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GENETIC PARAMETER ESTIMATION FOR AGRONOMIC TRAITS IN GRAIN-ONLY AND FORAGE-PLUS-GRAIN WINTER WHEAT SYSTEMS

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Abstract

Dual purpose winter wheat utilized for both livestock forage and grain yield is frequently grown throughout the Southern Great Plains of USA, yet no cultivars to date were bred specifically under a dual-purpose management system. This research was initiated to determine whether breeders should select winter wheat genotypes in a forage-plus-grain system, or continue the current practice of indirect selection in the grain-only system. Thirty-seven random winter wheat lines were evaluated in three experiments for 3 yr at the North Central Research Station, Lahoma, OK. Each experiment represented either an early-planted forage-plus-grain (FG) system, a normal-planted grain-only (GO) system, or a forage-plus-grain control (FGC) system, in which the forage was not removed. To simulate continuous grazing, the FG experiments were mechanically clipped three to four times from November until first-hollow-stem development in late-February. Though significant genetic variation was observed among wheat lines for all traits under each system, the genotype × system interactions were not significant due to strong genetic ($r_G \geq 0.94$) and phenotypic ($r_P \geq 0.71$, $P < 0.01$) correlations. Genetic variances and heritability estimates for all traits were equal to or slightly higher in the GO system than those in FG and FGC systems. Indirect selection in the GO system was as effective as direct selection for trait improvement in the FG system. It is concluded that separate selection of wheat genotypes should not be applied in FG and GO systems.

Introduction

Winter wheat (*Triticum eastivum* L.) for forage-plus-grain production is generally exposed to the potential stresses associated with early planting and forage removal—two main features of the dual-purpose system. A selection environment that features early planting would appear essential to selecting genotypes adapted to a dual-purpose system. Reductions in grain yields of currently used cultivars with early planting in August or September compared to a mid-October planting clearly demonstrate this requirement (MacKown & Carver, 2007; Krenzer *et al*., 2000). Besides crown and root rots (Lyon *et al*., 2001), early planting also increases exposure to insects vectoring wheat streak mosaic and barley yellow dwarf viruses (Arzadun *et al*., 2006; Kelley, 2001; Lyon *et al*., 2001), which newly released cultivars do not encounter to the same degree with most breeding regimes. Additionally, the removal of forage, either by clipping or grazing, would be advantageous for selecting genotypes with optimum recovery from defoliation and grain production (Hulmel *et al*., 2005; Edwards *et al*., 2007). Perhaps, cultivar selection is conducted under the grain-only system, because it is not only easily manageable but also more economical than the forage-plus-grain system, especially one that involves actual grazing.

Selection under the grain-only system may produce genotypes with acceptable yield performance in the forage-plus-grain system if the genetic correlation between grain yield in the grain-only and forage-plus-grain systems is large and positive and if heritability of grain yield is greater in the grain-only system than in the forage-plus-grain system. Research evidence indicates that rates of genetic gain for grain yield are smaller or even nonexistent in the dual-purpose system as compared to the grain-only system (Khalil *et al*., 2002), suggesting that selection be strictly conducted under the target system (Mahmood, 2009; Ceccarelli, 1989). However, past research in the Great Plains and elsewhere have mainly focussed on cultivar response to forage removal (Shearman *et al.*, 2005; Redmon *et al.,* 1995), rather than testing breeding strategies for maximizing cultivar performance in a forage-plus-grain system.

Therefore, the objectives of this study were to 1) estimate and compare genetic parameters relevant to genetic improvement in grain-only and forage-plus-grain systems, and 2) suggest an optimum selection strategy for simultaneous genetic improvement of grain yield in the two management systems.

Materials and Methods

This study was conducted at the Oklahoma State University (USA) during 1996-97 to 1998-99 crop seasons. Thirty-seven experimental winter wheat lines and three widely adapted hard red winter (HRW) wheat cultivars were evaluated in three management systems: i) forage-plus-grain (FG); ii) forage-plus-grain control, in which the forage was not removed (FGC); and, iii) grain-only (GO). The check cultivars were, Tomahawk, Jagger, and 2174, all recognized for their adaptation to forage-plus-grain management systems.

