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Modeling biomass allocation and grain yield in bread and durum wheat under abiotic stress

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Abstract

Differences between two wheat genotypes [*Triticum aestivum* and *T. durum* species (A and D, respectively)] in dry matter (DM) partitioning into stems, leaves and spikes, in response to multiple abiotic stresses were quantified during two years of contrasting rainfall regimes. The impact of normal (N, ~1830 accumulated growing degree days, GDD), and late (L, ~1750 GDD) planting, in combination with normal (450 live seed m^{-2}) or large (25% above normal) population density on 1000-kernel weight (TKWT), kernels m^{-2} (K m^{-2}), and grain yield (GY, Mg ha^{-1}) was quantified. Years, species, stress treatments, and their interactions explained 67, 73, and 75% of total variance in DM partitioned into stem (R-Stem), leaves (R-Leaves), and spike (R-Spike), respectively, 15 days after anthesis; and 50, 78 and 51% of variance in kernels m^{-2}, TKWT and GY, respectively, at physiological maturity. The two sets of variables were positively correlated (canonical r=0.90; p<0.0001); however, simple correlation coefficients between individual variables of both sets shifted in magnitude and significance in response to stress treatments. Partial least squares regression models were developed for each wheat species to quantify its response to stress.

Key words: Abiotic stress; Dry matter partitioning; models; wheat.

Introduction

Crop response to stress is dependent on numerous traits many of which are constitutive and expressed irrespective of availability of environmental resources, but such constitutive traits may be modified by stress (Craufurd and Wheeler, 1999). Stress caused by single or multiple factors suppresses leaf initiation and expansion, tillering, and leaf area index and, consequently reduces dry matter accumulation and grain yield (Kumar et al., 2006). Global climate change is causing yield reduction of cereals, including wheat (Gregory et al., 2005; Kotchi, 2007). On average, wheat yields were reduced by 5.4% for each °C rise in temperature, and the climate-driven yield change during the last 40 years was about -88.2 kg ha^{-1} (Gregory et al., 2005). The spatial variation in the effect of climate change was an explicit component of the study on potential yields of rainfed cereal crops (Fischer et al., 2002). The results of that study indicate that many parts of the world, including the western edge of the USA prairies where climatic extremes are predicted to increase in frequency and intensity, would suffer yield losses. Nevertheless, continued technological developments are anticipated to facilitate the adaptation of crops to changing environments (Kotchi, 2007).

Wheat productivity depends not only on dry matter accumulation, but also on its effective partitioning to the kernel; this is a key to yield stability under stress (Kumar et al., 2006). Dry matter accumulation in wheat stems, particularly water-soluble carbohydrates, may be reduced due to stress; however, water soluble carbohydrates may account for up to 60% of dry matter accumulation in the wheat kernel as a result of improved mobilization efficiency (Ehdaie et al., 2006). An improved partitioning of dry matter to the developing kernels will lead to increased number of kernels per unit area and increased kernel weight, the two most important yield components in wheat (Arduini et al., 2006). Wheat population density, although has no effect on phenology under no stress, may influence the use of environmental resources by changing the relative importance of inter- and intra-plant competition for environmental resources such as soil water, nutrients and light (Arduini et al., 2006); whereas, stress caused by short growing season may impact phenology, harvest index, and consequently potential grain yield (Craufurd and Wheeler, 1999).

Yield stability may become more important than large yields under stress conditions (Parry et al., 2005); therefore, production traits are more important than survival traits for wheat under stress, and the most important are traits that may stabilize, if not increase, grain yield. Notwithstanding the complex nature of stress tolerance in crop plants, an improved understanding of the mechanisms behind high stable yield under stress is needed (Chandrasekar et al., 2000; Villegas et al., 2007), and a more fundamental under-standing of genotype x environment interactions is necessary to determine the potential opportunities and disadvantages of specific traits, such as dry matter partitioning into stem, leaves and spike of wheat. A field experiment was conducted during two years of contrasting rainfall regimes to (1) quantify the magnitude of single and multiple plant and crop response indicators of two durum and bread wheat genotypes to stress and (2) model the impact of dry matter partitioning into stem, leaves and spike on number of kernels m^{-2} (K m^{-2}), thousand kernel weight (TKWT), and grain yield (GY) under stress and non-stress conditions.

Materials and Methods

Experimental setup

A factorial experiment in a split-plot design with three replicates was implemented on a piece of land uniformly cultivated for the three previous years and located at the Swan Lake Research Farm (45º 41′ N, 95º 48′ W, and elevation 370 m) near Morris, MN, USA. Annual precipitation in this region averages 645 mm and average monthly temperatures ranges from -13.1 ºC in January to 21.7 ºC in July (NOAA, 2002). Average wheat growing season growing-degree days (GDD) at the site is 1800 ºC (base 0 ºC for wheat). A summary of the environmental variables during 2006 and 2007 are presented in Table 1. The major soil series identified(USDA-SCS, 1971) within the experimental site was Barnes loam (fine-loamy, mixed, superactive frigid Calcic Haplotoll). Two levels each of three factors (wheat species, length of the growing season, and inter-crop competition for environmental resources) were evaluated for two years (2006-2007); therefore, there were eight species-stress treatment combinations, and will be referred to as "stress treatments." The same wheat species and factor levels were present on the same plots for both years in order to create stress progression. The experimental layout was comprised of two levels of wheat species (the bread wheat variety "Alsen" and the durum wheat variety "Lebsock") in vertical plots, two levels of planting date (normal planting date, N, and delayed planting date, L) in horizontal plots, and two levels of population density (normal sowing rate of 450 live seed m^{-2} and 25% above normal sowing rate) in intersection plots. Therefore, in addition to the normal planting date and seeding rate (N), there were three stress treatments: normal sowing date and a seeding rate 25% above normal (N25), late sowing date (L), and late sowing date and a seeding rate 25% above normal (L25). Permanent geo-referenced sampling sites were established within individual plots where plant data were sampled and recorded. Plots consisted of six rows each, 6 m in length and 20 cm between rows. Planting dates of the N and L stress treatments during 2006 were April 18 and May 5, respectively; and the respective harvesting dates were July 28 (1828 GDD) and July 31 (1741 GDD). During 2007, planting dates of the N and L stress treatments were April 27 and May 14, respectively; and the respective harvesting dates were July 30 (1847 GDD) and August 8 (1765 GDD). All management practices (tillage, fertilizers, and weed control) were performed according to recommendations for the experimental site and soil series.

