94	***	***	***	

* $P \leq 0.01$.
** $P \leq 0.001$.
*** $P \leq 0.0001$.
† Genotype × irrigation treatment interaction.
‡ ns, not significant at $P \leq 0.05$.
§ DAP = days after planting.

Table 3. The mean days to heading (HD), days to physiological maturity date (PMD), exposed peduncle length (EPL), kernel weight (KW), and kernel diameter (KD) of 30 spring wheat genotypes under three irrigation regimes: T1 (non-irrigated), T2 (50% evapotranspiration [ET] irrigated) and T3 (100% ET irrigated) in 2009 and 2010 seasons.

		T1		T2		T3		LSD
Year	Traits	Mean	SD	Mean	SD	Mean	SD	(0.05)
2009	HD, DAP†	60.8	2.96	61.3	2.77	62.3	2.62	0.83
	PMD, DAP	94.3	1.84	97.4	2.25	100.4	2.5	2.79
2010	HD, DAP	72.9	1.44	72.9	1.65	73.6	1.89	0.7
	PMD, DAP	98.5	1.84	108.8	1.83	112.3	1.62	1.49
	EPL, cm	3.9	2.25	9.6	2.75	13.4	3.46	2.46
	KW, mg	26.8	2.70	39.5	3.80	43.4	4.31	2.25
	KD, mm	2.1	0.16	2.7	0.18	2.8	0.19	0.11

† DAP = days after planting.

Days to Heading and Days to Physiological Maturity Responses to Drought

Days to heading did not differ much among irrigation regimes because irrigations occurred just before or during the heading stage, which slightly or not affected the HD of plants (Table 3). However, HD was different among the 30 genotypes ($P < 0.0001$), ranging from 57 to 67 d and from 70 to 76 d after sowing for 2009 and 2010 seasons, respectively. For both seasons, genotypes Agawam, Jerome, Cataldo, IDO694, Klasic and Snowcrest had earlier HD, while McNeal, Louise, Alpowa, WA8039, IDO686, IDO687, and Lolo had later HD.

Drought stress affected PMD among the 30 genotypes. The PMD under rainfed (T1) was earlier than that under well-watered regime (T3). The higher water stress level caused earlier physiological maturity (Table 3). Drought stress caused 6 and 14 d acceleration in the mean PMD of 30 genotypes under T1 compared with T3 in 2009 and 2010 seasons. Days to physiological maturity of genotypes in 2010 was several days later than that in 2009. High variations in PMD were observed among genotypes. Genotypes WB936, UI Winchester, Cataldo, IDO694, Klasic, and Snowcrest showed the earliest PMD, while IDO686 was the latest across all irrigation regimes. Genotypes Alpowa, Lolo, Alturas, and McNeal had late PMD under rainfed condition. The genotypes Agawam, Alpowa, and Snowcrest had relatively stable PMD across irrigation levels, while Hank was greatly influenced in PMD by drought stress.

Plant Height and Exposed Peduncle Length Responses to Drought

Plant height of 30 genotypes was different within each irrigation level. The HT of genotypes varied from 50.8 to 90.2 cm in 2009 season and 45.9 to 94.8 cm in 2010 season. Generally, drought stress caused a decrease in HT, up to 20 cm for the mean of genotypes in 2010 season (Fig. 1a). However, there were some exceptions that genotypes Agawam, Blanca Grande, Blanca Royale, Lolo, and IDO694 were taller under T2 than under T3 at least in one of the two seasons. Of these, Agawam had a consistent greater HT under T2 than T3 for both seasons.

In all irrigation regimes, genotypes Louise, IDO702, and Vida showed greater HT, while UC1600, WB936, Klasic,

