PERFORMANCE OF WINTER WHEAT

SEGREGATING FOR LEAF RUST

RESISTANCE AND AWN

EXPRESSION

By

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children in the world, I am the luckiest mother in the world. You are my inspiration, my greatest love, and my life.

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INTRODUCTION

Hard red winter wheat (*Triticum aestivum* L.) is one of the biggest crops in Oklahoma and the southern Great Plains. However, the use of awnletted hard red winter wheat (HRWW) cultivars in Oklahoma and the Great Plains region has been low due to the widespread emphasis among Great Plains breeding programs for the awned character. Many producers in the southern Great Plains region now prefer cultivars that are adapted for grazing as well as grain production. Awns in wheat, whether in the field or in bales fed to livestock, may cause mouth and eye irritation. Wheat lacking awns would then appear to be more desirable than awned wheat when wheat is used for grazing. Due to increased interest in the awnletted cultivars as a valuable source of cool season pasture for livestock, a few awnletted hard red winter wheat cultivars have been released. Previous research has shown a significant advantage of awns to grain yield and test weight especially under extreme drought conditions. Thus the awn is thought to provide some photosynthetic benefit to the wheat plant.

Just as the awn may provide some photosynthetic benefit to the wheat plant, the same benefit is provided by resistance to foliar diseases such as leaf rust. Leaf rust is caused by the pathogen *Puccinia triticina* Erikss. Leaf rust induces premature senescence of the flag leaf, thus impeding the plant's ability to photosynthesize. Leaf rust is one of the most wide spread diseases in the Great Plains, and can cause significant losses to grain yield and other agronomic characteristics. Urediniospores of *P. triticina* migrate north from Mexico and Texas via wind to Oklahoma and other Plains states in the spring. Spores can migrate as far north as Canada by the same method. Leaf rust requires warm temperatures and adequate moisture for infection and disease

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development. Spring in the Great Plains provides these optimum conditions for leaf rust development. Thus, leaf rust develops at a crucial time in Oklahoma, during the grain filling period, which results in production losses. Previous research has focused on the value of leaf rust resistance and awn expression independently. The goal of this research was to determine the individual and joint effects of leaf rust resistance and awn expression. Concerns with production of the awnletted cultivars are agronomic traits such as grain yield, test weight, and kernel weight. Other concerns are the end-use quality characteristics such as milling and flour quality, single kernel hardness, weight, and diameter.

RESEARCH AND LITERATURE REVIEW

The potential photosynthetic activity of the awns may improve kernel filling, increase grain yield, and raise test weights in the Great Plains, where drought stress and other factors may cause premature senescence of leaf tissue. Reports of the significance of awns are extensive but contradictory. A study by Evans et al. (1972) revealed that grain filling was positively affected by the presence of awns, especially under drought conditions. McKenzie's (1972) research showed awnletted lines to have higher grain yields than the awned cultivars under irrigated and non-irrigated conditions. A study by Olugbemi et al. (1976) using near-isogenic lines reported no significant difference in yields between awned versus awnletted cultivars, but kernel weight of the awnletted lines was somewhat heavier.

Differences in grain and flour quality characteristics, such as test weight, kernel weight, flour yield, and loaf volume, have been studied quite extensively. Awned cultivars of wheat (Atkins and Finney, 1957) had higher test weights, but the awnletted cultivars had slightly higher loaf volumes. Chemical, milling, and baking data indicated only slight differences. These differences were attributed to the color of the wheat and the presence of awns.

Weyhrich et al. (1994) studied the average effects of awn suppression on quality and agronomic characteristics in hard red winter wheat. Three awned cultivars (TAM 107, Century, and Mustang), and the awnletted cultivar, McNair 1003, were used to produce bulk populations containing either awned or awnletted plants. Among the characteristics analyzed were the number of spikes per meter squared (spike density), number of kernels per spike, grain yield, kernel weight, test weight, kernel texture,

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hardness, and protein content. As expected, no significant difference was found between awned and awnletted genotypes with respect to spike density. The number of kernels per spike closely followed the differences in yield. Grain yield for the awnletted TAM 107 showed a decrease of 157 kg ha^{-1} compared to awned TAM 107, while no notable difference occurred in the other two cultivars. Overall, the populations of awned wheat showed an average yield of only 6 kg ha^{-1} more than the awnletted varieties. Awn suppression did not affect kernel weight in any backgrounds. All awnletted populations had lower test weight than the awned populations. The decreases were 5.1 kg m^{-3} for Century, 10.3 kg m^{-3} for TAM 107, and 11.5 kg m^{-3} for Mustang. Awn suppression did not affect the protein concentration or kernel texture in a consistent manner. The absence of awns in the Mustang background resulted in a decrease in protein content from 128 g kg^{-1} for the awned to 125 g kg^{-1} for the awnletted populations. Kernel hardness was not changed by the presence of awns in the TAM 107 background. while the Century and Mustang backgrounds had a decrease of 16.1 and 5.3 hardness units, respectively, in the absence of awns (Weyhrich et al., 1994).

In a related study by Weyhrich et al. (1995). awns and awnletted near- isogenic lines of hard red winter wheat were evaluated for photosynthesis and water-use efficiency. This study showed that the presence of awns appeared to increase the photosynthetic capacity of the spike. Water-use efficiency (WUE) on a whole-plant basis, differed only slightly between the awned and awnletted lines. The well-watered treatments differed by 0.25 g kg^{-1} on average, with the awnletted lines having the higher WUE. For the water-stress treatments. the Mustang and Century lines differed in WUE by 0.12 g kg^{-1}, with the awned lines having the higher efficiency. The TAM 107

awnletted lines, however, had a higher WUE by 0.74 g kg^{-1}. Differences in kernel weight were observed, but no advantage of awns was found with respect to the developing kernel. Grain yield per plant did not show a definite pattern with respect to awn production. This led to the conclusion that agronomic characteristics were not affected by the increased photosynthesis of the awned spikes.

Resistance to leaf rust could provide benefits to agronomic and grain quality characteristics by extending the photosynthetic activity of the flag leaf during grain filling. *P. triticina* populations in the United States have distinct races that tend to be geographically isolated. This, along with the low amount of sexual recombination between races, results in the need for genetic mutation to occur in order for new rust races to originate. Thus, the most economical and efficient way to control the disease is through the use of resistant cultivars. Leaf rust undoubtedly affects performance and grain quality of wheat by causing decreases in grain yield, test weight, protein concentration, and kernel size. Yield losses due to leaf rust can approach 42% under heavy infection of susceptible cultivars (Cox et al., 1997). Rust resistance has, therefore, become an important trait to select for in the Great Plains. Resistance of some popular cultivars, such as Karl 92, Pioneer 2157, and Souixland has been defeated by one or more races of the pathogen. According to Singh (1993), a more diverse germplasm base is required to reduce vulnerability of future cultivars.