Sampling and measurements

For the purpose of this study, above-ground biomass was sampled (50 cm length x three central adjacent rows) each year and replicate at the 69 Zadoks scale, i.e., about 15 days after completion of anthesis, and at the 90 Zadoks scale, i.e., at physiological maturity (Zadoks et al., 1974) from permanent geo-referenced sampling sites. Plants sampled after the completion of anthesis were separated into stems, leaves and spikes, then dried in a forced-air oven at 60 °C for 48 hrs and weighed. Seed weight, number of kernels m^{-2}, and 1000-kernel weight at physiological maturity were estimated on three sub-samples from each sampling site and averaged for statistical analysis. Data is reported as (1) dry matter ratio partitioned into stem (R-Stem), leaves (R-Leaves), and spike (R-Spike), and (2) number of kernels m^{-2} (K m^{-2}), 1000-kernel weight (TKWT, g), and grain yield (GY, Mg ha^{-1}).

Statistical analyses

Data on R-Stem, R-Leaves, and R-Spike of each wheat species, grain yield and yield components in response to stress treatments during two cropping seasons were tested for homogeneity of variances, then subjected to analysis of variance (ANOVA) and mean separation (Tukey HSD, $p<0.05$). Data on R-Leaves were square root-transformed (range 8-30%) before statistical analysis to meet ANOVA assumptions, then back transformed for reporting. Principal components analysis, a dimension reduction and perceptual mapping statistical procedure[21] was employed to reduce the dimensionality of a matrix based on all factors (years, wheat species, stress treatments) and

Table 1. Average monthly air temperature, and total monthly growing degree days, precipitation (mm-equivalent snowfall and rainfall), and pan evaporation for 2006 and 2007 growing seasons at the Swan Lake Research Farm near Morris, MN.

Month	Air temperature		GDDs		Precipitation				Pan evaporation	
	°C maximum		°C		mm-equivalent				mm	
	2006	2007	2006	2007	2005/6 Snow	2006 Rain	2006/7 Snow	2007 Rain	2006	2007
April	15.3	11.2	192	156		53		48	86	66
May	20.5	22.8	341	380		47		75	163	200
June	26.0	26.4	488	501		28		84	189	180
July	30.0	28.3	597	567		27		10	216	161
August	27.0	26.4	524	488		35		58	156	127
Growing season GDD			1828	1847						
Sub total					1050	190	500	275		
Total			2142	2092	2140		775		810	734

variables (R-Stem, R-Leaves, R-Spike, GY, K m^{-2}, and TKWT) measured in this experiment. Canonical discriminant analysis was used to quantify multivariate relationships between stress treatments, based on their R-Stem, R-Leaves, R-Spike, K m^{-2}, TKWT, and GY. Canonical discriminant analysis (CDA), a combination of principal components and canonical correlation analyses, was used on the raw data to derive canonical variables that contain the largest possible multiple correlation with each stress treatment, and that best summarize variation between them. The differentiation of stress treatments was based on the correlation among the dependent variables (i.e., R-Stem, R-Leaves, R-Spike, GY, K m^{-2}, and TKWT) with the independent variable (i.e., stress treatments). The R^2 values in CDA were used to identify the traits that most significantly contributed to the discrimination among stress treatments. Total variance in each dependent variable, explained by differences among years, among wheat species, among stress treatments, and their 2-way and 3-way interaction using the restricted maximum likelihood (REML) method in a general linear model (GLM), was calculated and tested for significance. A whole model R^2 was calculated for each dependent variable and was partitioned according to its sources of variation (CAMO ASA, 2007; StatSoft Inc., 2008).

Modeling dry matter partitioning, grain yield and its components

The Partial Least Squares (PLS) regression option in the Non-linear Iterative Partial Least Squares (NIPALS) algorithm was used on the raw data to construct a set of components that accounts for as much variation as possible while modeling the R-Stem, R-Leaves, R-Spike, GY, K m^{-2}, and TKWT data. Comparison of the regression lines calculated for 2006 and 2007 verified that both the slope and intercept values were significantly different ($LSD_{0.05}$) for the two years. The PLS1 option in the Unscrambler software (CAMO ASA, 2007) was used for creating models to predict each of R-Stem, R-Leaves, and R-Spike as a function of plant dry matter in each stress treatment and to predict K m^{-2}, TKWT and GY as a function of R-Stem, R-Leaves, and R-Spike in each year and for each stress treatment. The models developed in this analysis were cross-validated by successively leaving out data one at a time and a model was built using the remaining data points, then the model created was used to predict the dependent variable. The root mean squares error (RMSE) was used to compare the prediction and validation errors of different PLS regression models and was based on the differences between the predicted and actual values, after all the samples have been held-out once.

Results

Environmental variables during the 2006 and 2007 growing seasons were different in that crops received less rainfall and the pan evaporation was larger during 2006 (Table 1). Total precipitation (i.e., mm-equivalent snowfall and rainfall) from November 2005 to August 2006 was twice as large (1050 mm) as total precipitation from November 2006 to August 2007 (500 mm). However; total rainfall during the growing season of 2006 and 2007 was 29% and 43% of the long-term average of 645 mm, respectively. Total growing degree days during both growing seasons were almost the same, with small variation among months and years.

