Article

Use of Genotype by Yield*Trait (GYT) Analysis to Select Hard Red Spring Wheat with Elevated Performance for Agronomic and Disease Resistance Traits

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ABSTRACT

Elevating resistance levels to bacterial leaf streak (BLS), caused by *Xanthomonas campestris pv. translucens* (Jones, Johnson, & Reddy) and Fusarium head blight (FHB) caused by *Fusarium graminearum* Schwabe (telomorph *Gibberella zeae* (Schwein.) Petch) are major objectives of several hard red spring wheat (*Triticum aestivum* L.; HRSW) breeding programs situated in the northern Great Plains of the USA. High grain yield significantly contributes to the success of HRSW cultivars. Other traits, such as disease resistance, are most useful when accompanied by high grain yield in a single genotype. The genotype by yield-trait (GYT) analysis method aids in selecting genotypes with elevated performance levels for traits of consideration in the presence of high grain yield. Replicated yield trial data was subjected to GYT analysis to demonstrate its utility for selecting HRSW genotypes for use as parents and further consideration toward cultivar release. Genotype selections were identified based on overall performance while strong and weak characteristics were also investigated. Several genotypes were selected for potential use as parents while three were chosen for further cultivar release consideration. Performance levels associated with two of the three candidate cultivars were greater than average for all traits considered.

KEYWORDS: biplot analysis; genotype by trait (GT) analysis; genotype by yield-trait (GYT) analysis; genotype selection; wheat; Fusarium head blight; bacterial leaf streak

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INTRODUCTION

Elevating resistance levels to bacterial leaf streak (BLS), caused by *Xanthomonas campestris pv. translucens* (Jones, Johnson, & Reddy) and Fusarium head blight (FHB) caused by *Fusarium graminearum* Schwabe

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(telomorph *Gibberella zeae* (Schwein.) Petch) are major objectives of several hard red spring wheat (*Triticum aestivum* L.; HRSW) breeding programs situated in the northern Great Plains of the USA. Both diseases have been documented as occuring in the USA for at least 100 years [1,2], and various levels of economic damage to wheat crops have been documented [3,4]. Each disease thrives when accompanied by elevated humidity at optimal temperatures. Likewise, reduced tillage practices in wheat production areas as well as alternate pathogen hosts tend to increase the likelihood of disease development due to inoculum accumulation. Fungicide application can help to reduce losses to FHB [5,6], though economically practical chemical control of BLS is not yet available. Even with fungicide application to control FHB damage, higher levels of control are achieved when moderately resistant cultivars are grown [7,8]. Taken together, these circumstances suggest that efforts by HRSW breeders to increase resistance levels for both diseases are a practical and economically sound means of disease management.

Wheat growers generally expect new cultivars to outperform old cultivars with respect to grain yield. Although elevated levels of disease resistance can help to achieve increased productivity, it is unlikely that new cultivars with high levels of disease resistance would receive widespread and consistent grower acceptance if they produce less grain than those presently available. Therefore, breeders strive to achieve a balance between grain yield and other traits of importance. Recently, Yan and Frégeau-Reid [9] formally introduced a genotype-by-yield*trait (GYT) approach to biplot analysis that specifically addresses genotype selection based on concurrent consideration of grain yield and other traits of interest.

A generalized method of biplot analysis was first proposed by Gabriel [10] as a means of analyzing data in a two-way table. The effectiveness of biplot analysis for studying multi-environment trial (MET) data, that also take the form of a two-way (e.g., genotype-by-environment; GE) table, was then demonstrated [11–13] and Yan [14] introduced the GGEbiplot software platform as a user-friendly means of analysis implementation. Utility of the GGEbiplot analysis software may be limited only by the imagination of users. Several approaches to biplot analysis have been demonstrated that range from examining single trial data for human errors [15] and exploring Net Blotch (*Pyrenophora teres* Drechs) isolates on barley (*Hordium vulgare* L.) genotypes [16] to the examination of quantitative trait loci-by-envrinoment interactions [17]. Among the numerous forms of biplot analysis, however, versions of GE and genotype-by-trait (GT) analysis are likely reported most prevalently.

Multi-environment trial evaluation of genotype performance for single traits can be carried out by coalescing “years” and “locations” into “environments” to create a two-way GE table. A few subsequent outcomes of GE biplot analysis include; genotype performance evaluation, megaenvironment detection, and evaluation of environments for representativness and discriminating ability. Genotype-by-trait analysis can aid with understanding trait relationships (i.e., correlations) within a group of genotypes and provide information regarding trait profiles for each genotype. An understanding of trait relationships can provide clues with regard to expectations for combining optimal values of multiple traits into a single genotype. Further, an understanding of trait profiles specific to individual genoptyes can aid in parental slection and identify unique charactersitics of potential cultivars.

Wheat genotypes possess a collection of traits for consideration when making selections, though grain yield is typically thought of as most important. The GYT biplot formulation is a simple extension of typical GT biplot analysis that allows simultaneous consideration of all traits with respect to grain yield. This is accomplished by creating new yield-trait combinations for each genotype [9]. A notable difference among GYT and GT biplot analysis is that a vector representing grain yield is absent from a GYT biplot because its values are captured within those of newly created yield-trait combinations. An additional unique characteristic of the GYT biplot approach, as compared to GT analysis, is that a superiority index is ultimately produced for making genotype selections [9].

For the purpose of parental selection, or further consideration toward eventual cultivar release, it is usually sufficient for HRSW breeders to make selections based on genotype performance from one or two growing seasons. However, prior to presenting data to release committees in the hope of going forward with a new cultivar, breeding programs typically evaluate performance of candidate breeding lines for at least three growing seasons in advanced METs.

The objective of this research was to illustrate the use of GYT biplot analysis as a means of identifying HRSW genotypes that possess high agronomic potential along with BLS and FHB resistance for the purpose of parental selection and additional consideration toward eventual release. This was accomplished by analyzing a datset composed of genotypes included in the South Dakota State University (SDSU) HRSW breeding program advanced yield trial (AYT) from growing seasons 2017–2018. With a framework to build upon provided by brief consideration of a typical GT analysis of the data, the same data was used to present the GYT analysis scheme for parental selection and further program consideration.