There are 47 alleles that confer resistance to leaf rust; of these, 23 have been transferred from outside the *Triticum aestivum* species. In 1996, three hard red winter wheat cultivars (TAM 107, TAM 200, and Century) and six BC$_2$F$_2$-derived wheat lines containing the *Lr41* gene were evaluated for various traits by Cox et al. (1997). The *Lr41*

gene was transferred from accession TA 2460 of *Triticum tauschii*, a wild diploid wheat. Traits evaluated in this experiment were grain yield, test weight, proportion of large and small kernels, hardness, flour yield, ash, color, protein concentration, mixing time and tolerance, baking absorption and mixing time, loaf volume, and crumb grain score. Differences between the backcrosses and their recurrent parents were generally non-significant in the absence of leaf rust, indicating the *Lr41* gene had a neutral effect on these traits. In the presence of leaf rust, the mean increases in grain yield for five of the leaf rust resistant backcross lines compared to their recurrent parents was 125 g m^{-2}. The mean increase in test weight was 41 kg m^{-3}, while the large-kernel fraction increased by 278 g kg^{-1}. Hardness had a mean increase of 5.8. The flour yield, color, and protein, along with the mixing time, tolerance, and bake absorption were slightly higher for the recurrent parents. This may be due to a pleiotropic effect of the *Lr41* gene, or more likely linkage drag. The backcross lines and their recurrent parents did not differ to any extent at any location for crumb-grain, loaf volume, or flour ash.

In another study, leaf rust resistance increased grain yield of spring wheat by 25% under moderate to heavy infestation of leaf rust. Milling quality and most other quality traits were increased due to the *Lr41* gene (Drijepondt et al., 1990).

Another leaf rust resistant gene, *Lr42*, was transferred from *T. tauschii*, accession TA2450. The *Lr42* gene is on chromosome 1D, is partially dominant, and is linked to the *Lr21* locus. In an experiment by Cox et al. (1994), the *Lr42* gene was studied along with *Lr41* and *Lr43* for reaction against 23 cultures of *P. triticina*. In this experiment, KS91WGRC11 (the line containing the *Lr42* gene) had low to intermediate infection types. The F$_2$ plants from the cross of KS91WGRC11 and line *Lr21*(TC) ('Tetra

Canthatch'/*T. tauschii* RL5289) segregated 50 resistant: 1 susceptible. This indicated that KS91WGRC11 containing the *Lr42* gene is linked to *Lr21*.

The objective of this research was to ascertain the individual and joint effects of leaf rust resistance and awn expression on grain yield, test weight, and various grain quality traits.

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CHAPTER II

GENE EFFECTS AND INTERACTION IN WINTER WHEAT

SEGREGATING FOR LEAF RUST RESPONSE AND

AWN EXPRESSION: AGRONOMIC TRAITS.

ABSTRACT

Incorporation of the awnletted trait into hard winter wheat cultivars would appear less detrimental to grain yield and related traits if flag leaf senescence is delayed via protection against foliar diseases. Our objective was to determine the relative benefit of awns and leaf rust resistance, both singly and in combination, to grain yield, kernel weight, and test weight. Two series of experimental lines were developed from crosses of a leaf rust-susceptible, awnletted near-isoline of 'Century' with two rust-resistant (*Lr41*- or *Lr42*-derived) awned near-isolines of Century. Field experiments were conducted in three Oklahoma environments, with varying levels of leaf rust infection. Large increases (>21%) in grain yield were found in the presence of either the *Lr41* or *Lr42* gene. averaged across awn types, relative to the susceptible controls. Negligible grain yield differences were found with respect to awn type, averaged across leaf-rust response types, though test weight increased 2 to 4% by the presence of awns. Kernel weight increased 8 to 12% with awns and 4 to 8% with leaf rust resistance averaged across the other factor. Gene interactions were generally lacking for grain yield, test weight. and kernel weight. The addition of awns provided a significant benefit to test weight and kernel weight with or without leaf rust resistance. Resistance to leaf rust provided the same proportional increase to grain yield whether in an awnletted or awned genotype, but the highest. The development of high yielding, awnletted cultivars appears achievable. but must be accompanied by selection for leaf rust resistance.

INTRODUCTION

One of the most significant diseases on hard winter wheat (*Triticum aestivum* L.) is leaf rust, caused by *Puccinia triticina* Erikss. Leaf rust attacks the living plant tissue and disrupts the epidermis. Yellowish-red pustules of urediniospores appear on the leaf surface first, then turn black (indicating the formation of teliospores), and eventually cause early leaf senescence. When rust attacks the photosynthetically active flag leaf, losses may occur in grain yield and other quality characteristics depending on the intensity and duration of infection (Cox et al., 1997; Drijepondt et al., 1990). Therefore, protecting the wheat plant from rust is an important breeding objective in the southern Great Plains, and many genes are being transferred into wheat to select for rust resistance (Singh, 1993).

Just as leaf rust resistance preserves photosynthetic activity late during the grain-filling period, photosynthetic benefits are believed to be provided also by the awns. Photosynthate produced by awns may partially support kernel filling, and thereby impact grain yield and test weight compared to awnletted genotypes (Weyhrich, 1994). Interest in awnletted cultivars has increased recently in the southern Great Plains where winter wheat can be used as a full-season, cool-season pasture resource. However, awns may decrease the palatability of wheat and cause mouth and eye irritation in cattle. Thus, awnletted cultivars adapted for this region would have extended usage for late season grazing, in addition to serving the traditional role as a grain source.

The value of awns to wheat production in the southern Great Plains may be most critical for leaf-rust susceptible genotypes, if heavy rust infection causes premature senescence of the flag leaf. Conversely, the presence of effective leaf rust resistant genes

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might compensate for the absence of awns in awnletted genotypes. This research was designed to determine the relative benefits of awns and leaf rust resistance, as governed by the action and interaction of single genes. Field experiments were conducted under conditions of natural infection of leaf rust to estimate the effect of awn expression in leaf rust-susceptible versus leaf-rust resistant near-isogenic lines. Our analysis will focus in this paper on grain yield, kernel weight, and test weight.