Interrelationships among factors and variables

When the data set was subjected to principal components analysis, the first and second PCs explained 56 and 32%, respectively, of total variance in all factors and variables included in the experiment (Fig. 1). The dry year (2007) was plotted with large positive loading on PC2 and was

Table 2. Percent variance explained by years, wheat species, stress treatments and their 2-way and 3-way interactions on percent dry matter partitioned in stem, leaves and spike of two wheat species and their yield and yield components.

Factors			R- Stem	R- Leaves	R- Spike	Kernels m^{-2}	TKWT mg	Grain yield Mg ha^{-1}
			--------Percent variance (significance level, p<0.05)------					
Year			0.0	0.0	0.0	38.2*†	0.0	39.4*
	Species		0.0	15.6*	60.2*	20.2*	7.6*	13.0*
		Treatment	0.0	0.0	0.0	0.0	10.6*	3.6
Year x	Species		16.8*	34.8*	11.5*	0.0	36.1*	2.2
Year x		Treatment	2.7	4.6	3.0	3.8	10.5*	0.0
	Species x	Treatment	33.4*	10.8*	12.1*	5.2*	0.0	0.0
Year x	Species x	Treatment	21.4*	17.7*	0.0	0.0	18.9*	5.7*
Adjusted R^2			0.67*	0.73*	0.75*	0.50*	0.78*	0.51*

† *, significant, Tukey HSD, p<0.05.

associated with durum wheat, TKWT and R-Spike; whereas 2006 was plotted with large negative loading on PC2 and was associated with R-Stem, R-Leaves, GY, and K m^{-2}. Loadings of the bread and durum wheats on PC1 reflect their contrasting performance under stress treatments. The bread wheat had larger R-Stem and R-Leaves, and produced larger GY as a result of larger K m^{-2}; whereas the durum wheat had larger R-Spike, and larger TKWT, even during the dry year. The non-stress (N) and three stress treatments (N25, L and L25) had very small loadings (range from -0.2 to +0.2) on both PCs; therefore, contributed very little by themselves to the explained variance in the whole experiment.

Sources of variation and variance components

Percent dry matter partitioned into stem, leaves and spike (R-Stem, R-Leaves and R-Spike, respectively) of both wheat species at the completion of anthesis, along with grain yield and its components at physiological maturity reacted in different quantitative manners to single factors and their 2-way and 3-way interactions (Table 2). The portion of total variance explained by years, species, stress treatments and their interactions ranged from 50% for K m^{-2} to 75% for R-Spike. Annual variation impacted GY and its most vulnerable yield component (i.e., K m^{-2}), but not TKWT or any of the dry matter ratios in stem, leaves and spike. Difference among species, unlike differences among stress treatments, explained significant (p<0.05) small (7.6%, TKWT) or large (60.2%, R-Spike) portions of variance in all traits except R-Stem. However, the 2-way and 3-way interactions accounted for small, albeit significant (p<0.05) portions of variance in most traits. Wheat species differed in R-Stem, R-Leaves, and R-Spike over years; whereas stress treatments impacted all traits in the same manner over years. Durum and bread wheat genotypes responded in different manners to stress treatments by partitioning significantly (p<0.05) different dry matter ratios into stem, leaves, and spike, in addition to K m^{-2}, but not TKWT or GY. However, the 3-way interaction significantly (p<0.05) influenced DM partitioning into stem and leaf, but not spike, and GY and TKWT, but not K m^{-2}.

Patterns of dry matter partitioning

The combined effects of species, stress treatments and years on how a plant partitioned its dry matter into stem, leaves and spike as a function of plant dry matter (Table 3), as indicated by the statistics of the PLS validation models, revealed major differences among wheat species and how they responded to stress treatments. Most models can estimate R-Stem, R-Leaves and R-Spike with large reliability as measured by the R^2 values, the majority of which (67%) exceeded 0.60. However; the main exception are the R^2 values for R-Leaves during 2006. Model intercepts (β_o) were positive except for R-Spike in late-planted bread wheat in 2006 (AL06) and 2007 (AL07) (Table 3) in which case it was associated with the largest positive regression coefficient (β). The regression coefficients reflected different dry matter partitioning patterns between years, species and stress treatments. With only a few exceptions, heavier plants tend to partition more dry matter into stems and spike, but not into leaves. Regression coefficients associated with R-Stem validation models of bread wheat during 2006 were exceptional in that they were all negative; indicating that less dry matter would be partitioned into stem and more into spike if plants accumulate larger amounts of dry matter. The remaining negative β values were for R-Stem for late-planted bread wheat in 2007 at normal (AL07) and large [AL07(25)] population density, and for R-Spike of durum wheat at large density, whether planted at the normal [DN06(25) and DN07(25)], or late planting dates [DL06(25) and DL07(25)].

Table 3. Validation partial least square (PLS) regression models and their statistics describing dry matter partitioned into stem (R-Stem), leaves (R-Leaves), and spike (R-Spike) as a function of plant dry weight for two wheat species and stress treatment combinations during two years.