To minimize environmental bias, the three systems were treated as independent experiments and planted adjacently in the field, using a randomized complete block design with four replicates per system. Each plot had five rows, spaced 0.23 m apart and 3 m long. Both the FG and FGC experiments were planted on 9 Sept. 1996, 28 Aug. 1997, and 18 Sept. 1998, using a seeding rate of 77 kg ha^{-1}, while the GO experiments were planted 14 Oct. 1996, 2 Oct. 1997, and 23 Oct. 1998, with a seeding rate of 58 kg ha^{-1}. To simulate continuous grazing, the FG experiments were mechanically clipped three to four times with a rotary mower to approximately 5 cm aboveground. Clipping commenced in November and was terminated when the non-clipped Jagger plots in the FGC system reached hollow stem (early jointing) development. Jagger is reputed to be very early in hollow stem development (mid to late February) among the current hard winter wheat cultivars in the southern Great Plains (Hossain *et al*., 2003; Krenzer, 2000); hence, clipping termination was often early for the experimental lines. The FGC system was included to determine if results similar to the FG system might be obtained without the added expense of forage removal. Nitrogenous fertilizer was applied according to the Oklahoma State University soil-test recommendations for a grain yield target of 3000 kg ha^{-1} in each system. The FG experiments were also top-dressed immediately following the last cutting based on a dry forage target of 3500 kg ha^{-1}, using 15 kg N for each 500 kg of harvested dry forage. All five rows of a plot in each system were combineharvested the same day. Grain yields were measured in all replicates, while 1000-kernel weight and test weight were measured in two to three of the four replicates.

Data collected for the 37 experimental lines were analyzed across years and systems using a Mixed-effects Model, with systems considered as a fixed effect, while replicates, years, and genotypes were considered random. Variance components across years in each system and their standard errors were estimated using the MIXED procedure and Covtest option in SAS (Anon., 1996). Heritability estimates were computed on an entry-mean basis in each system from the components of variance combined across years to reduce genotype-by-year bias. Exact 90-percent confidence intervals for heritabilities were determined according to Knapp *et al*., (1985). The estimate of genetic correlation, r_G, for a trait between two systems was obtained as, $r_G = COV_{G(XY)} / [V_{G(X)}\, V_{G(Y)}]^{0.5}$ where $COV_{G(XY)}$ is the genetic covariance among systems X and Y, and $V_{G(X)}$ and $V_{G(Y)}$ are the genetic variance of the same trait in systems X and Y, respectively. The genetic covariances were estimated using the MANOVA option in PROC ANOVA. Standard errors for the genetic correlations were determined according to Falconer & Mackay (1996).

Direct response, DR, to selection for a trait in system X was predicted as, $DR_X = i_X h^2_X [V_{PX}]^{0.5}$, wherein i_X is the selection intensity, h^2_X is the heritability, and V_{PX} is the phenotypic variance of the trait in system X. The correlated or indirect response for a trait in system X to selection in system Y, $CR_{X(Y)}$, was determined as, $CR_{X(Y)} = i_Y h_X h_Y r_G [V_{PX}]^{0.05}$, where i_Y is the selection intensity in system Y, h_X and h_Y are square roots of heritabilities of the trait in systems X and Y, respectively, and r_G is genetic correlation for the trait between the two systems. A similar selection intensity of 15% (i = 1.55; Falconer & Mackay, 1996) was assumed in predicting both direct and indirect selection responses.

Results and Discussion

The three management systems did not differ for average grain yield, kernel weight, or test weight, though significant interactions with years indicated that grain yield and test weight comparisons for the three systems varied during the 3-yr period (Table 1). Grain yields in the FGC system were consistently lower than the FG and GO systems during all years. Averaged across years, grain yields both in the FG and GO systems were 2700 kg ha^{-1} vs 2324 kg ha^{-1} in the FGC system, or a 14% reduction due to non-removal of excess forage or due to early planting in the FGC system (Table 2). Early planting in August or September often leads to reduced grain yields compared to the recommended early to mid-October planting dates for winter wheat (Hossain *et al*., 2003; Kelley, 2001).

Significant genetic variation was found among experimental lines for all traits, while genotype × system interactions were not significant (Table 1). Genetic variances tended to be larger in the FG and FGC systems than the GO system, but these differences were minor (Table 2). In contrast, genetic variances for 1000-kernel weight and test weight were 2- to 3-times greater in the GO system than the early-planted FG and FGC systems, while error variances for grain yield and test weight were reduced by about 30 to 60% in the GO system.