MATERIALS AND METHODS

Plant Materials and Growth Practices

Data used for analysis consisted of agronomic performance as well as BLS and FHB screening nursery resistance observations collected on all genotypes included in the SDSU-HRSW-AYT during both 2017–2018 growing seasons. Each year the AYT was composed of 48 genotypes, 28 of which were common over the two growing seasons. Of the 28 genotypes, 14 were previously released and named check cultivars included in each year of the AYT for purposes of comparison. The remaining 14 genotypes, generally designated as “SDXXXX”, were experimental breeding lines. The number of agronomic trial locations harvested in each growing season was variable because some sown locations were lost due to hail, drought, etc. Seven and ten locations were harvested in each of the respective study years. All trial locations were sown in April or May of each year as a randomized complete block (RCB) design composed of three replications. Plots were sown as 1.5 by 6.0 m in length consisting of seven rows (21.4 cm row spacing) though after heading, each was cut to final a harvest length of 5.3 m. Soil fertility levels and weed control practices were consistent with those of commercial production in the region.

Disease evaluations took place in nurseries where genotypes were sown as single rows measuring 1.5 m long with 35 cm spacing between rows and trials were formed as RCB designs composed of three replications. Each year, FHB resistance observations were collected from two nurseries grown near Brookings and Volga, South Dakota, while BLS resistance screening took place at a single nursery located near Brookings.

Disease Evaluation

Nearly all methods utilized for inoculation, resistance evaluation, and data collection in the disease nurseries were consistent with those routinely employed by the SDSU-HRSW breeding program [18,19]. An additional step not reported by Kadariya, et al. [18], however, was that after percent Fusarium damaged kernel (FDK) estimates were collected from each harvested FHB nursery row, samples were then ground with a Udy Cyclone sample mill (Udy Corporation, Fort Collins, CO, USA) to create a fine powder that was provided to the North Dakota State University Veterinary Diagnostic Laboratory for deoxynivalenol (DON) concentration determinations. Ultimately, three FHB resistance measures including Disease Index [20], FDK percentage, and DON concentration were aquired for each genotype. Resistance to BLS was reported as area under the disease progress curve (AUDPC) as in Kandel et al. [19].

Agronomic Evaluation

During each growing season, heading date (measured as ~50% spike emergence; expressed as days > 1 Jun) and plant height (cm) observations were collected at nearly all trial locations. At maturity, plots were harvested in July or August of each year with a Kincaid 8-XP (Kincaid, Haven, KS, USA) plot combine where grain yield ($kg \cdot ha^{-1}$) and test weight ($kg \cdot m^{-3}$) for each plot were collected. Grain protein content ($g \cdot kg^{-1}$) was then determined for each plot by passing samples through a FOSS Infratec 1241 grain analyzer (Foss, Laurel, MD, USA) and expressed on a 12 percent moisture basis (approved method 39-10) [21].

Data Analysis

Agronomic, BLS, and FHB resistance data from all trials were merged into a single dataset for analysis. All biplot analysis steps were carried out within the GGEbiplot software platform (http://GGEbiplot.com). By default, the GGEbiplot platform positions trait vector markers to represent high values. For GT analysis, vectors depciting disease resistance traits, plant height, and heading date were reversed to achieve a preferred orientation toward low values. Low values for each of these traits were also chosen as preferable in the GYT analysis. Log files associated with each analysis were used to create summary and correlation tables. Superiority index values for each genotype were calculated as the mean of its standardized yield-trait combinations.

RESULTS

Genotype by Trait Analysis of 2017–2018 AYT

Means of each genotype included in the 2017–2018 AYT are presented in Table 1, several of which were composed of values collected at 17 environments, though heading date and plant height were only collected at 16 environments. Levels of FHB and BLS resistance were reported only from inoculated nurseries. Correlations among trait means are presented in Table 2. A GT biplot (such as Figure 1) where “Scaling = 1”, “Centering = 2”, and “SVP = 2”, provides a graphical depiction of information presented in Tables 1 and 2. These constraints result in several noteworthy points of interest associated with a GT biplot [9,15].

Table 1. Genotype by trait means of 28 hard red spring wheat genotypes grown in 2017–2018 South Dakota State University advanced yield trial. Trait values are means across specified number of locations.

Genotype	YIELD	TW	GPC	DAYS	HEIGHT	AUDPC	DIS	FDK	DON
Advance	2968	775	152	19.4	69.6	346	20.7	21.3	1.9
Boost	2895	758	164	21.7	75.1	279	19.1	17.9	0.8
Brick	2791	779	160	15.3	71.5	421	13.9	15.4	0.8
Briggs	2765	758	162	17.3	71.4	403	21.6	28.8	1.6
Faller	2930	752	150	21.9	76.3	426	17.2	25.0	2.4
Focus	2777	779	166	15.3	73.0	403	15.5	17.1	1.4
Forefront	2980	773	160	16.9	78.2	403	14.6	23.8	1.0
LCS-Trigger	3315	761	144	23.9	74.6	300	24.6	19.2	1.5
Oxen	2911	747	158	18.1	69.1	455	24.1	43.3	1.9
Prevail	3154	762	154	18.3	71.7	347	18.4	19.2	1.4
Select	2767	778	157	16.6	71.4	444	19.5	24.6	1.6
Steele-ND	2832	763	161	19.6	75.7	455	22.3	33.3	3.7
Surpass	2872	755	158	17.2	68.1	323	16.8	20.4	1.3
Traverse	3051	732	151	18.7	74.7	403	21.3	49.2	1.8
SD4539	3057	765	159	20.3	78.0	338	18.2	20.8	1.3
SD4625	3172	769	157	19.3	73.1	328	18.2	19.6	1.4