MATERIALS AND METHODS

Two series of experimental lines were developed with the intent to restrict genotypic variation, except for genes segregating for leaf rust resistance and awn production. Each series featured a different leaf rust resistance gene derived from two germplasms in a common background, 'Century'. The first, designated KS93U50, is a selection from KS91WGRC11 (PI 56668) with the pedigree Century*3/TA2450, where TA2450 is a *T. tauschii* accession containing *Lr42*. K91WGRC11 seedlings produce low infection types when inoculated with several cultures of *Puccinia triticina* Erikss (PRTUS19, PRTUS24, and PRTUS25). The second germplasm, designated KS93U62, contains the resistance gene *Lr41*, and has the pedigree Century*3/TA2460, where TA2460 is another accession from *T. tauschii* (Cox et al., 1994)

KS93U50 and KS93U62 were each crossed with OK92G205 (PI 561731), an awnletted near-isoline of Century with the pedigree Century*5/'McNair 1003' (Carver et al., 1993). McNair 1003, a soft red winter wheat, was the donor of the awnletted gene. Each cross (KS93U50/OK92G205 and KS93U62/OK92G205) produced an F_2 population co-segregating at one of the leaf rust resistance loci (*Lr42* and *Lr41*, respectively) and a locus controlling awn production. Phenotypes were scored among >200 F_2 plants per cross grown in the greenhouse at Manhattan, KS, with artificial inoculation of seedlings with *P. triticina*. Four classes were identified: resistant, homozygous awned; susceptible, homozygous awned; resistant, homozygous awnletted; and susceptible, homozygous awnletted. Heterozygosity could be identified at the awn locus by intermediate expression of awn production, relative to the two classes (Wehyrich et al. 1994). The homozygous condition for leaf rust response was confirmed the following generation by

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evaluating $F_{2:3}$ families in the field (natural infection) at Stillwater, OK. Selected

families representing the four genotypic classes were grouped according to their original

cross (series 42A, KS93U50/OK92G205; series 41A, KS93U62/OK92G205) for further

testing (Table 1).

A third series was developed from crosses of KS93U50 and KS93U62 with

OK92G206, an awned near-isoline of OK92G205 (PI 561733)(Carver et al., 1993). This

series allowed additional determination of the value of leaf rust resistance, independent of

segregation for awn production. Resistant and susceptible awned genotypes were

combined into a single series (4142) from both crosses (Table 1). Selection procedures

were as described above for Series 42A and 41A.

Each series of lines were arranged in the field in a randomized complete block

design with four replications. In addition to the experimental lines, checks included

parents of the crosses, KS93U50, KS93U62, OK92G205, and OK92G206. Other checks

were 2174, a locally adapted cultivar with adult-plant resistance to leaf rust, and

WGRC15 (PI 566669), which has the pedigree 'Karl'// 'TAM 200'/KS86WGRC2

(*Lr21*). Adult plants of WGRC15 exhibit low leaf rust infection types.

The same cultural practices were applied to each series, including fertilizer

application (according to soil-test recommendations for a 2600 kg ha^{-1} yield goal),

planting date (grain-only management system), and plot size (either 1.38 m^2 or 3.45 m^2,

depending on the year). Disease development was dependent entirely on natural

infection, and was monitored on flag leaves during grain filling.

Experiments were conducted at Stillwater, OK in 1998 and at Stillwater and

Lahoma, OK in 1999. Leaf rust reaction was determined according to the modified Cobb

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scale (Peterson et al., 1948) and on a 1-to-9 scale. The 1-to-9 scale was a stay green scale, representing increasing levels of susceptibility, with 1= 4 leaves below the flag leaf mostly green; 2= 3 leaves below the flag leaf mostly green; 3= 2 leaves below the flag leaf mostly green; 4= pentultimate and flag leaf mostly green; 5= flag leaf mostly green; 6= flag leaf partially chlorotic; 7= flag leaf mostly chlorotic; 8= flag leaf severely chlorotic; 9= flag leaf necrotic (Table 2). The pathogenicity of the leaf rust population was monitored to help define the interaction between the wheat crop and *P. triticina* Erikss races occurring in the field plots. Bulk collections of urediospores were used from three Oklahoma locations (Kingfisher, Apache, and Lahoma) to inoculate a set of single-gene differentials and appropriate check cultivars. This information was used to determine the avirulence/virulence formula of the bulk collections, which was helpful in determining the presence of additional *Lr* genes in the test lines. Agronomic traits measured were grain yield, test weight, and 1000-kernel weight (based on a random 200-kernel sample per plot).

RESULTS AND DISCUSSION

Losses in grain production due to leaf rust can vary depending on disease severity. The severity observed in this study was sufficient to visually discern differences in rust infection of adult plants. General appearance of the flag leaf and lower leaves was summarized by a stay-green reading taken approximately two weeks after heading (mid-May) (Table 2). Readings in both years were indicative of the degree of chlorosis and necrosis caused primarily by leaf rust. Mean values for the four genotypic classes showed distinct differences between the resistant (flag leaves mostly green) and susceptible lines (flag leaves mostly chlorotic to necrotic). Divergence of susceptibility vs. resistance was more visually apparent among near-isogenic lines segregating for the *Lr41* gene than for the *Lr42* gene, as reflected in the difference between stay-green readings between *S* and *R* lines.

Flag leaf readings based on the modified Cobb scale showed no visible infection for the resistant lines in the *Lr41* series, while their near-isogenic susceptible lines showed a consistently high severity rating and susceptible infection type (Table 2). The resistant lines in the 42A series showed minimal visible infection (hypersensitive reaction), while the susceptible lines showed a severity rating of 65 to 90% susceptibility. Again, susceptibility was not as apparent, using this scale of rust response, among lines segregating for *Lr42*. As expected, no visual differences were noted in leaf rust reaction between awned and awnletted lines within rust response types. Rust reactions of seedlings were consistent with adult-plant reactions for lines segregating for *Lr41* resistance but not for lines segregating for *Lr42* (Table 2).

Genetic variation among the experimental lines was partitioned in an analysis of variance (not shown) for comparing means (as main effects) of resistant versus susceptible near-isolines and awned versus awnletted near-isolines, and for determining their interaction (Table 3). Averaged across awn types, grain yield declined by 39% (series 41A) and by 21% (series 42A) in lines lacking the corresponding gene for leaf rust resistance. Averaged across rust response types, grain yield declined by 6% (41A) in awnletted lines compared to their near-isogenic, awned sibs; however, the difference was not significant in the 42A series. In the 41A series only, the addition of awns increased grain yield regardless of rust response type (no interaction of rust response type x awn type), but in the 42A series, awns provided no additional benefit to grain yield in the presence of *Lr42* (interaction significant at P=0.05).