Treatment	R-Stem				R-Leaves				R-Spike			
	β_o	β	RMSE	R^2	β_o	β	RMSE	R^2	β_o	β	RMSE	R^2
AN06	0.61	-0.081	0.005	0.85	0.28	-0.07	0.015	0.32	0.11	0.150	0.011	0.82
AN06(25)	0.35	-0.016	0.009	0.55	0.19	-0.012	0.005	0.74	0.46	0.028	0.009	0.79
AL06	1.02	-0.400	0.069	0.65	0.19	-0.081	0.062	0.45	-0.1	0.404	0.077	0.59
AL06(25)	0.67	-0.130	0.063	0.64	0.21	-0.079	0.055	0.58	0.16	0.135	0.057	0.71
DN06	0.21	0.061	0.050	0.38	0.32	-0.092	0.054	0.56	0.21	0.180	0.019	0.68
DN06(25)	0.21	0.035	0.009	0.79	0.14	-0.084	0.058	0.69	0.68	-0.03	0.007	0.83
DL06	0.22	0.037	0.008	0.85	0.37	-0.222	0.040	0.54	0.49	0.072	0.008	0.86
DL06(25)	0.18	0.048	0.011	0.77	0.12	-0.02	0.016	0.23	0.71	-0.03	0.005	0.87
AN07	0.28	0.079	0.042	0.31	0.61	-0.229	0.010	0.96	0.11	0.150	0.052	0.57
AN07(25)	0.21	0.058	0.005	0.97	0.47	-0.147	0.003	0.98	0.32	0.089	0.002	0.97
AL07	0.99	-0.420	0.008	0.98	0.26	-0.106	0.002	0.98	-0.3	0.525	0.009	0.98
AL07(25)	0.66	-0.161	0.028	0.80	0.30	-0.091	0.020	0.70	0.04	0.252	0.008	0.98
DN07	0.26	0.021	0.002	0.96	0.28	-0.046	0.004	0.93	0.46	0.025	0.003	0.91
DN07(25)	0.20	0.036	0.002	0.97	0.12	-0.004	0.002	0.80	0.68	-0.032	0.004	0.96
DL07	0.24	0.025	0.009	0.86	0.25	-0.086	0.006	0.93	0.55	0.067	0.006	0.89
DL07(25)	0.14	0.060	0.006	0.98	0.17	-0.030	0.018	0.69	0.69	-0.031	0.011	0.86

The regression coefficients in few cases indicate that the same stress treatment exhibited the same dry matter partitioning pattern during both years. For example, heavier plants of AL06 and AL07 tended to partition smaller, and larger amounts of dry matter into stem and spike, respectively; whereas, the opposite was true for DN06(25) and DN07(25). Other β values were similar in sign and magnitude (e.g., R-Spike in DL06 and DL07) regardless of the value of the regression coefficients for R-Stem and R-Leaves. The overall relationship between RMSE and R^2 was negative and nonlinear ($r=-0.63$; $p<0.05$); however, when R-Stem, R-Leaves, and R-Spike were considered separately, the respective r-values were -0.69, -0.51, and -0.83, indicating differences in the precision with which these three variables can be predicted.

Leaves, invariably, had the smallest percent dry matter partitioned into them (R-Leaves, <30%), followed by stem (R-Stem; 30-56%) then spike (R-Spike; 30-60%; Table 4). The stress year (2007), bread wheat, and the N and N25 stress treatments resulted in significantly ($p<0.05$) larger R-Leaves, but not R-Spike, as compared to non-stress year (2006), durum wheat and the L and L25 stress treatments, respectively. However, there were significant differences among the four stress treatments for R-Stem. The 3-way interaction between years, species and stress treatments resulted in significant differences among levels of these factors in R-Stem, R-Leaves and R-Spike. The late-planted (L) bread and durum wheat, respectively, partitioned the largest and smallest dry matter into stems in both years. Bread wheat partitioned the largest dry matter into leaves in 2007 under the N treatment; whereas, durum wheat partitioned the smallest dry matter into leaves under the L25 stress treatment in both years. The maximum (>55%) amounts of dry matter were partitioned into spike by both wheat species, especially under the L and L25 stress treatments; whereas the smallest (<30%) was partitioned by bread wheat planted at the normal date (N) in 2007. The N25 stress treatment resulted in a slightly, but not significantly, larger GY as compared with the N

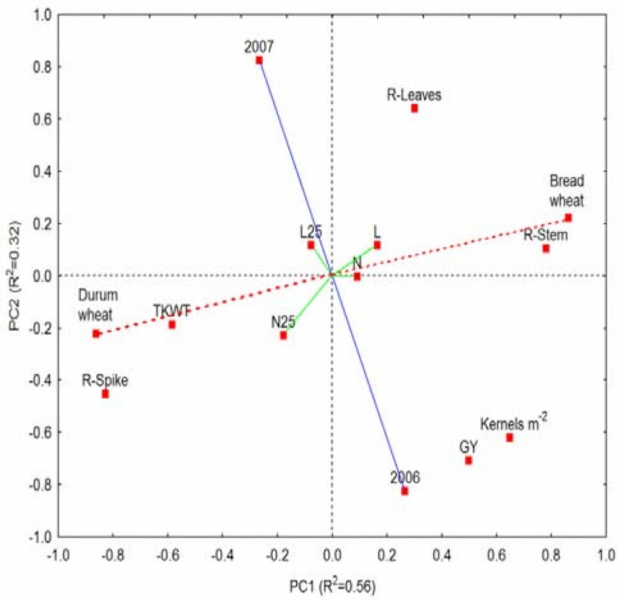

Fig 1. Loadings (correlation coefficients between factors or variables and the principal component) of factors and variables on the first two principal components in a field experiment to evaluate bread and durum wheat genotypes under stress treatments.

Table 4. Percent dry matter ratio partitioned into stem (R-Stem), leaves (R-Leaves) and spike (R-Spike) of two wheat species and their yield and yield components in response to diminishing environmental resources during two cropping seasons.