Table 1. *Cont.*

Genotype	YIELD	TW	GPC	DAYS	HEIGHT	AUDPC	DIS	FDK	DON
SD4706	3065	762	156	16.3	74.1	455	19.3	34.2	2.8
SD4707	2683	733	165	18.3	69.7	444	25.1	37.1	1.8
SD4708	3010	773	160	18.4	72.8	384	18.1	26.7	1.0
SD4711	2949	774	160	15.7	71.8	519	18.7	29.6	1.7
SD4719	3142	762	155	20.6	75.0	409	19.4	30.4	2.4
SD4720	2747	751	173	19.5	74.2	386	20.7	30.0	2.2
SD4721	2832	756	163	18.4	67.0	409	17.7	32.9	2.8
SD4740	2774	770	158	17.6	70.5	426	18.4	22.5	1.3
SD4745	2809	768	170	19.1	74.6	369	18.9	39.2	2.2
SD4746	2773	784	163	18.1	69.9	438	23.9	28.3	1.7
SD4748	2708	754	161	16.6	69.1	449	17.9	25.0	1.4
SD4752	2833	774	162	19.9	74.3	392	16.4	22.5	0.8
Mean	2913	763	159	18.5	72.7	398	19.3	27	1.7
Std Dev	160	13	6.0	2.0	2.9	54	2.9	8.3	0.7
Environments	17	17	17	16	16	2	4	4	4

Traits include: YIELD: grain yield ($kg \cdot ha^{-1}$); TW: test weight ($kg \cdot m^{-3}$); GPC: grain protein content ($g \cdot kg^{-1}$); DAYS: heading date (~50% head emergence > 1 Jun); HEIGHT: plant height (cm); AUDPC: area under Bacterial leaf streak disease progress curve (area); DIS: Fusarium head blight disease index (%); FDK: Fusarium damaged kernels (%); DON: deoxynivalenol concentration (ppm).

Table 2. Pearson Product Moment correlations among nine traits collected from 28 genotypes grown in 2017–2018 South Dakota State University advanced yield trial.

Traits	YIELD	TW	GPC	DAYS	HEIGHT	AUDPC	DIS	FDK
TW	−0.01							
GPC	−0.71	0.09						
DAYS	−0.47	0.27	0.34					
HEIGHT	−0.41	−0.07	0.09	0.42				
AUDPC	0.44	−0.01	−0.16	−0.57	−0.21			
DIS	−0.05	0.43	0.12	0.36	−0.18	0.08		
FDK	0.11	0.60	−0.12	−0.04	−0.06	0.46	0.52	
DON	0.03	0.28	−0.03	0.14	0.02	0.38	0.38	0.55

Thresholds for significant correlations are $P < 0.05 = 0.382$, and $P < 0.01 = 0.483$. Traits include: YIELD: grain yield ($kg \cdot ha^{-1}$); TW: test weight ($kg \cdot m^{-3}$); GPC: grain protein content ($g \cdot kg^{-1}$); DAYS: heading date (~50% head emergence > 1 Jun); HEIGHT: plant height (cm); AUDPC: area under Bacterial leaf streak disease progress curve (area); DIS: Fusarium head blight disease index (%); FDK: Fusarium damaged kernels (%); DON: deoxynivalenol concentration (ppm).

Total variation of the 2017–2018 AYT datset depicted in the first two dimensions used to generate the GT biplot was 57.9% (Figure 1). Each of the three FHB disease resistance traits (DIS, FDK, and DON) were drawn with acute angles to one another (Figure 1) and their correlations were generally significant ($P < 0.01$) although the correlation between DIS and DON did not achieve significance (Table 2). None of these traits were correlated with grain yield, protein content, heading date, or plant height, but DIS and FDK values were significantly correlated with test weight, and FDK was significantly correlated with AUDPC (Table 2). The AUDPC trait was significantly correlated with grain yield and significantly negatively correlated with heading date (Table 2). Figure 1 reveals obtuse angles between the grain yield vector and each of the protein content, heading date, and plant height vectors. Each of these correlations was negative and significant (Table 2). The nearly right angle drawn between the grain yield and test weight vectors revealed that the two traits were uncorrelated (Figure 1; Table 2).