Lines which were both leaf-rust resistant and awned held a distinct advantage for grain yield (Table 3). However, the relative benefits of these two traits were not equal. Leaf rust resistance was highly beneficial to grain yield, whereas the contribution of awns was small to none. The awnletted character is perceived to be detrimental to grain yield in the Great Plains; indeed, only two cultivars have occupied significant acreage in the past 10 to 15 years – 'Longhorn' and more recently 'Lockett'. Our data show that in the presence of moderate to severe leaf rust pressure, the incorporation of leaf rust resistance deserves greater attention than preservation of the awned character when improving grain yield.

Genotypic class responses in test weight and kernel weight were similar and will thus be considered concurrently. Previous research has shown a significant advantage to test weight through leaf rust resistance (Drijepondt et al., 1990) or by the presence of

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awns (Weyhrich et al., 1994). Averaged across awn types, test weight declined by 3.0 to 4.0%, depending on the series, in lines lacking the corresponding gene for leaf rust resistance (Table 3). Averaged across rust response types, test weight declined by 1.7% in awnletted lines of both series compared to their near-isogenic, awned sibs. Kernel weight declined in proportionate amounts, though the percentage decreases (ranging from 4.2 to 12.2%) were larger than for test weight. We found a slight advantage to emphasizing rust resistance over awn type. Resistant, awned genotypes produced the largest kernels with highest test weights, whereas susceptible, awnletted genotypes had the opposite effect. Differences between these two classes amounted to about 40 kg m^{-3} in test weight, or about 4 g in 1000-kernel weight, approximating between the two series. The absence of awns in a resistant genotype was less detrimental to test weight and kernel weight than the lack of resistance in an awned genotype.

A third series of lines (series 41/42) segregated for the same leaf-rust resistance genes but was non-segregating for the awned character. This series allowed direct comparison of the two sources of leaf rust resistance because the derived lines were evaluated in the same field experiments. Averaged across the two resistance genes *Lr41* and *Lr42*, grain yield declined by 29%, test weight declined by 2.7%, and kernel weight declined by 10.1% in lines lacking the gene for leaf rust resistance (Table 4). These results provide additional verification of the benefits of leaf rust resistance and are consistent with the main effects determined independently for series 41A and 42A (Table 3, R vs. S main effect). Resistant lines of the two gene sources did not differ for yield or test weight, but the susceptible lines derived from the *Lr42* source had greater grain yield than susceptible lines derived from the *Lr41* source. The greater divergence in yield

among *Lr41*-derived *R* and *S* lines was not surprising considering the wider separation in visual ratings of rust infection and damage observed on flag leaves (Table 2).

Our results show that genes conferring rust resistance and awn production act largely independently. The agronomic value of *Lr41* and *Lr42* exceeded expectations based on our own unpublished observations and limited published results (Cox et al., 1997). The addition of awns proved beneficial to test weight and kernel weight in resistant and susceptible genotypes, but did not provide a consistent yield advantage, and certainly not on par with the yield advantage of rust resistance. Genotypes which were both susceptible to leaf rust and awnletted were consistently lower yielding, and they had lower test weight and kernel weight. This genotype should be avoided in hard winter wheat selection programs. The development of high-yielding, awnletted cultivars appears to offer promise in hard winter wheat breeding programs as long as resistance to leaf rust is maintained and selection for test weight and kernel weight is adequately applied.

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Table 1. Summary of F$_2$-derived hard red winter wheat lines selected for differential leaf rust reaction and presence of awns.

Series	Pedigree	Respone Type	Awn type	No. of genotypes
41A	KS93U62/OK92G205	Resistant	Awned	6
			Awnletted	10
		Susceptible	Awned	10
			Awnletted	6
42A	KS93U50/OK92G205	Resistant	Awned	11
			Awnletted	8
		Susceptible	Awned	7
			Awnletted	6
4142	KS93U50/OK92G206	Resistant	Awned	6
		Susceptible	Awned	7
	KS93U62/OK92G206	Resistant	Awned	11
		Susceptible	Awned	8

Table 2. Adult plant and seedling responses of near-isogenic experimental lines with 'Century' background, including several checks.

Experimental line series or checks	Genotypic class description			No. of genotypes	Stay-green[+] rating (1-9)	Predominant[+] leaf rust reaction	Seedling[§] response
	Rust response type	Rust gene source	Awn type				
Series							
41A	R[¶]	*Lr41*	Awned	6	5.0	0R	;
			Awnletted	10	4.9	0R	;
	S		Awned	10	8.7	90S	3+
			Awnletted	6	8.7	90S	X3cn;
t(SD)[#]					1.3		
42A	R	*Lr42*	Awned	11	5.3	0-1R	X3-cn;
			Awnletted	8	5.1	0-1R	3cn
	S		Awned	7	7.5	65-90S	X3-cn;
			Awnletted	6	7.6	65-90S	3cn
t(SD)[#]					2.4		
41/42	R	*Lr41*	Awned	6	5.0	0R	;
	S			7	8.8	80-90S	X3cn;
	R	*Lr42*		11	5.9	0R	X3-cn;
	S			8	8.5	40-65S	3cn
t(SD)[#]					1.5		
Checks							
Danne[††]	S	-	-	-	-	-	3
Lr19[††]	R	-	-	-	-	-	;
Century isoline	S	-	Awned	-	8.8	90S	X3cn;
Century isoline	S	-	Awnletted	-	8.9	90S	3cn
KS93U62	R	*Lr41*	Awned	-	4.8	0R	;
KS93U50	R	*Lr42*	Awned	-	5.4	0-1R	X3-cn;
McNair 1003	S	-	Awnletted	-	-	-	3

[+] Taken approximately two weeks after heading at Stillwater. OK during May 1998 and 1999, where 5=flag leaf mostly green and 9=flag leaf necrotic.

[+] Modified Cobb scale, recorded 19 May 1998 at Stillwater on adult plants.

[§] Results of single-gene differential observed in 1999 according to E.C. Stakman (USDA Bull. #E617. 1962. 153 pp.)

[¶] R= resistant, S=susceptible to leaf rust.