Factors			R-			Kernels	TKWT	Grain yield
Year	Species	Treatment	Stem	Leaves	Spike	m^{-2}	mg	Mg ha^{-1}
2006			37a	13b	50a	9628a†	35.34a	3.37a
2007			35a	18a	47a	6160b	36.97a	2.19b
	A		24a	19a	57a	9179a	34.22b	3.13a
	D		28a	13b	59a	6609b	38.09a	2.43b
		N	37a	18a	45a	8192a	37.36a	3.01a
		N25	30b	17a	53a	8307a	38.70a	3.16a
		L	31b	13b	46a	7896b	33.50b	2.53b
		L25	38a	13b	49a	7180b	35.06b	2.43b
2006	A	N	43b	14a	43b	10964b	36.22a	3.98a
		E25	31c	15a	54a	11936a	38.51a	4.59a
		L	56a	11bc	33b	11000b	32.51b	3.43b
		L25	46b	16a	38b	9745b	33.23b	3.19b
	D	N	34c	13b	53a	10014b	34.35b	3.46b
		N25	33c	10c	57a	8246c	40.80a	3.36b
		L	29c	16a	55a	8862c	39.44a	2.55c
		L25	32c	08c	60a	8325c	37.80a	2.41c
2007	A	N	42b	30a	28b	5873c	34.20ab	2.69a
		N25	30c	29a	41b	7747a	35.00ab	2.69a
		L	55a	15bc	30b	7837a	33.00b	2.02b
		L25	49a	20b	31b	6256b	31.12b	2.46b
	D	N	34b	12c	54a	5917c	44.70a	2.59a
		N25	32bc	11c	57a	5303d	40.51a	2.21b
		L	24c	15bc	60a	3884f	39.22a	1.46c
		L25	28c	10c	62a	4389e	38.12a	1.43c

†, Means, within each factor and variable, followed by the same letter do not differ significantly (Tukey HSD, $p<0.05$)

treatment; however, the L and L25 stress treatments achieved 80 and 77% of that maximum yield, respectively; this reduction in grain yield was accompanied with reduced K m^{-2} and TKWT for both stress treatments. Patterns of dry matter partitioning into stem, leaves, and spike, and the concomitant differences in K m^{-2}, TKWT and GY due to the 3-way interactions between years, species, and stress treatments were more complex as compared to 2-way interactions between years and species, or between species and stress treatments (data not presented). Larger significant ($p<0.05$) differences in K m^{-2}, but not in TKWT, were found between the stress treatments during 2007 as compared to 2006. Durum wheat invariably had smaller K m^{-2} and larger TKWT during both years and in response to most stress treatments.

A considerable weather-induced yield potential variation between years was found in this study (Table 4). The drought stress during 2007 negatively impacted GY and its components of both wheat species and of all stress and non-stress treatments. On average, GY in 2007 was 35% smaller than that in 2006. In 2006, GY was 30 and 30% smaller in bread and durum wheat, respectively, as a result of the L25 stress treatment (i.e., maximum stress) as compared with the N treatment (i.e., non-stress); the respective values during 2007 were 25 and 45%.

Discrimination between stress treatments

The eight stress treatments exhibited significant differences at the multivariate level (Fig. 2). Two canonical discriminant functions (CAN) accounted for 81% of total variance and were derived from R-Stem, R-Leaves, R-Spike, and GY and its components. CAN1 accounted for 55% of total variance and separated durum and bread wheat based on differences in R-Stem, R-Leaves, R-Spike, and differences in GY and TKWT; CAN2 accounted for a smaller and significant portion (26%) of total variance, and separated the L and L25 from the N and N25 treatments. The correct classification of plants belonging to a certain treatment averaged 88% and ranged from 70% for the DL to 100% for the AN, and AN25 treatments. However, when only the N25, L and L25 stress treatments were considered, average percent correct classification (92%) was a little larger, and ranged from 80-100%. The AL and AL25 stress treatments exhibited smaller percent correct classification and larger variation along the axis of both canonical functions as compared with DL and DL25.

Alternatively, the AN, and AN25 stress treatments exhibited the largest (100%) correct classification and the narrowest variation along both canonical functions; whereas the DN and DN25 were intermediate in their spread and percent correct classification.

Dry matter partitioning and grain yield

The test statistic in the canonical model for biomass partitioning, tested here for R-Leaves in relation to R-Stem (Fig. 3), did not statistically deviate from the expected value (i.e., 0.75) under non-stress (i.e., AN and DN) treatments. However, it was significantly larger (AN25, AL25) or smaller (DN25, AL, DL, and DL25) than the expected value when plants were subjected to stress. A positive and significant ($r=0.90$; $p<0.0001$) canonical correlation coefficient was found between GY and its components (CAN1; $R^2=0.38$) on one hand and percent dry matter partitioned into stem, leaves and spike (CAN1; $R^2=0.49$) on the other (Fig. 3). The AL, AL25, DL and DL25 stress treatments were tightly plotted below the origin of both canonical functions; whereas, the remaining stress treatments (i.e., AN, AN25, DN, and DN25) were plotted on the positive side of both canonical functions with a wider spread. Correlation coefficients between the two sets of variables (Fig. 3) exhibited a wide range of values and are illustrated by presenting the correlation matrices for the non-stress (N) and the maximum stress (L25) treatments. R-Stem was positively ($p<0.05$) correlated with K m^{-2} and with GY under N treatment; however, a stronger correlation, especially with K m^{-2}, was found under L25 stress treatment. A large shift was found in the correlation between R-Stem and TKWT under N ($r=0.08$, ns) and L25 ($r=-0.80$, $p<0.05$). R-Leaves was negatively ($p<0.05$) correlated with GY and with its components under N; however, the strength of this correlation was diminished under L25, except with TKWT. Similarly, R-Spike was positively ($p<0.05$) correlated with GY and with its components under N; however, although it maintained a stronger correlation with TKWT under L25, it developed a strong and negative correlation with GY ($r=-0.41$; $p<0.05$) and with K m^{-2} ($r=-0.61$; $p<0.05$).