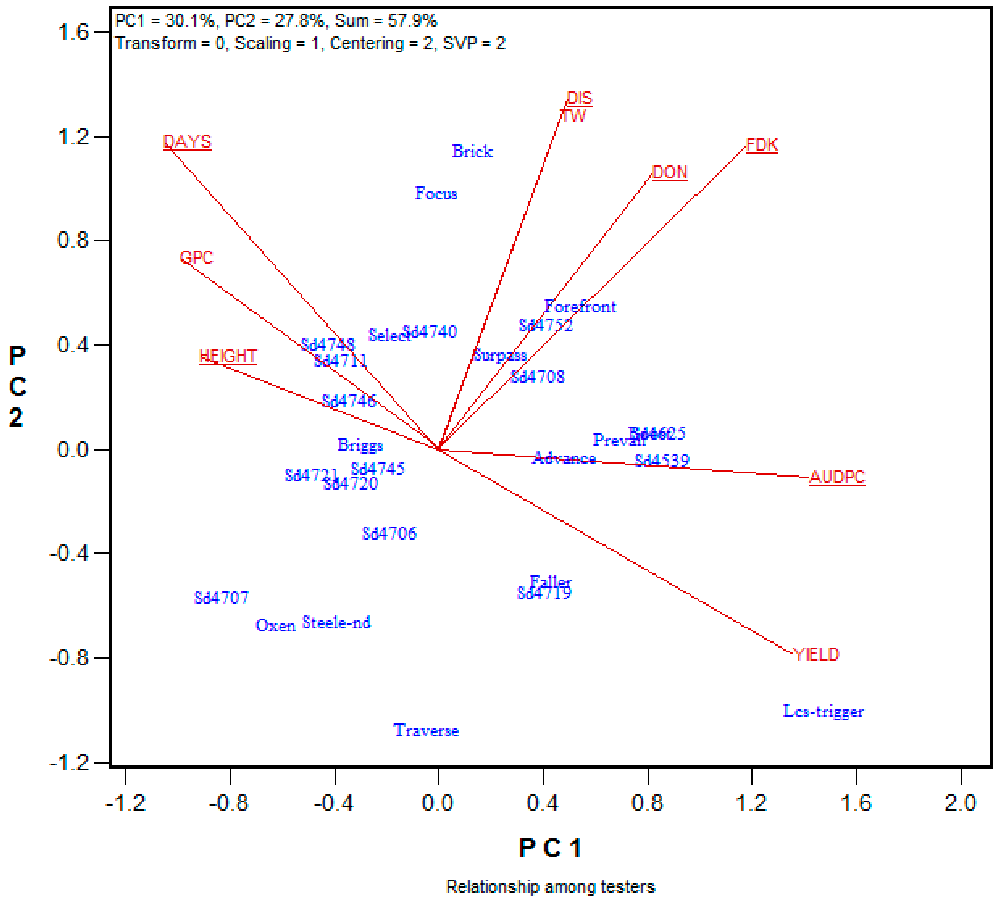

Figure 1. Genotype by trait (GT) biplot of mean data for 28 hard red spring wheat genotypes grown in 2017–2018 South Dakota State University advanced yield trial based on singular value decomposition of trait-standardized data ("Scaling = 1, Centering = 2") and trait-focused singular value partition ("SVP = 2"). Traits include: YIELD: grain yield (kg·ha^{-1}); TW: test weight (kg·m^{-3}); GPC: grain protein content (g·kg^{-1}); DAYS: heading date (~50% head emergence > 1 Jun); HEIGHT: plant height (cm); AUDPC: area under Bacterial leaf streak disease progress curve (area); DIS: Fusarium head blight disease index (%); FDK: Fusarium damaged kernels (%); DON: deoxynivalenol concentration (ppm). Underlined trait vector markers indicate those that were reversed to display preferred orientation.

The cultivar "LCS-Trigger" was included in the AYT as a high-yielding check that produced more grain than all other genotypes (Table 1). Figure 1 also revealed that this was the case with its long projection on the YIELD vector, though it was also among those with the lowest AUDPC scores.

Figure 1 also revealed that it was among genotypes with the latest heading date, lowest protein content, and tallest plant height. In fact, its heading date was latest, it had lowest protein content, and was eighth tallest among all 28 genotypes (Table 1). Other high yielding genotypes included experimental lines SD4539, SD4625, and SD4719 along with the check cultivars “Boost”, (hidden behind SD4625) “Prevail”, “Faller”, “Advance”, and “Traverse” (Figure 1). Among the three experimental lines, SD4539 was characterized with the sixth highest grain yield mean and second highest plant height with better than average performance for the remaining traits (Table 1). SD4625 had the second highest grain yield mean with somewhat less than average grain protein content. It was also slightly taller and later than average, though its disease resistance levels were all better than average (Table 1). SD4719 was fourth best in terms of grain yield production, though its performance levels for each of the remaining traits were lower than average.

Among the check cultivars, Boost was most notable for the lowest AUDPC score, better than average values for the FHB resistance traits, third latest heading date, and fifth highest grain protein average, though its grain yield mean was lower than average. With the third highest grain yield mean, Prevail would best be described as producing grain with slightly low test weight and less than average grain protein, but was better than average for the remaining traits (Table 1). Advance, Faller, and Traverse also produced more grain than average, and had protein content means that were well below average. Faller and Traverse also had low test weight means. With high average values for each of the FHB resistance traits, Traverse was among the most susceptible, especially with regard to FDK values (Table 1).

In further selecting for productivity as well as FHB and BLS resistance, Figure 1 shows that experimental lines SD4708 and SD4752 as well as checks “Forefront” and “Surpass” warranted consideration. SD4708 was better than average for each of the disease resistiance traits and had the eighth highest grain yield mean as well as ninth heaviest test weight. SD4752 was quite similar, though its grain yield mean was less than average. Both of these genotypes had high levels of resistance to DON accumulation. SD4752 was tied with Boost for the second lowest, while SD4708 was next with third lowest, mean DON accumulation (Table 1). Forefront and Surpass had similar and better than average levels of resistance to FHB while Surpass had a lower than average AUDPC score (Table 1). Forefront had a higher than average AUDPC mean and was tallest among all genotypes while the plant height of Surpass was less than average. Both had early heading dates and Forefront had a higher grain yield mean (Table 1).

Genotype by Yield Trait Analysis of 2017–2018 AYT

Table 3 contains standardized yield-trait combinations of the GYT data for each genotype that were derived by combining traits presented in

Table 1 with grain yield. As an example, Y*TW is the standardized version of the product of grain yield and test weight. Those yield-trait combinations followed by "-1" such as, Y*DIS-1 represent products of grain yield and trait values that were chosen with preference toward lower numerical scores. As a result, high values are always preferable in the standardized GYT table.

Table 3. Standardized genotype by yield*trait (GYT) data and superiority index of 28 hard red spring wheat genotypes grown in 2017–2018 South Dakota State University advanced yield trial.