^a Compute LSD(0.05) as $t(SD)([n_1 + n_2]/n_1n_2)^{1/2}$, where n_1 and n_2 are the number of observations (no. of genotypes x replications [4] x no. of environments [3]) used to compute each mean.
^{††} Only used for seedling tests.

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Table 3. Means for grain yield, test weight, and kernel weight of near-isogenic wheat lines selected for differential leaf rust reaction and awn expression and evaluated in three Oklahoma environments.

Rust Response	Awn Type	No. of genotypes in class 41A	42A	Grain yield 41A	42A	Test weight 41A	42A	1000 kernel weight 41A	42A
		----------no.--------		---------kg ha⁻¹------		------- kg m⁻³-------		------------g------------	
Main effects									
R	A', A⁻	16	19	2880**	2970**	720**	726**	26.3**	26.5**
S	A', A⁻	16	13	1770	2350	688	704	23.1	24.3
R, S	A'	16	18	2400**	2700	710**	721**	25.5**	25.9**
R, S	A⁻	16	14	2260	2620	698	709	24.0	24.8
Interactions									
R	A'	6	11	2930	2930	729	731	27.4	26.9
	A⁻	10	8	2840	3010	712	721	25.3	26.0
S	A'	10	7	1870	2460	692	711	23.6	24.9
	A⁻	6	6	1680	2230	684	697	22.7	23.6
t(SD)‡				1413	1356	63	59	8.7	6.1

** Main-effect means (resistant vs. susceptible or awned vs. awnletted) significantly different at the 0.01 level of probability according to F-test.

† R=resistant, S=susceptible to leaf rust; A⁺=awned, A⁻=awnletted; 41A=lines co-segregating for $Lr41$ resistance and awns; 42A=lines co-segregating for $Lr42$ resistance and awns.

‡Compute LSD(0.05) as $t(SD)([n_1 + n_2]/n_1 n_2)^{1/2}$, where n_1 and n_2 are the number of observations (no. of genotypes x replications [4] x environments [3]) used to compute each mean.

Table 4. Means for grain yield, test weight, and kernel weight of near-isogenic awned wheat lines selected for differential leaf rust reaction and evaluated in three Oklahoma environments.

Resistance gene source	Genotypic class description[+]		Grain yield	Test weight	1000-kernel weight
	Rust response	No. of genotypes in class			
			kg ha^{-1}	kg m^{-3}	g
Main effects					
Lr41	R, S[+]	19	2330*	720**	26.6
Lr42	R, S	13	2430	730	26.2
Lr41, Lr42	R	17	2780**	730**	27.8**
Lr41, Lr42	S	15	1980	710	25.0
Interactions					
Lr41	R	11	2850	730	28.4
	S	8	1820	700	24.8
Lr42	R	6	2700	740	27.3
	S	7	2150	710	25.2
t(SD)[+]			1063	33	5

*, ** Main-effect means significantly different at P=0.05 or 0.01, respectively (*Lr41* vs. *Lr42* background or resistant vs. susceptible) according to F-test.

[+] R=resistant lines; S=susceptible to leaf rust.

[+] Compute LSD(0.05) as t(SD)[(n$_1$ + n$_2$)/n$_1$n$_2$]$^{1/2}$, where n$_1$ and n$_2$ are the number of observations (no. of genotypes x replications [4] x environments [3]) used to compute each mean.

CHAPTER III

GENE EFFECTS AND INTERACTIONS IN WINTER

WHEAT SEGREGATING FOR LEAF RUST

RESPONSE AND AWN EXPRESSION:

QUALITY TRAITS.

ABSTRACT

The value of awns to quality characteristics would seem to be less critical if adequate protection against foliar diseases is achieved. Our objective was to ascertain the individual and joint effect of leaf rust resistance and awn expression on various quality characteristics. Two series of near-isogenic lines were developed with the intent to restrict genetic variation among experimental lines. Each series featured a different seedling resistance gene, transferred from the wild diploid wheat *Triticum tauschii*. Field experiments were conducted in three Oklahoma environments, Stillwater in 1998, and Stillwater and Lahoma in 1999. Quality characteristics measured were grain protein, kernel size, hardness, and weight, based on the single kernel characterization system, NIR spectroscopy, and mixing properties. Hardness values were higher for the awnletted lines. A significant interaction was observed for the 42A series. Lines which were resistant had lower hardness values for the 41A series, but lines segregating for the *Lr42* gene had the opposite effect. Leaf rust resistance increased kernel weight 8 to 12%, averaged across awn type. The presence of awns increased average kernel weight approximately 4%, averaged across rust response. Average kernel diameter followed the same trend as kernel weight, with significant increases of 5 to 8% for the resistant lines, averaged across awn type. Awn production increased kernel diameter 3.5% in both series. Flour protein was significantly increased in the resistant lines averaged across awn type for lines segregating for the *Lr41* gene. Significant increases were observed in the 42A series for flour yield, but increases for the 41A series were non-significant. Sedimentation volume was decreased by rust resistance, averaged across awn type, in the 41A series. Rust resistance or awn expression had little effect on mixograph properties.

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Significance was only observed in the 42A series for resistance to mixing. The value of leaf rust resistance proved to be more beneficial to quality characteristics overall than the presence of awns. However, for flour properties such as flour protein and flour yield significance was more affected by the gene conferring resistance.

INTRODUCTION

Wheat (*Triticum aestivum* L.) is one of the world's most important food crops. Processing characteristics of wheat such as milling yield, kernel texture or hardness, protein content, and mixing properties are as equally important to the breeder as agronomic characteristics. Wheat with poor quality is of little value to producers and processors, so maintenance of acceptable end-use quality is a critical component of yield improvement in cultivar development programs.

Leaf rust (*Puccinia triticina* Erikss.) is a serious yield deterrent in southern Great Plains wheat production. The disease forces premature senescence of the flag leaf, thus cutting off a critical supply of photosynthate to the developing grain. The most economically feasible way to protect against leaf rust is through production of resistant cultivars. Besides the expected benefit to reduction in yield losses, leaf rust resistance may also reduce losses in grain quality. Cox et al. (1997) found that resistant genotypes with the *Lr41* gene had higher kernel hardness, flour yield, and flour protein content than their susceptible counterparts lacking the *Lr41* gene. The incorporation of resistance genes may, however, introduce undesirable genes, via linkage drag that may produce a net loss in quality. For example, the *Lr34* gene actually reduced flour yield, sedimentation volume, and mixograph mixing time (Drijepondt et al., 1990).