Modeling grain yield and its components

Validation models developed to predict GY and its components as functions of R-Stem, R-Leaves and R-Spike in response to stress treatments are presented in Table 5. Number of kernels m^{-2} was best predicted by all three independent variables under AN, and AN25 treatments; however, all other stress treatments reduced the power of prediction, especially under AL, DN and DL treatments. R-Stem exerted positive and significant impact on K m^{-2}, except under DL25. R-Leaves exerted negative and significant impacts on K m^{-2} under all stress treatments, except DL25, and this impact was larger in magnitude for durum wheat. R-Spike displayed wide variation in predicting K m^{-2}, with significant impact on bread, but not durum wheat, except under DL25. Validation models displayed a wide range of reliability in predicting TKWT, the final yield component to be determined by the wheat plant, with the largest (0.85) and smallest (0.52) R^2 values under AN25 and DL treatments, respectively. No clear pattern was detected of the impact of all three independent variables on TKWT under different stress treatments. Larger R-Stem values mostly tend to reduce and increase TKWT of bread and durum wheat, respectively; whereas larger R-Spike values had the opposite effect on TKWT of both wheat species. R-Leaves, except under AL25, had significant, albeit variable impact on TKWT, especially in durum wheat. The validation model for GY was more reliable and resulted in larger R^2 values as compared with validation models for K m^{-2} or TKWT.

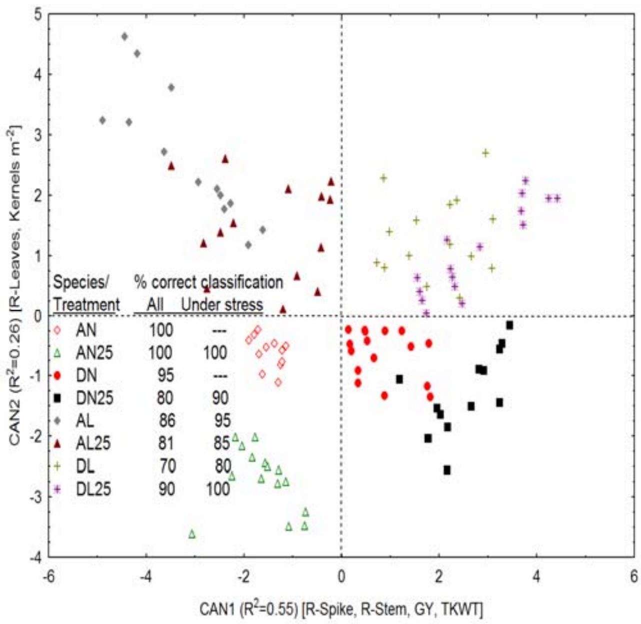

Fig 2. Scatter plot, percent correct classification and variance accounted for by the first two canonical discriminant functions derived from (1) grain yield, thousand kernel weight (TKWT), percent dry matter in spike (R-Spike) and in stem (R-Stem), and (2) percent dry matter in leaves (R-Leaves), and kernels m^{-2} of two wheat species (A and D) subjected to diminishing environmental resources during two cropping seasons.

The largest R^2 values for GY were found under AN, and AN25 and the smallest under DN; however, the remaining R^2 values were >0.70. All three independent variables (i.e., R-Stem, R-Leaves and R-Spike) had significant impact on GY, except R-

Table 5. Validation partial least square (PLS) regression models and their test statistics to predict grain yield and its components as functions of dry matter ratios partitioned into stem (R-Stem), leaves (R-Leaves) and spike (R-Spike) of two wheat species subjected to diminishing environmental resources during two cropping seasons.

Dependent variable	Species/ treatment	Validation model β_o	Regression coefficient, β			RMSE	R^2
			R-Stem	R-Leaves	R-Spike		
Kernels m^{-2}	AN	6648	4013*†	-1434*	1032*	911	0.91
	AN25	12645	4871*	-2786*	-2085*	604	0.95
	AL	-2000	1926*	-3636*	1710*	1642	0.44
	AL25	2941	1716*	-2412*	6958*	785	0.78
	DN	-1238	1278	-3037*	1760	3157	0.40
	DN25	-18464	7329*	-9140*	1811	1278	0.79
	DL	2913	3178*	-2524*	-6536	1842	0.39
	DL25	4776	-6910*	5368*	1542*	2012	0.70
TKWT, mg	AN	33.5	13.5	-9.0*	-4.4	0.94	0.60
	AN25	24.0	-75.0*	8.6*	66.4*	1.14	0.85
	AL	38.7	-14.3*	13.6*	0.7	0.88	0.72
	AL25	38.6	-27.2*	16.9	10.3*	1.71	0.77
	DN	35.5	12.2	-10.5*	-3.6*	1.04	0.59
	DN25	63.3	15.5	38.9*	-54.4*	0.96	0.66
	DL	20.8	-10.6	-18.7*	29.2*	3.6	0.52
	DL25	64.3	36.3*	24.8*	-61.0*	1.28	0.68
GY, Mg ha^{-1}	AN	2.31	1.60*	-5.6*	3.95*	0.29	0.92
	AN25	2.17	2.03*	-7.3*	5.32*	0.23	0.95
	AL	0.24	4.49*	-9.3*	4.80*	0.24	0.80
	AL25	1.31	3.60*	-7.2*	3.60*	0.21	0.76
	DN	-0.6	4.02	-11.2*	7.11*	0.96	0.51
	DN25	-6.3	30.2*	-34.9*	4.71*	0.54	0.79
	DL	1.26	19.6*	-10.7*	7.22*	0.60	0.75
	DL25	-4.5	14.3*	-21.7*	6.81*	0.61	0.70

† *, significant, Tukey HSD, $p<0.05$.

Stem under DN. Larger values of R-Stem and R-Spike resulted in larger GY; whereas larger R-Leaves resulted in smaller GY of both species and under all stress and non-stress treatments. R-Stem and R-Leaves had the largest positive and negative impact on GY under DN25, respectively; whereas, R-Spike had the largest and smallest impact on GY under DL and AL25, respectively.

Both K m^{-2} and TKWT contributed significantly to predicting GY under all stress treatments, except K m^{-2} under AL and DL25 (Table 6). Most models, except the one for AL25, had large reliability (small RMSE and large R^2 values). However, when the interaction term between yield components was introduced into the model, reliability of model estimates (especially under AL25) was improved for all stress treatments, except AL. Comparisons among regression coefficients of both yield components indicated that K m^{-2} had the largest significant and positive impact on GY under AN and AN25, and a large significant and negative impact on GY under DL; however it had a comparatively smaller, positive and negative significant impacts on GY under DN and DN25, respectively. Regression coefficients of TKWT were all positive and significant, with the largest under DL25 being almost twice as large as the smallest under AL.