Genotype	Y*TW	Y*GPC	Y*DAYS-1	Y*HEIGHT-1	Y*AUDPC-1	Y*DIS-1	Y*FDK-1	Y*DON-1	INDEX
SD4625	1.72	1.96	0.55	1.58	1.63	1.01	1.29	0.91	1.33
Prevail	1.43	1.23	1.09	1.85	1.28	0.9	1.31	0.86	1.24
LCS-Trigger	2.37	0.82	−1.77	2.03	2.43	−1.09	1.59	0.92	0.91
SD4708	0.82	1.04	0.48	0.6	0.4	0.63	0.18	1.24	0.67
Forefront	0.64	0.69	1.18	−1.02	0.04	1.76	0.47	1.16	0.62
SD4539	0.91	1.32	−0.43	−0.51	1.2	0.73	0.94	0.76	0.62
Surpass	−0.43	−0.49	0.56	0.91	0.99	0.73	0.67	0.5	0.43
SD4719	1.35	1.4	−0.31	0.84	0.27	0.48	−0.08	−0.69	0.41
Brick	−0.37	−0.97	1.2	−0.48	−0.58	1.45	1.08	1.04	0.29
Advance	0.61	−0.61	−0.26	1.19	0.88	−0.36	0.74	−0.14	0.26
SD4706	0.88	0.82	1.87	0.6	−0.59	0.37	−0.63	−1.44	0.24
Boost	−0.24	0.62	−1.76	−0.74	1.67	0.04	0.99	1.23	0.23
SD4711	0.47	0.44	1.72	0.48	−1.73	0.31	−0.25	0.07	0.19
Focus	−0.48	−0.2	1.14	−0.95	−0.36	0.91	0.87	0.25	0.15
SD4752	−0.25	−0.26	−1.01	−0.92	−0.09	0.77	0.38	1.11	−0.03
Traverse	0.08	−0.09	0.44	0.35	0.18	−0.38	−2.43	0.07	−0.22
SD4721	−0.63	−0.16	−0.22	0.94	−0.33	0.34	−0.77	−1.67	−0.31
SD4740	−0.68	−1.37	−0.04	−0.35	−0.69	−0.02	0.28	0.41	−0.31
Select	−0.55	−1.59	0.46	−0.61	−0.94	−0.38	0.05	−0.06	−0.45
SD4745	−0.51	0.86	−0.7	−1.15	0.19	−0.11	−1.48	−0.88	−0.47
Oxen	−0.39	−0.22	0.25	0.92	−0.85	−1.62	−1.85	−0.25	−0.5
SD4748	−1.42	−1.51	0.22	−0.45	−1.12	−0.03	−0.09	0.11	−0.54
Faller	−0.15	−1.33	−1.75	−0.82	−0.4	0.74	0.25	−0.95	−0.55
Briggs	−1.01	−0.93	0.1	−0.63	−0.39	−1.08	−0.41	−0.12	−0.56
SD4746	−0.39	−0.62	−0.28	−0.22	−0.85	−1.8	−0.35	−0.18	−0.59
SD4720	−1.25	0.74	−1.1	−1.43	−0.18	−0.82	−0.56	−0.85	−0.68
Steele-ND	−0.48	−0.35	−0.89	−1.28	−0.99	−1.14	−0.82	−2.96	−1.11
SD4707	−2.02	−1.24	−0.74	−0.75	−1.09	−2.32	−1.39	−0.46	−1.25
Mean	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
Std Dev	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	

Traits include: Yield (Y)*TW: test weight; Y*GPC: grain protein content; Y*DAYS: heading date; Y*HEIGHT: plant height; Y*AUDPC: area under Bacterial leaf streak disease progress curve; Y*DIS: Fusarium head blight disease index; Y*FDK: Fusarium damaged kernels; Y*DON: deoxynivalenol concentration; and INDEX: superiority index. Traits including -1 indicate those that were chosen with preference for low values.

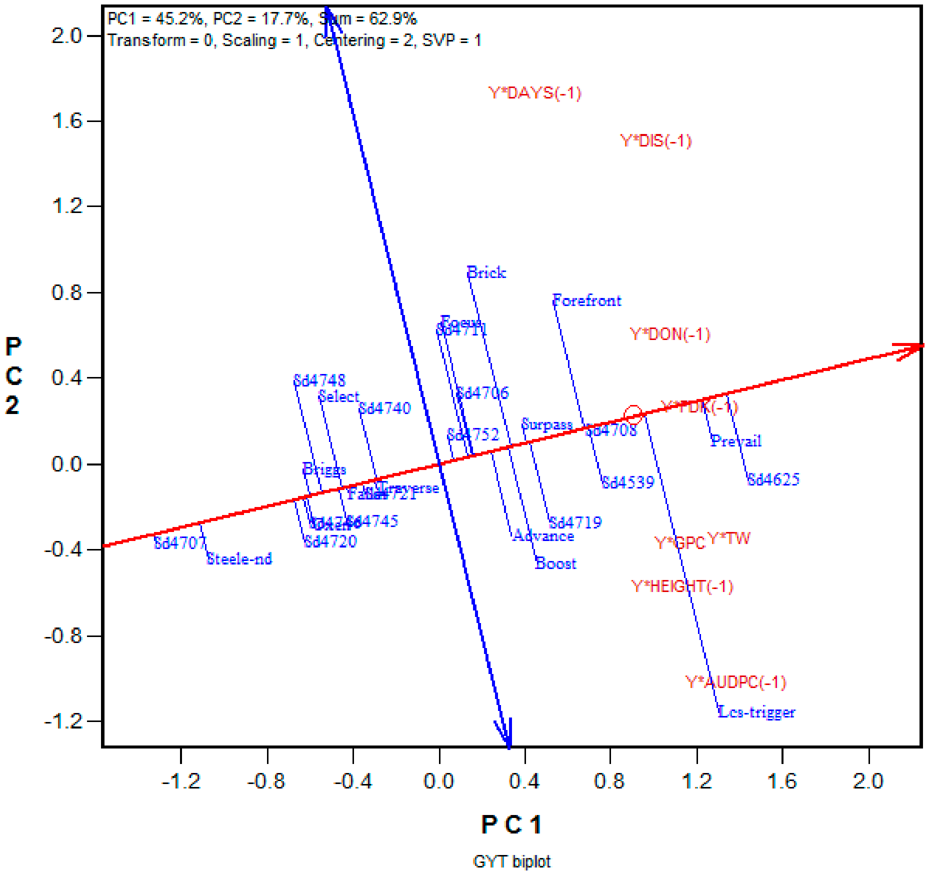

Figure 2. Average tester coordinate view of Genotype by yield*trait (GYT) biplot for consideration of overall superiority, strengths, and weaknesses of 28 hard red spring wheat genotypes grown in 2017–2018 South Dakota State University advanced yield trial based on singular value decomposition of trait-standardized data (“Scaling = 1, Centering = 2”) and genotype-focused singular value partition (“SVP = 1”). Traits include: Yield (Y)*TW: test weight; Y*GPC: grain protein content; Y*DAYS: heading date; Y*HEIGHT: plant height; Y*AUDPC: area under Bacterial leaf streak disease progress curve; Y*DIS: Fusarium head blight disease index; Y*FDK: Fusarium damaged kernels; Y*DON: deoxynivalenol concentration. Trait vector markers including -1 indicate those chosen with preference for low values.