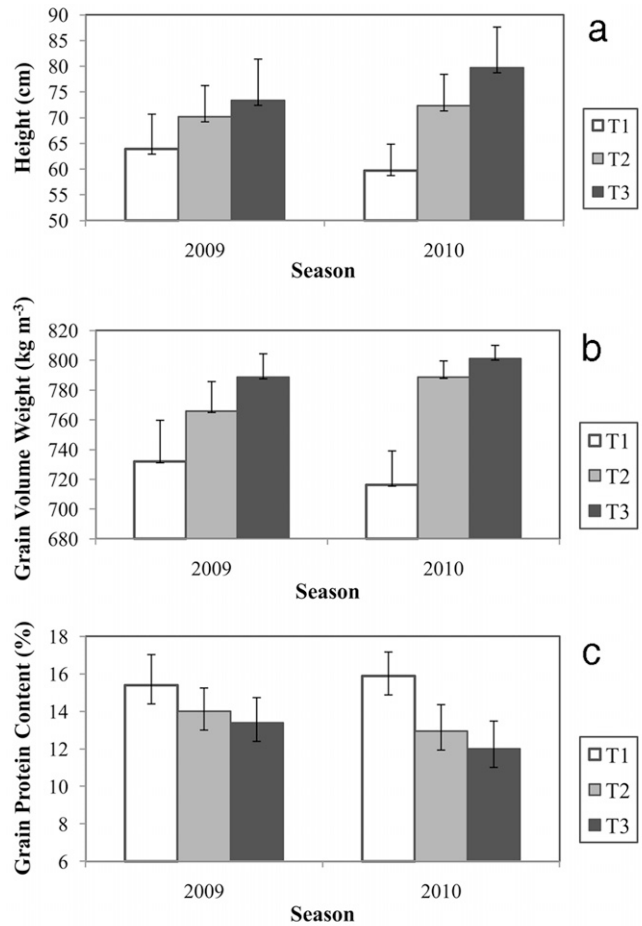

Fig. 1. The mean plant height (cm) ± SD, grain volume weight (kg m^{-3}) ± SD and grain protein content (%) ± SD of 30 spring wheat genotypes under three irrigation regimes: T1 (non-irrigated), T2 (50% evapotranspiration [ET] irrigated), and T3 (100% ET irrigated) in 2009 and 2010 seasons.

Blanca Royale, Hank, and Snowcrest showed shorter HT. Besides Louise and IDO702, Agawam and McNeal showed taller HT under rainfed also. The HT of genotypes IDO686, Conan, Alpowa, and Alzada were most significantly affected by water stress, whereas Klasic, IDO694, UC1600, and Agawam produced plants with similar HT across irrigation levels.

Drought stress decreased the mean EPL for 30 genotypes by approximately 10 cm (Table 3). Lassik, IDO694, IDO702, and Alzada had longer EPL, while WB936, UC1600, and Blanca Grande had shorter EPL in all irrigation regimes. The EPL of genotypes IDO599, WA8039, Louise, Vida, McNeal, and Alzada was shortened greatly by drought stress, while Hank, UC1600, Snowcrest, Blanca Grande, and Blanca Royale possessed relatively stable EPL across irrigation regimes.

Grain Yield Responses to Drought

In 2009 season, drought stress reduced GY significantly ($P < 0.0001$). The mean GY for all genotypes were 181.2, 319.5 and 429.1 g m^{-2} for T1, T2, and T3, respectively (Table 4). Within each of the irrigation regimes, differences ($P < 0.001$) in GY among 30 genotypes were also observed in 2009. The GY of genotypes ranged from 103.6 to 544.8 g m^{-2} across irrigation regimes. Whereas in 2010 season, GY was greatly affected by the interaction of drought stress and genotype ($P < 0.001$). For irrigated regimes (T2 and T3), the seven-row

Table 4. The grain yield (GY, g m^{-2}) of 30 spring wheat genotypes under three irrigation regimes: T1 (non-irrigated), T2 (50% evapotranspiration [ET] irrigated), and T3 (100% ET irrigated) in 2009 and 2010 seasons.