Awns are perceived to enhance grain yield, particularly when disease pressure or harsh climatic conditions forces premature senescence of the flag leaf. Effects on grain quality were reported by Weyhrich et al. (1994) and found no significant effect of awns on kernel hardness or protein content. McNeal et al. (1969) evaluated awnletted and awned backcross breeding lines of spring wheat for flour quality and found that the

awnletted population had 3.7% higher flour yield than the awned population. Differences were not observed in flour protein or mixing time. However, loaf volume for the awnletted population was higher. These results do not necessarily pertain to hard winter wheat, nor would they be necessarily expected to occur in the Great Plains environments.

Field experiments were conducted to further clarify the individual and joint effects of leaf rust resistance and awns on grain quality, using near-isolines to increase the precision of estimating gene effects. We examined the *Lr41* gene due to its current adoption in bread wheat programs in the Great Plains, as did Cox et al. (1997), but expanded our study to include the *Lr42* gene, also currently deployed in breeding programs. We were especially interested in knowing if leaf rust resistance may compensate for the lack of awns, or reciprocally, if the presence of awns may compensate for the lack of resistance. We chose to examine quality characteristics subjected to constant selection pressure in hard wheat breeding programs. These included grain protein, kernel size and texture based on the single kernel characterization system and NIR spectroscopy, and mixing properties.

MATERIALS AND METHODS

Experimental materials consisted of two series of near-isogenic lines, each featuring a different seedling resistance gene. Materials were developed to restrict genotypic variation, except for genes segregating for leaf rust resistance and awn expression. Each series was developed by the same method within the 'Century' background. Sources of leaf rust resistance were $Lr41$ and $Lr42$, tranferred from the wild diploid wheat, *Triticum tauschii* (Cox et al. 1994). KS93U50 (Century*3/TA2450; $Lr42$) and KS93U62 (Century*3/TA2460; $Lr41$) were each crossed with OK92G205 an awnletted near-isoline of Century, with the pedigree Century*5/'McNair 1003' (Carver et al., 1993). Each cross (KS93U50/OK92G205 and KS93U62/OK92G205) produced an F_2 population co-segregating for leaf rust response and awn type. Four homozygous genotypic classes were identified in the F_2 generations of each cross: resistant awned, resistant awnletted, susceptible awned, and susceptible awnletted. Multiple lines were developed for each genotypic class as described in Chapter II. The two series of lines, each containing a different leaf rust resistance gene, will be referred to as 41A (KS93U62/OK92G205) and 42A (KS93U62/OK92G205).

The two series of lines were arranged in the field in separate randomized complete block designs with four replications each. Tests were conducted in three Oklahoma environments: Stillwater in 1998, and Stillwater and Lahoma in 1999. In addition to the experimental lines, the following checks were used: 2174, a locally adapted cultivar; parents of the original crosses; and WGRC15 a leaf-rust resistant germplasm containing the $Lr40$ gene (PI 566669). The same cultural practices were

applied to each series as described in Chapter II. Disease development was dependent entirely on natural infection.

To determine milling and flour quality 125 g grain samples were taken from two replicates of each line at Stillwater, OK in 1998 and 1999. These samples were cleaned and tempered to a moisture basis of 155 g kg^{-1}. Samples were then milled using a laboratory scale Brabender Quadrumat senior mill (C. W. Brabender Instruments, South Hackensack, NJ). Flour yield was determined by weighing three flour streams per kg of tempered wheat. Flour protein concentration was determined by NIR spectroscopy using InfraAlyzer 400 (Tarrytown, NY) according to method 39-70 (AACC, 1983), and was adjusted to a moisture basis of 140 g kg^{-1}.

Mixograph characteristics were measured with a National Manufacturing Co. mixograph (Lincoln, NE). Approximately 10 grams of flour was used for this test (Method 54-40, AACC 1983). Mixing time was estimated by the number of minutes needed to achieve peak development of the dough. The mixograph curve of each sample was scored to measure tolerance to overmixing using a scale of 1 to 10: 1-2, weak; 3-6, acceptable; 7-10, highly tolerant. Mixing tolerance was estimated by measuring the width of the curve 2 minutes after the peak.

Sodium dodecyl sulfate (SDS) sedimentation was measured according to Lorenzo and Kronstad (1987) to predict potential loaf volume. A 4.3 g flour sample was suspended in a 100-mL solution containing 0.96 g lactate liter^{-1}. The samples were allowed to settle for 30 minutes, the volume of the precipitate was recorded, and the final volume was expressed as a ratio with flour protein content.

Kernel hardness and whole-grain protein were determined on separate samples collected in these replications of three environments: Stillwater 1998 and 1999, and Lahoma in 1999. These samples were ground on an Udy Cyclone Sample Mill with an Udy Sample Mill Feed Controller (Fort Collins, CO) and measured for NIR hardness and protein via the Technicon InfraAlyzer 400. Values for protein were adjusted to 140 g kg^{-1} moisture basis before data analysis.

An additional 25-g sample was taken from three replications and the same three environments to determine single kernel hardness, kernel weight, and kernel diameter using the Perten Single Kernel Characterization System (Perten Instruments, NA, Reno, NV).

Data was combined across three environments after determining error homogeneity, and then analyzed using Statistical Analysis System procedures. Genetic variation was partitioned into single-degree of freedom contrast of resistant versus susceptible, awned vs. awnletted, and their interaction. The error term used for testing their effects was variation pooled within classes.

RESULTS AND DISCUSSION

Environmental conditions for natural infection of leaf rust were adequate to visually differentiate between resistant and susceptible lines. Distinguishing between resistant and susceptible lines was visually more apparent in lines segregating for the *Lr41* gene than lines segregating for the *Lr42* gene as discussed in Chapter II.

Due to its kernel hardness, hard red winter wheat is best suited for the production of bread flour (Cornell and Hoveling, 1998). Hardness values for both series were above the acceptable criteria of >40. NIR hardness and single kernel hardness tests in this experiment showed a significant increase for the resistant lines segregating for the *Lr41* gene, averaged across awn type (Table 1). A substantial increase in single kernel hardness was observed in the awnletted lines, averaged across rust response in the 41A series. A significant interaction was observed for single-kernel hardness in the 42A series. This interaction was likely due to the susceptible awned lines having higher hardness values than the resistant awnletted lines (according to LSD tests). Significantly larger increases in single-kernel hardness were observed in the awnletted genotypes (vs. the awned) in the susceptible background compared to the resistant background. Resistance to leaf rust and the presence of awns significantly increased kernel weight in both series. Kernel weight was increased 12.3% for the resistant lines, averaged across awn type in the 41A series. The main effects of awns provided about half the benefit to kernel weight as rust resistance. Awned lines in the 41A series produced 4.8% heavier kernels than their awnletted sibs. Kernel diameter, like kernel weight, was positively affected by the presence of awn and rust resistance. Kernels for the 41A resistant lines

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were 8.3% larger than the susceptible lines, averaged across awn type. Awned lines, averaged across rust response, were 3.5% larger than awnletted lines in the 41A series.