Figure 2 is the average tester coordinate (ATC) biplot view based on genotype-focused singular value partitioning (“SVP = 1”) of the standardized GYT data (Table 3). Figure 3 is the tester vector view of the same data though based on trait-focused singular value partitioning (“SVP = 2”). Total variation depicted in the first two dimensions of this data was 62.9%. By default, the GGEBiplot software program produces Figure 2 upon completion of the GYT analysis routine. Its formulation is best-suited to focusing on genotypes while Figure 3 is best for examining relationships among yield-trait combinations [9]. In a GYT biplot analysis, each yield-trait combination includes grain yield as a component. Consequently, correlations among most yield-trait combinations tend to be positive. These relationships are easily viewed on Figure 3, though it is also immediately apparent that not all yield-trait combinations were positively correlated. The most notable example was that of the relationship between

Y*DAYS-1 and Y*AUDPC-1 ratings, which were negatively associated, though their correlation was not significant (Table 4). The characteristic of generally positive correlations among yield-trait combinations allows genotype selection to take place because a meaningful average vector can be calculated. Yield-trait combinations are equivelent to testers in a GYT biplot analysis. Figures 2 and 3 each poseess two bold lines that intersect at the biplot origin; one with a single arrow point and one that is double-arrowed. The line with a single arrow is the average tester axis (ATA). Location of the ATA on the figure denotes the average placement of all yield-trait combination vectors. The small circle located on the ATA indicates the average value of each yield-trait combination. The ATA points in the direction of high mean performance. The double-arrowed line separates genotypes with better than average overall performance from those with less than average overall performance. Since the ATA arrow points towards high performance, genotypes situated to the right of the double-arrowed line are those of most interest for selection. The double-arrowed line also provides information as to whether a genotype's triat profile was quite well-rounded or obviously strong or weak for a certain trait or group of traits. Genotypes with short projections on the double-arrowed line are more balanced while those placed farther from the ATA, regardless of direction, have obvious strong or weak characteristics.

Table 4. Pearson Product Moment correlations among eight yield-trait combinations collected from 28 genotypes grown in 2017–2018 South Dakota State University advanced yield trial.

Traits	Y*TW	Y*GPC	Y*DAYS-1	Y*HEIGHT-1	Y*AUDPC-1	Y*DIS-1	Y*FDK-1
Y*GPC	0.72						
Y*DAYS	0.14	0.09					
Y*HEIGHT	0.68	0.38	0.24				
Y*AUDPC	0.66	0.60	−0.30	0.49			
Y*DIS	0.40	0.33	0.41	0.07	0.26		
Y*FDK	0.50	0.22	0.00	0.25	0.57	0.54	
Y*DON	0.33	0.19	0.16	0.21	0.48	0.41	0.59

Thresholds for significant correlations are $P < 0.05 = 0.382$, and $P < 0.01 = 0.483$. Traits include: Yield (Y)*TW: test weight; Y*GPC: grain protein content; Y*DAYS: heading date; Y*HEIGHT: plant height; Y*AUDPC: area under Bacterial leaf streak disease progress curve; Y*DIS: Fusarium head blight disease index; Y*FDK: Fusarium damaged kernels; Y*DON: deoxynivalenol concentration; and INDEX: superiority index. Traits including -1 indicate those that were chosen with preference for low values.