		GY 2009			GY 2010		
No.	Genotype	T1	T2	T3	T1	T2	T3
1	Choteau	177.6	226.1	406.2	132.0	457.0	673.0
2	Vida	178.1	403.0	544.8	187.9	557.8	727.9
3	McNeal	202.1	321.5	408.1	217.3	596.0	641.8
4	Alzada	152.6	325.3	399.2	210.6	514.6	721.6
5	Agawam	215.4	354.1	360.8	254.7	612.1	655.7
6	Conan	148.0	358.6	464.7	257.2	500.4	652.0
7	Hank	191.4	272.1	517.4	228.4	571.6	720.3
8	WB936	221.6	235.8	434.5	165.3	567.3	728.6
9	Lassik	162.6	362.0	456.8	262.8	615.5	792.1
10	UC1600	156.2	284.0	350.6	142.4	478.3	656.1
11	Louise	196.0	253.2	404.0	190.1	677.5	735.9
12	Alpowa	268.5	317.4	390.3	206.4	513.0	703.8
13	WA8039	337.7	349.3	435.4	177.3	584.8	817.8
14	UI Winchester	146.0	325.0	504.2	260.1	549.9	792.6
15	Jerome	189.9	350.8	344.6	142.8	521.2	807.5
16	IDO702	200.2	356.8	474.7	223.4	578.0	841.1
17	Jefferson	201.1	369.7	401.2	182.3	593.0	709.8
18	Alturas	200.1	327.3	497.0	213.1	624.3	822.5
19	Cataldo	137.3	248.1	359.7	159.6	502.3	727.0
20	Lolo	147.5	263.4	489.1	143.9	653.9	757.8
21	UI Lochsa	146.5	349.2	453.3	262.4	496.2	725.0
22	IDO694	176.1	276.0	367.3	261.6	668.3	781.2
23	IDO686	147.5	384.5	495.6	118.1	599.6	764.0
24	IDO687	145.0	293.7	383.9	237.5	595.4	770.1
25	IDO599	237.4	330.8	515.6	223.8	586.5	969.7
26	IDO644	218.5	288.2	478.4	130.9	634.8	793.5
27	Klasic	105.7	269.5	344.1	163.1	479.4	661.1
28	Snowcrest	103.6	282.8	325.8	190.2	517.2	618.7
29	Blanca Grande	156.2	412.9	430.5	212.7	588.2	736.5
30	Blanca Royale	168.4	393.7	435.8	204.3	676.5	665.0
Mean		181.2c†	319.5b	429.1a	198.7	570.4	739.0
LSD (0.05)		–	–	–	70.74	70.74	70.74

† Means followed by different letters are significantly ($P \leq 0.05$) different.

plots in 2010 produced higher GY than the four-row plots in 2009. For the non-irrigated regime (T1), GY did not increase much by the increase of row number in the same plot area. Among 30 genotypes, IDO599, Alturas, and IDO702 had greater GY under all irrigation regimes for both seasons, indicating that these genotypes possess better GY performance in both water limited and water sufficient environment. The GY of Klasic, Choteau, UC1600, Snowcrest, and Cataldo were less than other genotypes under all irrigation regimes.

In 2010 season, IDO686 and Lolo produced less GY under rainfed and relatively greater GY under irrigated regimes. Genotypes Agawam, McNeal, and Alpowa produced greater GY under rainfed, and intermediate GY than other genotypes under irrigated regimes. There were seven genotypes (Agawam, Alpowa, McNeal, IDO694, Louise, Jefferson, and Blanca Royale) that had better yield stability across irrigation regimes. Another four genotypes (Choteau, Cataldo, Lolo, and IDO686) had inferior yield stability, with two genotypes (Choteau and Cataldo) that had lower GY for all irrigation regimes.

Grain Volume Weight and Grain Protein Content Responses to Drought

The relationship between GVW and different water stress levels was significant, and there was sufficient evidence for lower GVW to be associated with higher stress levels (Fig. 1b). High variation in GVW among 30 genotypes was observed, which ranged from 716.4 to 801.1 kg m^{-3}. Across irrigation regimes, Agawam, IDO686, Alzada, and IDO694 had consistently bigger GVW, while Blanca Royale, Cataldo, UC1600, and IDO644 had smaller GVW. The genotype IDO599 had bigger GVW under non-irrigated and intermediate GVW under irrigated regimes. Across irrigation regimes, the GVW of Agawam, Alzada, and Alpowa differed relatively less than other genotypes, while the GVW of IDO702, Blanca Grande, IDO644, and Louise were more responsive to drought stress.

The effect of different drought stress levels was clear on GPC of all 30 genotypes and the lack of water caused an increase in GPC (Fig. 1c). Genotypes McNeal, Choteau, Vida, Conan, Hank, and WB936 showed higher GPC in all irrigation treatments, while IDO686, IDO599, IDO687, Alturas, WA 8039, IDO644, Louise, and Alzada showed lower GPC. Relatively stable GPC across irrigation treatments were observed in genotypes Agawam, Choteau, and UI Lochsa, whereas GPC for Blanca Grande, UC1600, Louise, and UI Winchester were affected greatly by drought stress.