Table 1. Mean squares for grain yield, 1000-kernel weight, and test weight of 37 hard winter wheat lines evaluated in three management systems for 3 yr at Oklahoma.

Source of variation	df	Grain yield	1000-kernel weight (g^2)	Test weight $(kg\ hL^{-1})^2$
Year (Y)	2	17263	271	127815**
System (S)	2	20628	64	4160
Y x S	4	11648**	43	4554*
Reps (Y x S)	27, 15, 9†	924	28	1162
Genotypes (G)	36	11317**	32**	953**
G x Y	72	374**	3**	125**
G x S	72	146	2	81
G x S x Y	144	139**	2	66
Error	972, 540, 324†	95	1	68
Coefficient of variation (%)		12.0	4.0	1.1

†Degrees of freedom for grain yield, 1000-kernel weight, and test weight, respectively.

Table 2. Estimates of genotypic (V_G), genotype × year (V_{GY}) and residual error (V_E) variances, and means for grain yield, kernel weight, and test weight measured on 37 hard winter wheat lines in three management systems for 3 yr at Oklahoma, USA.

Trait	Parameter	Management system†		
		FG	FGC	GO
Grain yield	V_G	25734‡	29239‡	24817‡
	V_{GY}	25428‡	37545‡	28577‡
	V_E	128941	93188	63865
	Mean (kg ha^{-1})	2701	2324	2693
1000-Kernel weight	V_G	0.9‡	1.0‡	1.8‡
	V_{GY}	0.1	0.2	0.3‡
	V_E	1.3	1.7	1.3
	Mean (g)	28.9	29.3	29.8
Test weight	V_G	43‡	26‡	73‡
	V_{GY}	0	10	20‡
	V_E	68	98	39
	Mean (kg hL^{-1})	76.3	75.8	76.7

† FG = Forage-plus-grain; FGC = Forage-plus-grain control; GO = Grain-only.
‡ Variance component significantly greater than zero if the variance estimate is twice its standard error.

There was no consistent relationship between genetic variance and the magnitude of heritability (Table 3). As noted above, genetic variances for grain yield were numerically greater in the early-planted FG and FGC systems, but the resultant heritabilities were comparatively smaller than the GO system due to higher genotype-by-year and/or error variances. The differences in heritability estimates for all traits were indistinguishable based on their confidence intervals except for test weight in the GO system, which was 49% greater compared to the FGC system. Similar differences in heritability estimates for yield related traits have also been reported by Yagdi & Sozen (2009) under different environments in durum wheat. Genetic correlations among the three systems were high ($r_G \geq 0.94$) for all traits (Table 3), indicating that at least 88% or more of the genetic variation for a trait was common in any given pair of the three systems. Interestingly, the heritabilities for test weight under the GO (0.85) and FGC (0.57) systems differed significantly, but the genetic correlation between the two systems was 1.03. Thus, the grain-only environment might not only be more conducive to improving test weight but also serve as a proxy to improving test weight in the early- planted forage-plus-grain system. A genetic correlation coefficient exceeding 1.0 between selection environments was previously reported for yield in white clover (Rowe & Brink, 1993) and for several yield components in sugarcane (De Sousa-Vieira & Milligan, 1999).

Table 3. Heritabilities and genetic correlations among three management systems for grain yield, 1000-kernel weight, and test weight measured on 37 hard winter wheat lines for 3 yr at Oklahoma, USA.

Parameter	Trait	Management system†		
		FG	FGC	GO
Heritability (90% CI)	Grain yield	0.57 (0.32, 0.73)	0.59 (0.34, 0.74)	0.63 (0.40, 0.77)
	Kernel weight	0.84 (0.64, 0.86)	0.79 (0.71, 0.89)	0.88 (0.80, 0.92)
	Test weight	0.79 (0.71, 0.89)	0.57 (0.32, 0.73)	0.85 (0.75, 0.90)
Genetic correlation		FG vs/ FGC	FGC	GO
	Grain yield	0.96 ± 0.02	1.04 ± -0.02	0.94 ± 0.03
	Kernel weight	1.04 ± -0.01	0.97 ± 0.01	0.98 ± 0.01
	Test weight	1.05 ± -0.02	0.97 ± 0.01	1.03 ± -0.01

† FG = Forage-plus-grain; FGC = Forage-plus-grain control, forage not removed; GO = Grain-only.