Discussion

Understanding the factors that determine how efficiently wheat can utilize environmental resources under different stresses may allow for better modeling of grain yield and its components as functions of dry matter partitioning into different plant parts. Wheat productivity and yield depend not only on dry matter accumulation, but also on its effective partitioning, especially into spikes (Moragues et al., 2006), a key to yield stability under stress (Kumar et al., 2006). Simple measurements of wheat dry matter 15 days after the completion of anthesis and its partitioning into stem, leaves and spike, when jointly analyzed with estimates of K m^{-2}, TKWT and GY under stress and non-stress conditions using multivariate procedures, helped model the response of bread and durum wheat to diminishing environmental resources. Inter-specific differences (i.e., bread vs. durum wheat), as demonstrated by PC (Fig. 1) and PLS regression (Table 3) analyses, confirm their differences for yield components (Otteson et al., 2007), and suggest that they require different management strategies to optimize grain yield under stress.

Stress tolerant landraces and genotypes, as compared to non-tolerant wheat landraces (Moragues et al., 2006) and genotypes (Ehdaie et al., 2006), partition more dry matter into their stems, which may or may not contribute to larger GY (Kumar et al., 2006). A wide range of values for R-Stem (24-56%) were recorded under stress treatments in this study. However; unlike the large R-Spike values (28-62%), the large R-Stem values did not always contribute to larger GY under stress (Table 4). This was the case in wheat landraces adapted to drought stress, which allocated ~16% more weight on the main stem than non-adapted landraces, and produced 48% more grain than the non-tolerant landraces (Moragues et al., 2006).

Enhanced tolerance to stress caused by competition for environmental resources can lead to increased, or at least stabilized, crop yield (Davis and May, 2005). This study demonstrated that GY of bread and durum wheat was increased under non-stress and stabilized under stress treatments (e.g., N vs. N25, and L vs. L25; Table 4). However, genotypes with large yield potential may experience the largest yield reduction when subjected to stress (Davis and May, 2005; Ehdaie et al., 2006) as demonstrated in this study by a 31 and 54% reduction of GY in bread and durum wheat in 2006 and 2007, respectively. Therefore, in order to increase productivity and yield, wheat genotypes that can be planted earlier to more closely match crop growth to the availability of environmental resources (Parry et al., 2005), or that can be planted at larger population densities to optimize the use of these resources should be used, if available, otherwise should be developed.

Yield stability may become more important than large yield under stress conditions (Kato and Yokoyama, 1992; Arduini et al., 2006); therefore, an improved understanding of the mechanisms behind high stable yield under stress (e.g., genotype x environment interaction) is needed. Percent variance in R-Stem, R-Leaves, and R-Spike explained by years, species, stress treatments and their interactions (R^2=0.67, 0.73 and 0.75, respectively; Table 2) indicate that species and their 2-way and 3-way interactions, but not temporal variation or stress treatments alone, were the most important factors in partitioning dry matter, especially into spikes. Therefore, and in view of the unexplained variance in the data, a more fundamental understanding of genotype x environment interactions is necessary to determine the potential opportunities and disadvantages of specific phenological (Kato and Yokoyama, 1992; Villegas et al., 2007), yield-stabilizing, and survival traits (Parry et al., 2005) under stress. The portion of unexplained variance, particularly in K m^{-2} and GY (0.50 and 0.49, respectively) as compared to TKWT (0.78) demonstrates the stronger dependence of GY on K m^{-2} (Fig. 1) and the need to know the extent to which differences in TKWT are a result of intra-plant competition among kernels in order to maximize GY. Nevertheless, maintaining a large TKWT, especially under stress, is important not to only stabilize or increase GY, but also because of its impact on end-use quality (Gupta et al., 2006).

Discrimination among the stress treatments (Fig. 2) was large (70-100% correct classification) and, notwithstanding the potential suppression of variation under stress (Dhanda et al., 2004), was improved further (80-100%) when only stress treatments were considered. This indicates that plants differed in both the magnitude and direction of phenological responses to stress progression. This "phenotypic plasticity" is known (Weiner, 2004) to optimize the capture of different resources in a manner that maximizes plant growth. The trait associations on CAN1 and CAN2 (Fig. 2) and the scatter plot of the stress treatments, provide a visual and, when combined with PLS model statistics (Table 5), quantitative selection criterion as to the magnitude and importance of certain traits for bread and durum wheat under stress or non-stress conditions.

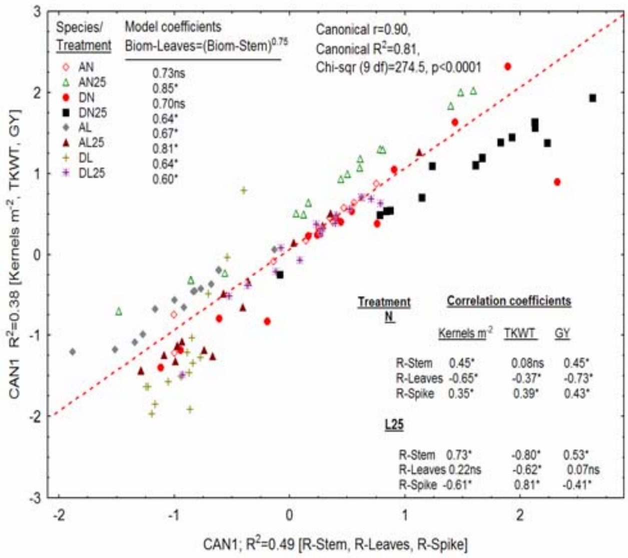

Fig 3. Scatter plot, canonical correlation coefficient between, and variance accounted for by the first canonical function derived from (1) dry matter ratio partitioned into stem (R-Stem), leaves (R-Leaves), spike (R-Spike), and coefficients of a canonical model relating biomass in leaves (Biom-Leaves) to biomass in stem (Biom-Stem), and (2) kernels m^{-2}, thousand kernel weight (TKWT) and grain yield (GY), of two wheat species subjected to stress treatments averaged over two cropping seasons. Simple correlation coefficients among variables in (1) and (2) for the no-stress (N) and maximum stress (L25) treatments are presented [*, $p<0.05$; ns=non-significant].