Kernel Weight and Kernel Diameter Responses to Drought

The interaction of drought stress and genotype significantly ($P < 0.01$) influenced KW. The KW varied from 22.7 to 52.7 mg for genotypes across irrigation regimes. Drought stress resulted in decrease in KD (Table 3). Significant variations ($P < 0.0001$) were observed in KD across genotypes, the KD varied from 1.74 to 3.13 mm. In all irrigation regimes, genotypes Alzada, Agawam, Hank, and WB936 had bigger KW and KD, while Choteau, IDO702, and Blanca Royale had smaller KW and KD. Besides Alzada, Agawam, Hank, Alpowa, and UC1600 had bigger KW and KD as well under T1. The genotypes Conan, Lassik, Alpowa, Alturas, and IDO599 had relatively stable KW and KD across different irrigation regimes, while KW and KD of Klasic, Lolo, Jerome, Louise, and WB936 were more responsive to drought stress.

Correlations and Regression

Evaluation of all agronomic traits except HD in 2010 was correlated with GY ($r > 0.3$, $P < 0.001$) for both years (Tables 5 and 6). Negative correlation of GY was observed with GPC, while GY was positively correlated with all other evaluated traits (HD, PMD, HT, EPL, KW, KD, and GVW) for both seasons. The greatest correlation occurred between PMD and GY ($r = 0.87$ and 0.95, $P < 0.001$) for 2009 and 2010 seasons, respectively. Days to heading and GY were correlated in 2009, but not in 2010, the correlation was markedly weaker than that between other agronomic traits and GY. Among evaluated agronomic traits, the correlations were always significant, except for the cases that correlation of HD with GVW, EPL, KW, and KD. Grain protein content was always negatively associated with other traits, while in other cases, the correlation coefficients were all positive.

The linear regressions of GY on PMD, HT, GVW, and GPC were significant at $P < 0.0001$, which explained 30 to 90% of the total phenotypic variation of GY, individually. Results from stepwise regression indicated that the combination of PMD, HT, and GVW explained 81.8% of the total phenotypic variation of GY in 2009; and the combination of PMD, HT, and GPC explained 92.7% of the total phenotypic variation of GY in 2010, respectively (Table 7).

Table 5. Pearsons' correlation coefficients between grain yield (GY), days to heading (HD), days to physiological maturity (PMD), plant height (HT), grain volume weight (GVW), and grain protein content (GPC) in 30 genotypes across three irrigation regimes: T1 (non-irrigated), T2 (50% evapotranspiration [ET] irrigated) and T3 (100% ET irrigated) for the 2009 growing season.

	GY	HD	PMD	HT	GVW
HD	0.385***				
PMD	0.869***	0.552***			
HT	0.665***	0.658***	0.671***		
GVW	0.697***	ns†	0.606***	0.347***	
GPC	–0.552***	–0.239*	–0.465***	–0.437***	–0.567***

* $P \leq 0.05$.
*** $P \leq 0.001$.
† ns, not significant at $P \leq 0.05$.

Summary of 30 Wheat Genotypes

Superior agronomic performance contributed to high GY while inferior ones tended to result in low GY (Table 8). The stability of agronomic traits and GY for selected genotypes is reported in Table 9. On the basis of agronomic and yield stability across different irrigation regimes, selected genotypes were classified into drought resistance or drought susceptibility on target traits. Comparison of the mean GY of genotypes in each of the four types and the mean GY of 30 genotypes under three irrigation regimes based on 2-yr data is reported in Fig. 2.