Lines segregating for the *Lr42* gene followed the same trend as the *Lr41* series, with significant benefit provided by the presence of awns and resistance to leaf rust. However, the percent decrease in kernel weight and diameter for the susceptible lines, averaged across awn type, and awnletted lines, averaged across rust response, was much smaller than the 41A series. Kernel weight in the 42A series was increased 8.2% for the resistant lines averaged across awn type. The presence of awns provided a 4.0% increase (averaged across rust response) in kernel weight. Increases of 5.5% were observed in kernel diameter for the resistant lines compared to their susceptible sibs. The main effect of awns substantially increased kernel diameter 3.5% for the 42A series (Table 1). Resistance to leaf rust was beneficial to kernel weight and kernel diameter for both series. Lines which were susceptible and awnletted were at a distinct advantage for hardness.

In preparing a wheat blend for milling, protein quality and quantity are two important considerations. Near-infrared reflectance is now used as a faster means for determining protein quantification (Posner and Hobbs, 1997). Grain protein concentration measured by NIR in this experiment showed no observable differences for either series (Table 2). Flour protein, however, was significantly increased 3% by the presence of leaf rust resistance in the 41A series (main effects). Means for the awned and awnletted lines, averaged across awn type were almost identical.

Flour yield plays a major part in the buying decision of millers. If a cultivar of wheat fails to meet the standards of millers it may be rejected regardless of other satisfactory characteristics (Posner and Hibbs, 1997). Flour yield was positively affected

by leaf rust resistance in the 42A series; with a 2% increase for the resistant lines averaged across awn type (Table 2). Awned lines averaged across rust response showed minimal increases in flour yield for both series.

SDS sedimentation is a measure of potential loaf volume using sodium dodecyl sulphate, which maximizes separation of flours with contrasting loaf volumes (Carver, 1994). Observable decreases were found in the 41A series for the resistant genotypes, averaged across awn type (Table 2). Drijepondt et al. (1990) studied the effects of the *Lr34* resistance gene on leaf rust development, on grain yield and baking quality in wheat. Results of this study showed that the presence of the *Lr34* gene generally reduced SDS-sedimentation volume. In this experiment, sedimentation values were decreased with respect to rust resistance. Awns did not effect sedimentation values, averaged across awn type (Table 2).

Physical dough properties measured in this experiment were mixing time, mixograph rating, and mixing tolerance, using the mixograph method (AACC Method 54-40A). These characteristics have been used by breeders to determine desirable bread making potential in early-generation selection of genotypes (Carver, 1994). Short mixing times were observed in this study was not effected by rust response or awn type. Mixing time was in the questionable range for both series, with times ranging form 4.5 to 6.4 minutes (Table 3). In a study by Lofgren et al., (1967), evaluating awnletted and awned backcross breeding lines of bread wheat, no differences were found for mixing times. Ratings for mixograph were not consistent with respect to awn type, and no significant differences were found for rust response or awn type. Mixing tolerance was well above the acceptable level of >3 mm for both series. A significant 15% larger curve width was

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observed for the susceptible lines in the 42A series, averaged across awn type. No differences were observed for mixing tolerance with respect to awn type, averaged across rust response for either series.

Overall resistance was beneficial to kernel weight, kernel diameter, flour protein, and flour yield. However, benefit varied dependent on resistance gene source. Resistance in lines segregating for *Lr41* provided significant benefit to NIR and single-kernel hardness, kernel weight and diameter, and flour protein. Awns in the 41A series provided benefit to kernel weight and diameter. However, awns were not beneficial to single kernel hardness in the 41A series. Resistance in lines segregating for *Lr42*, provided benefit to kernel weight, kernel diameter, and flour yield. The presence of awns in this series significantly increased kernel weight and diameter. Mixograph properties showed few differences for rust response or awn type. Resistance to leaf rust compensated for the lack of awns in this experiment, with respect to kernel weight, kernel diameter, and flour yield. The value of leaf rust resistance was more apparent to quality characteristics than the presence of awns. However, in a susceptible background the presence of awns was beneficial to kernel weight and diameter. Awnletted cultivars with acceptable quality characteristics appears to be achievable as long as rust resistance is maintained.

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Table 1. Means for physical characteristics of near-isogenic wheat lines selected for differential leaf rust reaction and awn expression and evaluated in three Oklahoma environments.

	Genotypic class description[†]					Single Kernel Characterization					
Rust response	Awn type	No. of genotypes in class		NIR hardness		Average kernel hardness index		Average 1000-kernel weight		Average kernel diameter	
		41A	42A	41A	42A	41A	42A	41A	42A	41A	42A
						-----0 – 150----		----------g----------		--------mm--------	
Main effects											
R	A⁻, A⁻	16	19	48.2*	50.5	76.7*	75.0**	26.0**	25.6**	2.04**	2.00**
S	A⁺, A⁻	16	13	46.2	50.7	76.4	76.7	22.8	23.5	1.87	1.89
R, S	A⁺	16	18	47.0	49.9	75.4**	75.2**	25.0*	25.1**	1.99*	1.98**
R, S	A⁻	16	14	47.4	51.3	77.7	76.5	23.8	24.1	1.92	1.91
Interactions											
R	A⁻	6	11	48.2	50.2	75.3	74.8	26.9	26.0	2.09	2.03
	A⁻	10	8	48.2	50.8	78.1	75.2	25.1	25.2	1.99	1.97
S	A⁻	10	7	45.8	49.7	75.5	75.6	23.1	24.1	1.88	1.92
	A⁻	6	6	46.7	51.8	77.2	77.8	22.5	22.9	1.85	1.85
t(SD)[§]				12.9	12.3	6.8	7.1	7.9	4.9	.46	.20

*, ** Main effect means significantly different at the 0.05 or 0.01 level of probability respectively (resistant vs. susceptible or awned vs. awnletted) according to Fischer's F-test.