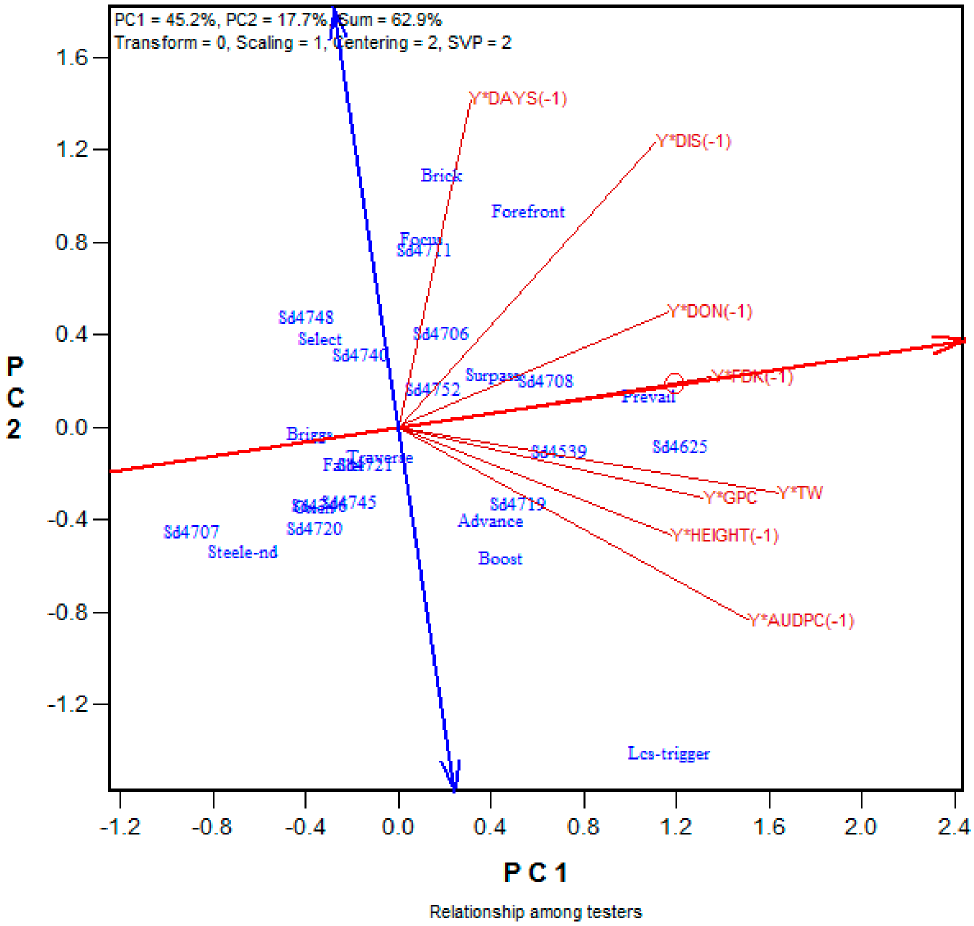

Figure 3. Tester vector view of Genotype by yield*trait (GYT) biplot for revealing associations among the yield-trait combinations of 28 hard red spring wheat genotypes grown in 2017–2018 South Dakota State University advanced yield trial based on singular value decomposition of trait-standardized data ("Scaling = 1, Centering = 2") and trait-focused singular value partition ("SVP = 2"). Traits include: Yield (Y)*TW: test weight; Y*GPC: grain protein content; Y*DAYS: heading date; Y*HEIGHT: plant height; Y*AUDPC: area under Bacterial leaf streak disease progress curve; Y*DIS: Fusarium head blight disease index; Y*FDK: Fusarium damaged kernels; Y*DON: deoxynivalenol concentration. Trait vector markers including -1 indicate those chosen with preference for low values.

With these points in mind, overall genotype performance can be judged in reference to ATA placement while strong or weak characteristics can be evaluated with respect to projections on the double-arrowed line. By moving from right to left on the ATA (Figure 2), SD4625 was found to have the best overall performance. This was followed by Prevail, LCS-Trigger, SD4539, SD4708, Forefront, SD4719, and so on. At the far left end of the ATA, "Steele-ND" and SD4707 were clearly worst in overall performance (Figure 2). Superiority index values (Table 3), calculated as the mean of standardized yield-trait combinations for each genotype, are in close agreement with overall performance gathered by observing placement order beginning from the arrow point on the ATA.

Of the genotypes ranked highest for ovrall performance, the projection of LCS-Trigger onto the double-arrowed line of Figure 2 was clearly largest, followed by Forefront, SD4625, and SD4719. Strong or weak characteristics associated with each of these genotypes could be determined through inspection of Table 3, however, Figure 2 graphically provided similar information. For example, the projection of LCS-Trigger in the direction of Y*AUDPC-1, Y*HEIGHT-1, Y*GPC, and Y*TW suggests strong performance levels with regard to those yield-trait combinations. The opposite was true of its performance concerning yield-trait combinations in the reverse direction. In actuality, LCS-Trigger had the highest standardized values among all genotypes for the Y*AUDPC-1, Y*HEIGHT-1, and Y*TW yield-trait combinations while it was lowest for Y*DAYS-1 and among the lowest for Y*DIS-1 (Table 3). Forefront was notable for its high Y*DIS-1 and Y*DON-1 and low Y*HEIGHT-1 values. SD4625 and SD4719 were generally similar, though SD4719 had lower values for Y*DAYS-1 and was among lowest of all genotypes for Y*DON-1. SD4625 was placed away from the ATA because of its high Y*TW, Y*GPC, and Y*HEIGHT-1 values. SD4708 was placed very near to the ATA indicating a consistent or well-rounded level of performance. In contrast to genotypes with high overall performance, SD4707 was ranked lowest, but also in a consistent fashion. None of its yield-trait combination values were close to average (Table 3) and this was reflected by its close proximity to the ATA (Figure 2).

DISCUSSION

Genotype by Trait Analysis of 2017–2018 AYT

Traits relating to disease resistance are typically scored in a fashion where low numerical values are preferred for selecting higher resistance while high values of other traits, like grain yield or test weight, are concurrently used for selection. To remove need for remembering which traits displayed on a GT biplot would best be selected based on high or low levels, the GGEbiplot software platform allows users to reverse individual trait vectors at will. Growers located in South Dakota prefer HRSW cultivars to be relatively early in terms of maturity and relatively short in stature. Therefore, the SDSU-HRSW breeding program usually favors genotype selections as depicted on Figure 1 (i.e., high values for grain yield, test weight, and protein content along with low values for each remaining trait). After trait vector reversal, signs of relevant correlation coefficients were adjusted to have opposite signs as presented in Table 2.

In general, the GT biplot analysis (Figure 1) revealed that FHB resistance traits were correlated amongst themselves and as a group most closely associated with test weight and then perhaps AUDPC. Table 2 revealed that was mostly the case, though DIS was not significantly correlated with neither DON nor AUDPC as might have been expected from vector placement on Figure 1. Figure 1 and Table 2 also showed that grain yield was significantly positively correlated with AUDPC, though uncorrelated with the FHB resistance traits and test weight. Placement of the grain yield vector on Figure 1 hinted that it was significantly and negatively correlated with heading date, protein content and plant height and Table 2 revealed that to be the case. Finally, the only trait significantly negatively correlated with protein content was grain yield, and none of the disease resistance traits were correlated with protein content or plant height (Table 2).

Generalities of this GT biplot analysis suggest that going forward with high-yielding materials from this genotype collection would almost certainly result in choosing those with higher than average heading date, lower than average protein content, and taller than average plant height. Interestingly, high yielding genotypes tended to have lower AUDPC levels. This may have been an artifact of previous selection cycles where genotypes with some resistance to BLS outperformed those with more susceptibility and were therefore brought to the AYT stage of development. Lastly, choosing high yielding genotypes would not necessarily influence test weight or FHB resistance traits.