High-yield type had three genotypes IDO599, Alturas, and IDO702 that exhibited better agronomic performance and produced greater GY under all irrigation regimes for both growing seasons. These genotypes possessed agronomic and GY stability across different water conditions. Drought-susceptibility type (DS) had two genotypes IDO686 and Lolo that produced less GY under rainfed and greater GY under irrigated regimes than other genotypes in both growing seasons. The two genotypes showed drought susceptibility in GY and at least one agronomic trait as well. Drought-resistance type (DR) contained three genotypes Agawam, McNeal, and Alpowa that produced higher GY under non-irrigated regime, and intermediate GY under irrigated regimes. These genotypes showed drought resistance in GY and one to several agronomic

Table 6. Pearsons' correlation coefficients between grain yield (GY), days to heading (HD), days to physiological maturity (PMD), plant height (HT), exposed peduncle length (EPL), kernel weight (KW), kernel diameter (KD), grain volume weight (GVW), and grain protein content (GPC) in 30 genotypes across three irrigation regimes: T1 (non-irrigated), T2 (50% evapotranspiration [ET] irrigated) and T3 (100% ET irrigated) for the 2010 growing season.

	GY	HD	PMD	HT	EPL	KW	KD	GVW
HD	ns†							
PMD	0.950***	0.326**						
HT	0.829***	0.208*	0.786***					
EPL	0.833***	ns	0.776***	0.909***				
KW	0.845***	ns	0.852***	0.719***	0.744***			
KD	0.821***	ns	0.833***	0.706***	0.758***	0.974***		
GVW	0.906***	ns	0.923***	0.759***	0.774***	0.891***	0.881***	
GPC	–0.821***	–0.245*	–0.806***	–0.653***	–0.620***	–0.678***	–0.577***	–0.797***

* $P \leq 0.05$.
** $P \leq 0.01$.
*** $P \leq 0.001$.
† ns, not significant at $P \leq 0.05$.

Table 7. Single variable and stepwise regression between grain yield (GY, Y) and agronomic traits of days to physiological maturity (PMD), plant height (HT), grain volume weight (GVW), and grain protein content (GPC).

Year	Trait	Regression equation	R^2	P
2009	PMD, X_1	$Y = 31.413\ X_1 - 2715.615$	0.755	<0.0001
	HT, X_2	$Y = 10.090\ X_2 - 355.244$	0.442	<0.0001
	GVW, X_3	$Y = 2.661\ X_3 - 1685.381$	0.486	<0.0001
	GPC, X_4	$Y = -40.835\ X_4 + 926.008$	0.305	<0.0001
	PMD, HT, and GVW	$Y = 20.753\ X_1 + 2.734\ X_2 + 1.095\ X_3 - 2701.770$	0.818	<0.0001
2010	PMD, X_1	$Y = 36.577\ X_1 - 3393.454$	0.902	<0.0001
	HT, X_2	$Y = 18.710\ X_2 - 818.229$	0.687	<0.0001
	GPC, X_3	$Y = -89.998\ X_4 + 1727.458$	0.673	<0.0001
	GVW, X_4	$Y = 9.599\ X_3 - 3560.310$	0.82	<0.0001
	PMD, HT, and GPC	$Y = 25.704\ X_1 + 4.700\ X_2 - 16.134\ X_3 - 2347.519$	0.927	<0.0001

traits. Low-yield type (LY) represented the group of five genotypes (Klasic, Choteau, UC1600, Snowcrest, and Cataldo) that produced less GY than other genotypes under all three irrigation regimes. Of these LY genotypes, Choteau and Cataldo also showed drought susceptibility in GY.

DISCUSSION

Grain yield is frequently used in crops such as wheat as the main criteria for drought resistance. Generally, selection for drought resistance typically involves evaluating genotypes for either HY potential or stable performance under varying degrees of water stress (Ahmad et al., 2003). Grain yield is a product of several contributing factors and can be estimated on the basis of performance of various components. In our study, DR was determined by GY and agronomic observations, which referred to the ability of persisting relatively stable performance in evaluated traits across different water conditions: severe drought (T1), moderate drought (T2), and well-watered (T3).

The most widely used criteria for selecting HY performance are mean yield, mean productivity (average yield performance under stress and nonstress conditions) and relative yield performance in drought-stressed and moist environments. However, in fact, mean yield could not reflect the specific yield changes across different water conditions. For example, in the current study, there were three genotypes that showed similar mean yield across irrigation regimes (Lolo, IDO687, Agawam). However, the specific performances of GY under each of the three irrigation regimes (T1, T2, and T3) were diverse. Compared with other genotypes, Lolo produced relatively high yield under T3, IDO687 produced intermediate yield across three irrigation regimes, while Agawam produced relatively HY under T1. Therefore, characterizing GY of genotypes under all different water conditions is necessary.