Table 6. Validation partial least square (PLS) regression models and their test statistics for grain yield as a function of kernels m^{-2} and TKWT of two wheat species subjected to diminishing environmental resources and averaged over two cropping seasons.

Species/ Treatment	Validation model β_o	Regression Coefficient for		RMSE	R^2	R^2 (Model plus Interaction)
		Kernels m^{-2}	TKWT			
AN	-0.21	1.441e-07*†	3.821e-04*	0.09	0.97	0.98
AN25	-0.24	2.671e-07*	3.914e-04*	0.44	0.84	0.92
AL	1.21	6.622e-09	1.992e-04*	0.27	0.71	0.71
AL25	0.91	7.766e-08*	2.290e-04*	0.29	0.58	0.85
DN	-0.10	7.061e-08*	4.124e-04*	0.10	0.96	0.98
DN25	0.36	-8.430e-08*	3.245e-04*	0.39	0.91	0.95
DL	0.38	-1.877e-07*	2.505e-04*	0.22	0.95	0.96
DL25	-0.40	5.556e-08	4.424e-04*	0.23	0.95	0.96

† *, significant, Tukey HSD, $p<0.05$.

For example, larger population density in durum wheat can compensate for shorter growing season in stabilizing GY through larger number of kernels m^{-2} as a result of larger R-Stem and R-Spike.

Biomass data obtained under non-stress conditions conforms to the model (Niklas, 2003) describing the partitioning of biomass at the level of individual plants and asserts a "canonical" pattern such that standing leaf biomass is expected to scale as the 0.75-power of stem biomass, unless disrupted by stress as indicated by the model coefficients (Fig. 3). This disruption can be explained on the basis of differential response of R-Stem and R-Leaves to 2-way and 3-way interactions of years, wheat species, and stress treatments (Table 2). More variance in R-Stem, as compared to R-Leaves, was explained by the wheat species responding differently to stress treatments, and to their combined temporal variation; whereas, more variance in R-Leaves, as compared to R-Stem, was explained by temporal differences among the wheat species.

Increased population density can contribute to better exploitation of environmental resources as it tends to increase above-ground dry matter before and at physiological maturity (Arduini et al., 2006) and may increase (Carr et al., 2003a; Arduini et al., 2006) or decrease GY under stress or non-stress environments (Otteson et al., 2007). On average, no significant differences were found in this study between large and normal population densities in K m^{-2}, TKWT or GY, whether planted at the recommended or late planting dates. When wheat species in different years were considered, GY of bread wheat was increased by 15 and 22% in 2006 and 2007, respectively; and GY of durum wheat was decreased by 15% in 2007, due to larger population density when both species were planted at the recommended planting date. However; GY of bread and durum wheat was significantly reduced, and remained unchanged in 2006, respectively, and remained unchanged for both species in 2007 in response to increased population density.

Stress had a small, but important effect on phenology (Craufurd and Wheeler, 1999). In 2006 and 2007, crops planted 17 and 36 days (L treatment), respectively, after the normal planting dates (N treatment) required only three and nine more days to reach physiological maturity. These late-planted crops lost 87 and 82 potential GDDs and their grain yield was reduced by 30 and 20% as compared with crops planted on normal dates, respectively. Nevertheless, phenotypic adjustments could lead to increased R-Spike as a means to increased number of fertile florets and grain yield (Whitechurch et al., 2007). Kernel weight was less affected by population density adjustment than K m^{-2} (Table 4). It may decrease, increase (Arduini et al., 2006), or remain relatively unchanged (Carr et al., 2003b); however, usually it is heavier under non-stress than under stress environments (Kumar et al., 2006). In this study, kernel weight in bread and durum wheat varied as much as 7.4 and 3 mg kernel^{-1}; respectively, as compared to 2.2 mg in five hard red spring wheat cultivars in the Great Plains (Carr et al., 2003b). In bread wheat, a kernel on average was four mg heavier under non-stress treatment; however, due to a significantly smaller number of K m^{-2} under stress, durum wheat kernels were as heavy under stress and non-stress treatments.

The dynamic interrelationships among R-Stem, R-Leaves and R-Spike were successfully used in developing, for the most part, reliable models to predict GY and its components under a range of resource-limiting scenarios. The different combinations of planting dates and population densities created different micro-environments where a genotype is capable of giving rise to different phenotypes (Weiner, 2004). This environment-dependent phenotypic expression was expressed by wheat at different levels of complexity (Table 5; Fig. 3) and was quantified, for the most part, by significant coefficients of the validation models. The R-Stem and R-Spike, in particular, responded quantitatively in different manners to changes in environmental resources, and provided insights into how single plants interact with their environment, adjust their dry matter partitioning, and determine grain yield. Differences in magnitude and sign among model statistics illustrate the dynamics of interrelationships among independent variables predicting GY and its components as functions of R-Stem, R-Leaves and R-Spike (Table 4), or predicting GY as a function of its two major components (i.e., K m^{-2} and TKWT; Table 5) under different stress and non-stress conditions and for both wheat species. Additionally, reliability in validating predicted GY and its components displayed a wide range, as quantified by model β_o (in comparison with mean values for Km^{-2}, TKWT and GY in Table 3), RMSE and R^2 values.

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