Difficulties underlying genotype selection based on GT biplot analysis would be lessened in the presence of either no adverse trait interrelationships, (negative correlations) or neutral interrelationships, (no correlations) but this is not usually the situation faced by breeders. Hence, the task of genotype selection is not easily accommodated through GT analysis.

Genotype by Yield Trait Analysis of 2017–2018 AYT

Negative trait correlations that hinder genotype selections with GT biplot analysis are considerably reduced in GYT biplot analysis because a great majority of yield-trait combinations are positively correlated (Table 4). This feature of GYT analysis alone allows for creation of a useful ATA. With GYT analysis, selections are largely made based on superiority index values which correspond to ATA placement. The ATA is a virtual representation of the average yield-trait combination. Under these circumstances, negative yield-trait interrelationships would only be troublesome when compared against the ATA.

Selections from this genotype collection based on either superiority index values (Table 3) or ATA placement (Figure 2) would first include SD4625, Prevail, LCS-Trigger, SD4708, Forefront, SD4539, and so on. These genotypes produced the most grain in conjunction with possessing the highest values for other traits. Among these genotypes, LCS-Trigger and SD4708 were most distinct in terms of projections onto the double-arrowed line of Figure 2, while others had intermediate projections. These differences were indicative of strong and weak versus well-rounded performance levels. LCS-Trigger was included in the AYT as a high-yielding check and was known for its high BLS resistance, low grain protein content, and late maturity prior to analysis. Experimental genotypes with trait profiles similar to LCS-Trigger would likely have been discarded at an early point in the evaluation process, primarily because of low grain protein content, but also it was too late for most HRSW growers in South Dakota (reflected by heading date). Ultimately, such decisions are based on breeder objectives as well as his or her understanding of market requirements. Its presence within this collection does illustrate the importance of careful scrutinization of genotypes with large projections onto the double-arrowed line. For example, yield-trait vectors for Y*AUDPC-1, Y*GPC, Y*HEIGHT-1, and Y*TW were all in close proximity to one another (Figure 3) and most correlations were significant among the group (Table 4). Standardized yield-trait combination values for LCS-Trigger were highest for each of these combinations except Y*GPC, for which it was eighth highest. Likewise, its standardized yield-trait combination value was lowest of all genotypes for Y*DAYS-1, which was far removed from this group of yield-trait vectors (Figure 3). Placement of LCS-Trigger on Figures 2 and 3 was appropriate, though in the way that grain yield can contribute to success of a HRSW cultivar, low grain protein can contribute to its failure. Regardless of analysis output, from the standpoint of most experienced HRSW breeders, ranking LCS-Trigger as eighth highest for its Y*GPC yield-trait combination would seemingly exaggerate its true worth given a grain protein content that was lowest of all genotypes (Table 1). For similar reasons, Yan and Frégeau-Reid [9] suggested that entries be removed via independent culling prior to GYT analysis. This would remove those with undesirable performance levels for any trait prior to further consideration and thereby, ensure an acceptable range from which genotypes may be selected for all traits.

The choice as to whether independent culling might be carried out prior to GYT analysis would also be guided by experience and objectives of the breeder. Along with evaluating genotypes for eventual cultivar release, HRSW breeders must also choose parents for use in development of new segregating populations. Some may suggest that independent culling could reduce potential to maximize genetic diversity while selecting parents. Alternatively, when cultivar release candidates are considered, grower and end-user requirements and expectations may require culling to maintain satisfactory levels. In either case, GYT analysis is a useful approach to selection because performance for any or all traits is observed in the context of productivity (i.e., grain yield) and can be readily identified either by numerical examination, viewing the biplot image, or both.

In this instance, and from the standpoint of identifying parents, genotypes would be selected by moving leftward on the ATA or by choosing those with the highest superiority index values. As described, however, a breeder may also wish to carefully scrutinize genotypes with long projections onto the double-arrowed line to uncover the cause. Using a similar approach among experimental genotypes, those selected for further consideration towards potential cultivar release included SD4539, SD4625, and SD4708, with SD4625 being the most likely candidate. Performance levels for all agronomic and disease resistance yield-trait combinations associated with SD4625 and SD4708 were better than average (Table 3). Because SD4539 was nearly tallest among all genotypes and had a late heading date (Table 1), its performance with regard to these yield-trait combinations were less than average, though the remaining yield-trait combinations were also greater than average (Table 3).

CONCLUSIONS

This work was carried out to demonstrate use of GYT biplot analysis as a means of selecting genotypes for population development and further consideration toward eventual cultivar release. Specifically, HRSW genotypes with high agronomic performance levels and elevated resistance to BLS and FHB were identified. A GYT analysis is an extension of GT analysis where grain yield values are first combined with those of other traits to generate new yield-trait combinations. Because each yield-trait combination includes grain yield in its calculation, their correlations are generally positive. It is genotype placement with respect to the ATA and double-arrowed line on a GYT biplot image that allows for genotype selection. Alternatively, or in conjunction with a biplot image, numerical values can also be inspected for making selections.

For demonstration purposes, this work was carried out using data gathered over two growing seasons. For the purpose of cultivar release recommendation, data from a third or fourth growing season may be required. On the other hand, for parental selection, data from a single growing season could be sufficient. Regardless of the particular goal, similar analyses of different genotype collections would likely result in somewhat dissimilar correlations among yield-trait vectors, and genotype rankings would also be unique to the collection. Nevertheless, analysis and selection methods highlighted in this study would remain unchanged.

DATA AVAILABILITY

The dataset of the study is available from the authors upon reasonable request.

AUTHOR CONTRIBUTIONS

LM, KG, DY, and EB designed the study. LM and KG performed agronomic performance trials. LM, KG, DY, and EB performed disease resistance trials. LM and KG analyzed the data. LM, KG and EB wrote the paper with input from all authors.

CONFLICTS OF INTEREST

The authors declare that they have no conflicts of interest.

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