Some genotypes (Agawam, McNeal, and Alpowa) only produced higher GY under rainfed (T1), while some other genotypes (IDO686 and Lolo) only produced higher GY under well-watered condition (T3) than other genotypes. Our results indicate that the high GY of genotypes in sufficiently irrigated conditions is not necessarily related to high GY under drought stress, and vice versa. However, GY is a product of several contributing factors and can be estimated on the basis of performance of various components. In other words, wheat genotypes must have the best combination of several agronomic traits for obtaining the highest yield potential. Selection based on above yield components would result in yield increases.

Days to heading and PMD of genotypes in 2010 was several days later than that in 2009 due to the cool spring of 2010. Exposed peduncle length was highly correlated with HT ($r = 0.91$, $P < 0.001$), considering that measuring HT is much easier than measuring EPL, our study suggests that choosing to measure HT could represent EPL to some extent. Similarly, KD was highly correlated with KW ($r = 0.97$, $P < 0.001$), which indicates that recording KW may also represent KD. Among evaluated traits, PMD was associated with GY with the highest coefficients, which could be the superior component for estimating and improving GY.

The overall correlation coefficients between evaluated agronomic traits and GY were all significant except HD. In both growing seasons, negative correlation of GY was observed with GPC, while GY was positively correlated with all other

Table 8. Summary of the performance of days to heading (HD), days to physiological maturity (PMD), plant height (HT), exposed peduncle length (EPL), grain volume weight (GVW), grain protein content (GPC), kernel weight (KW), kernel diameter (KD), and grain yield (GY) for 30 spring wheat genotypes across three irrigation regimes: T1 (non-irrigated), T2 (50% evapotranspiration [ET] irrigated) and T3 (100% ET irrigated) in both 2009 and 2010 seasons.

No.	Genotype	HD†	PMD†	HT‡	EPL§	GVW¶	KW¶	KD#	GPC¶	GY¶
1	Choteau	††					L		H	L
2	Vida			T					H	
3	McNeal	L							H	
4	Alzada				L	H	H	B	L	
5	Agawam	E				H	H	B		
6	Conan								H	
7	Hank			S			H	B	H	
8	WB936		E	S	S		H	B	H	
9	Lassik				L					
10	UC1600			S	S	L				L
11	Louise	L		T					L	
12	Alpowa	L								
13	WA8039	L							L	
14	UI Winchester		E							
15	Jerome	E								
16	IDO702			T			L			H
17	Jefferson									
18	Alturas							S	L	H
19	Cataldo	E	E			L		S		L
20	Lolo	L								
21	UI Lochsa									
22	IDO694	E	E		L	H				
23	IDO686	L	L			H		S	L	
24	IDO687	L						S	L	
25	IDO599								L	H
26	IDO644					L		S	L	
27	Klasic	E	E	S						L
28	Snowcrest	E	E	S						L
29	Blanca Grande				S					
30	Blanca Royale			S		L	L	S		

† E, early; L, late.
‡ T, tall; S, short.
§ L, long; S, short.
¶ H, high; L, low.
# B, big; S, small.
†† Blank cell, intermediate performance of target trait.

Table 9. Evaluation of the 30 spring wheat genotypes on agronomic traits (days to physiological maturity [PMD], plant height [HT], exposed peduncle length [EPL], grain volume weight [GVW], kernel weight [KW], and kernel diameter [KD]) and grain yield (GY) respond to drought stress in both 2009 and 2010 seasons.