Table 4. Predicted direct and indirect responses for grain yield, 1000-kernel weight, and test weight at 15% selection intensity for 37 hard winter wheat lines in the grain-only and forage-plus-grain systems at Oklahoma, USA.

Response system	Type of selection †	Grain yield kg ha^{-1}	Kernel weight g	Test weight kg hL^{-1}
FG	Direct in FG	187	1.4	2.3
	Indirect in FGC	183	1.3	2.2
	Indirect in GO	197	1.4	2.3
GO	Direct in GO	195	1.9	2.6
	Indirect in FGC	177	1.8	2.4
	Indirect in FG	185	1.8	2.6

† FG = Forage-plus-grain; FGC = Forage-plus-grain control, forage not removed; GO = Grain-only.

The perfect genetic (r_G = 0.94-1.0) correlations among the three systems for all traits indicate that selection in this population of wheat lines in any system is likely to produce similar responses in other systems. This was evident from the relatively small differences in predicted direct and indirect selection responses for each system (Table 4). Assuming a similar selection intensity of 15%, responses to indirect selection in the FGC system were always lower for all traits than direct selection in the FG system, excluding the possibility of considering this system as a substitute for the clipped FG system. Direct selection for grain yield in the GO system was 10% more effective than indirect selection in the FGC system, while only 2% more effective for the FG system. Similarly, direct selection for kernel weight and test weight was 6 and 8% higher in the GO, while 8 and 5% higher in the FG system, than indirect selection in the FGC system. In contrast, selection in the GO system for indirect improvement of grain yield in the FG system was 5% more effective than direct selection in the FG system. The direct responses for other traits (kernel weight and test weight) in the FG system were virtually identical in magnitude to that of indirect selection for these traits in the GO system, and *vice versa*.

Selection differentials, calculated as the difference in mean grain yield of the six highest yielding lines and the overall mean of 37 lines, from direct selection in the GO (264 kg ha^{-1}) and FG (304 kg ha^{-1}) systems were 43 and 40% greater than selection differentials from indirect selection in the FGC system (Table 5). Interestingly, the selection differential for the FG system through indirect selection in the GO system was 97 kg ha^{-1}, or 32% less than that from direct selection in FG (304 kg ha^{-1}), suggesting efficiency of direct selection under the FG system.

Table 5. Mean grain yields of six selected winter wheat lines ($\overline{X}_s$) and of the entire population ($\overline{X}_o$), selection differential (S), and expected direct and indirect responses (R) to selection in grain-only and forage-plus-grain systems at Oklahoma, USA.

Response system	Type of selection †	$\overline{X}$s	$\overline{X}$o	S‡	R§
		kg ha^{-1}			
GO	Direct in GO	2957	2693	264	166
	Indirect in FGC	2877	2693	184	116
	Indirect in FG	2948	2693	255	161
FG	Direct in FG	3005	2701	304	173
	Indirect in FGC	2918	2701	217	124
	Indirect in GO	2908	2701	207	118

† FG = Forage-plus-grain; FGC = Forage-plus-grain control, forage not removed; GO = Grain-only
‡S = $\overline{X}$s - $\overline{X}$o, wherein each mean computed across 3 yr
§R = S × h^2 (from Table 3).

Results from a companion study indicated that yield potential of a historical set of winter wheat cultivars bred in a grain-only system was not fully realized in a dual-purpose grazing system (Khalil *et al*., 2002). Our results here would suggest that progress should be expected in FG system following selection in a GO system. This discrepancy in results may be due to lower levels or different types of stresses in the forage-plus-grain system (where forage is mechanically clipped) than in a dual-purpose grazing system. To achieve maximum response under the target forage-plus-grain production system, indirect selection of early segregating generations under the grain-only system might be supplemented with simultaneous evaluation and selection in a dual-purpose system with actual grazing. This approach will increase the probability of selecting genotypes with optimum adaptation to stresses encountered in the target dual-purpose system, though a high degree of genetic spillover is expected between systems.

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