[†] R=resistant, S=susceptible to leaf rust; A⁻=awned, A⁻=awnletted; 41A=lines co-segregating for $Lr41$ resistance and awns; 42A=lines co-segregating for $Lr42$ resistance and awns.

[‡] Compute LSD(0.05) as $t(SD)([n_1 + n_2]/n_1 n_2)^{1/2}$, where n_1 and n_2 are the number of observations (no. of genotypes x replications [3] x environments [3]) used to compute each mean.

Table 2. Means for sedimentation tests, grain protein, flour protein, and flour yield of near-isogenic wheat lines selected for differential leaf rust reaction and awn expression and evaluated in either two or three Oklahoma environments.

Genotypic class description[†]		No. of genotypes in class		Grain protein		Flour protein		Flour yield		SDS sedimentation	
Rust response	Awn type	41A	42A	41A	42A	41A	42A	41A	42A	41A	42A
				---------------------------------g kg^{-1}-------------------------------						---------mL--------	
Main effects											
R	A·, A⁻	16	19	12.4	12.3	11.6**	11.2	68.2	65.2**	6.7**	6.9
S	A⁺, A⁻	16	13	12.3	12.2	11.2	11.0	66.2	63.7	6.9	7.1
R, S	A·	16	18	12.4	12.2	11.4	11.2	67.9	64.7	6.8	6.9
R, S	A⁻	16	14	12.4	12.2	11.4	11.0	66.6	64.1	6.8	7.1
Interactions											
R	A·	6	11	12.4	12.3	11.7	11.2	69.6	65.6	6.6	6.8
	A⁻	10	8	12.4	12.2	11.6	11.1	66.8	64.6	6.7	7.0
S	A·	10	7	12.3	12.2	11.1	11.1	66.1	63.8	6.9	7.0
	A⁻	6	6	12.4	12.2	11.3	11.0	66.3	63.6	6.9	7.1
t(SD)[‡]				.8	1.0	1.0	.7	8.4	5.7	.9	.9

** Main effect means significantly different at the 0.01 level of probability (resistant vs. susceptible or awned vs. awnletted) according to Fischer's F-test.

[†] R=resistant, S=susceptible to leaf rust; A·=awned, A⁻=awnletted; 41A=lines co-segregating for *Lr41* resistance and awns; 42A=lines co-segregating for *Lr42* resistance and awns.

[‡] For SDS sedimentation, flour protein, and flour yield compute LSD(0.05) as $t(SD)([n_1 + n_2]/n_1 n_2])^{1/2}$, where n_1 and n_2 are the number of observations (no. of genotypes x replications [2] x environments [2]) used to compute each mean; for grain protein compute LSD(0.05) as $t(SD)([n_1 + n_2]/n_1 n_2])^{1/2}$, where n_1 and n_2 are the number of observations (no. of genotypes x replications [3] x environments [3]) used to compute each mean.

Table 3. Means for mixograph properties of near-isogenic wheat lines selected for differential leaf rust reaction and awn expression and evaluated in two Oklahoma environments.

Rust response	Awn type	No. of genotypes in class		Mixing time		Mixograph rating		Curve width at 2 min.	
	Genotypic class description[+]	41A	42A	41A	42A	41A	42A	41A	42A
				--------min--------		--------1-10--------		--------mm--------	
Main effects									
R	A', A"	16	19	6.3	4.6	4.6	4.1	11.4	9.5**
S	A', A"	16	13	6.0	4.8	4.9	4.3	12.5	11.2
R, S	A'	16	18	6.1	4.8	4.7	4.2	11.8	10.6
R, S	A"	16	14	6.2	4.6	4.8	4.2	12.2	10.1
Interactions									
R	A'	6	11	6.1	4.6	4.5	4.1	11.1	9.3
	A"	10	8	6.4	4.5	4.7	4.1	11.8	9.7
S	A'	10	7	6.0	5.0	4.8	4.4	12.5	11.9
	A"	6	6	5.9	4.6	5.0	4.3	12.5	10.6
t(SD)[+]				2.1	4.2	1.7	3.4	4.4	5.9

** Main effect means significantly different at the 0.01 level of probability (resistant vs. susceptible or awned vs. awnletted) according to Fischer's F-test.

[+] R=resistant. S=susceptible to leaf rust; A'=awned. A"=awnletted; 41A=lines co-segregating for $Lr41$ resistance and awns; 42A=lines co-segregating for $Lr42$ resistance and awns.

[+] Compute LSD(0.05) as $t(SD)([n_1 + n_2]/n_1 n_2)^{1/2}$, where n_1 and n_2 are the number of observations (no. of genotypes x replications [2] x environments [2]) used to compute each mean.

APPENDIX

SUPPLEMENTAL INFORMATION FOR

NEAR-ISOGENIC EXPERIMENT

Table 1. Overall means for NIR test and Single kernel hardness tests of near-isogenic awned wheat lines selected for differential leaf rust response and evaluated in three environments.

Genotypic class description[†]			NIR		Single Kernel Characterization		
Resistance gene source	Rust response	No. of genotypes in class	Protein concentration	Hardness	Kernel hardness	Kernel weight	Kernel diameter
Lr41	R, S	19	12.3	46.0	74.9	25.6	2.02
Lr42	R, S	13	12.3	45.5	75.2	25.2	1.99
Lr41, Lr42	R	17	12.4**	47.0**	74.4**	26.8**	2.08**
Lr41, Lr42	S	15	12.1	44.5	75.8	24.0	1.94
Lr41	R	11	12.5	48.4	74.1	27.5	2.11
	S	8	12.0	43.6	75.7	23.8	1.93
Lr42	R	6	12.3	45.5	74.7	26.1	2.04
	S	7	12.2	45.4	75.8	24.3	1.94
t(SD)[‡]			1.0	13.9	7.7	4.6	.28

** Means significance at the 0.01 level of probability according to Fischer's F-test.

[†] R=resistant; S=susceptible to leaf rust.

[‡] Compute LSD(0.05) as $t(SD)([n_1 + n_2]/n_1 n_2)^{1/2}$, where n_1 and n_2 are the number of observations (no. of environments [3] x no. of replication [3] x no. of genotypes) used to compute each mean.

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VITA

Joy Martin

Candidate for the Degree of

Master of Science

Thesis: PERFORMANCE OF WINTER WHEAT SEGREGATING FOR LEAF RUST
RESISTANCE AND AWN
EXPRESSION

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