No.	Genotype	PMD	HT	EPL	GVW	KW	KD	GY	Type†
1	Choteau	‡						s§	LY
2	Vida			s					
3	McNeal	g¶	g	s				r#	DR
4	Alzada		s	s	r, g	g	g		
5	Agawam	r	r, g		r, g	g	g	r, g	DR
6	Conan		s			r	r, g		
7	Hank	s		r		g			
8	WB936					s	s		
9	Lassik			g		r	r		
10	UC1600		r	r		g	r		LY
11	Louise		g	s	s,	s		r	
12	Alpowa	r, g	s		r	r, g		r	DR
13	WA8039			s			s		
14	UI Winchester								
15	Jerome					s	s		
16	IDO702		g	g	s				HY
17	Jefferson							r	
18	Alturas	g				r	r		HY
19	Cataldo							s	LY
20	Lolo	g				s	s	s	DS
21	UI Lochsa			g					
22	IDO694		r	g				r	
23	IDO686		s		g		r	s	DS
24	IDO687								
25	IDO599			s	g	r		g	HY
26	IDO644				s	s			
27	Klasic		r				s		LY
28	Snowcrest	r		r, g					
29	Blanca Grande			r	s				
30	Blanca Royale			r				r	

† HY, high yield genotype; LY, low yield genotype; DR, drought resistance genotype; DS, drought susceptibility genotype.
‡ Blank cell, the genotype showed neither drought resistance nor drought susceptibility in corresponding trait.
§ s, susceptible to drought stress.
¶ g, good performance under drought condition in corresponding trait.
# r, resistant to drought stress.

evaluated traits (PMD, HT, EPL, KW, KD, and GVW), indicating that selection for one of these traits can improve GY. Similar results were reported by previous studies (Law et al., 1978; Aycicek and Yildirim, 2006; Jamali and Ali, 2008; Khan et al., 2010). Stepwise regression identified the combination of PMD, HT, and GVW/GPC explained 81.8 and 92.7% of the total phenotypic variation of GY in 2009 and 2010. Results suggest that a combination of PMD, HT, and GVW/GPC could be used as an indicator for selecting high GY.

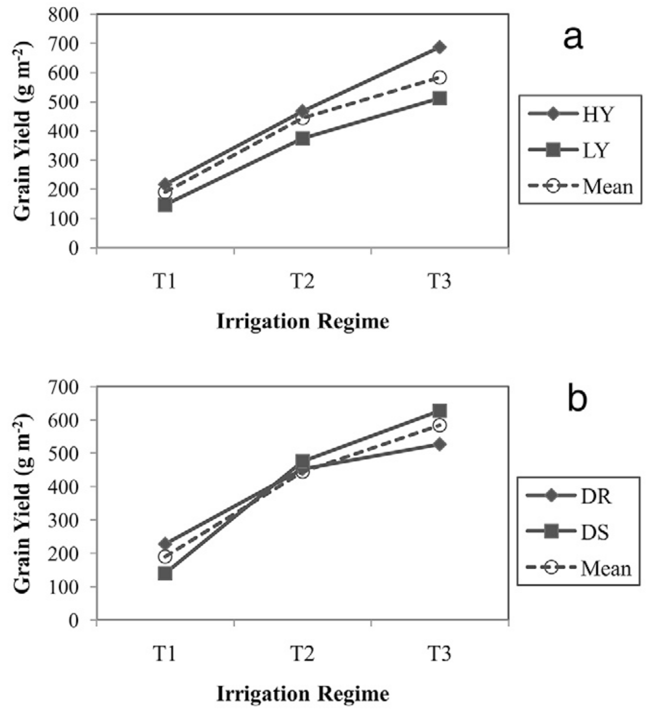

Fig. 2. The comparison of the mean grain yield (g m^{-2}) of 30 spring wheat genotypes (Mean) and the mean grain yield of genotypes in each of four types [high-yield (HY), low-yield (LY), drought-resistance (DR) and drought-susceptibility (DS)] under three irrigation regimes: T1 (non-irrigated), T2 (50% evapotranspiration [ET] irrigated), and T3 (100% ET irrigated) based on data from 2009 and 2010 seasons.

However, there were also conflicting results reported in previous studies (Cuthbert et al., 2008; Khan et al., 2010). Cuthbert et al. (2008) indicated the correlations between GY and HD and PMD were negative in a spring wheat doubled haploid (DH) population. The different result may be due to different plant materials in different studies. In the study of Khan et al. (2010), negative correlation of GY was observed with HT, peduncle length, and 1000-grain weight in 14 wheat recombinant inbred lines (RILs) and two varieties under rainfed condition. This may be due to lodging in taller plants in their studies. In our study, no lodging occurred for both growing seasons even for the taller genotypes. In addition, Fischer and Quail (1990) and Richards (1992) have reported that there is an optimum HT (70–100 cm) at which maximum GY could be achieved. Plant height of genotypes in our study varied from 45.9 to 94.8 cm among irrigation treatments, which was below the upper limit of 100 cm.

Results from this study indicated that genotypes that showed earlier heading, showed earlier physiological maturity as well; taller genotypes showed longer EPL; genotypes with bigger KW tend to possess bigger KD, and vice versa. The height of plant affects photosynthesis, which could result in the change of GY (Jamali and Ali, 2008). In our study, drought stress shortened the HT for most genotypes. Similarly, Inamullah et al. (1999) and Mirbahar et al. (2009) also observed that HT in wheat varieties reduced significantly under water stress when it was compared with irrigated. Almost all genotypes had increased HT under high irrigated treatment during both seasons. However, there were two exceptions, genotypes Agawam and Blanca Royale showed close or even taller HT under T2 than that under T3 in both seasons.

Genotypes that produced high GY tended to possess low GPC and vice versa, which can be limited factors for wheat breeding. Efforts have been attempted to alter the negative relationship between GY and grain N concentration in wheat, such as changing the rate and timing of N application during growing season, but minimal success has been achieved (Peltonen, 1993; Nakano et al., 2008). Our results suggest that it may be possible and easier to select genotypes with both high GY and relatively high GPC.

In the three HY genotypes (IDO599, IDO702, and Alturas), IDO599 and Alturas showed low GPC while IDO702 showed intermediate. In the LY genotypes Klasic, Choteau, UC1600, Snowcrest, and Cataldo, only Choteau showed high GPC. In the three DR genotypes (Agawam, McNeal, and Alpowa) identified from this study, McNeal showed high GPC concurrently. Therefore, in the 30 spring wheat genotypes, IDO702 could be the recommended genotype which possessed both high GY and relative high GPC across different water conditions, and McNeal may be an ideal genotype for planting in water deficit environment which possessed both higher yield and protein.

CONCLUSIONS

Exposure of plants to drought led to noticeable earlier PMD, shorter HT and EPL, smaller GVW, higher GPC, smaller KW and KD, and lower GY. The correlation coefficients between evaluated agronomic traits and GY were all significant except HD. In both seasons, GY was negatively correlated with GPC, and was positively correlated with other traits (PMD, HT, EPL, KW, KD, and GVW). Stepwise regression identified that the combination of PMD, HT, and GVW explained 81.8% of the total phenotypic variation of GY in 2009; the combination of PMD, HT, and GPC explained 92.7% of the total phenotypic variation of GY in 2010, respectively. Our results indicate that selection for agronomic traits would improve GY.

Selected genotypes were classified into four types based on their agronomic and yield performance across three irrigation regimes. High-yield genotypes IDO599, Alturas, and IDO702 exhibited better agronomic performance and produced greater GY under all irrigation regimes. These genotypes could be recommended for both water limited and sufficient environments, and appeared to be a promising parent for wheat breeding programs. Drought-susceptibility genotypes IDO686 and Lolo produced less GY under rainfed and greater GY under irrigated treatments than other genotypes. The two genotypes showed drought susceptibility in GY and at least one agronomic trait as well, and would be recommended for moist environment. Drought-resistance genotypes Agawam, McNeal, and Alpowa that produced higher GY under rainfed and intermediate GY under irrigated treatments. These genotypes had drought resistance in GY and one to several agronomic traits. The DR genotypes showed drought resistance and can be recommended for water deficit environment. Low-yield genotypes (Klasic, Choteau, UC1600, Snowcrest, and Cataldo) produced less GY than other genotypes under all three irrigation regimes. Of these LY genotypes, Choteau and Cataldo also had drought susceptibility in GY, which could be replaced by other genotypes in the future.

The high GY of genotypes could be due to late HD, late PMD, tall HT, long EPL, high GVW, high KW, or big KD, or the combination of one or several of them, and vice versa. Preliminary results indicate that GY could be estimated on the basis of performance of agronomic components, and selecting proper type of genotypes for different water environments may be important for improving yield productivity. However, breeding wheat for drought resistance is a difficult, long-term project, so further tests need to be conducted for other drought confirming characteristics.

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