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Agronomic and Quality Evaluation of Common Wheat Near-Isogenic Lines Carrying the Leaf Rust Resistance Gene *Lr47*

Juan Carlos Brevis, Oswaldo Chicaiza, Imtiaz A. Khan, Lee Jackson, Craig F. Morris, and Jorge Dubcovsky*

ABSTRACT

Wheat leaf rust (*Puccinia triticina*) causes significant yield losses in wheat production worldwide. Genetic resistance is a cost-effective way to reduce these losses. Among the known leaf rust (*Lr*) resistance genes, nearly half are from alien sources. However, their deployment into wheat (*Triticum aestivum* L.) cultivars has been limited, likely because of fear of potential negative effects of linked alien genes. We report here the effects of the *Lr47* introgression from *Triticum speltoides* on agronomic and quality traits in common wheat. Five pairs of hard red spring near-isogenic lines were tested in replicated field trials from 2002 to 2004. The presence of the *Lr47* introgression was associated with an overall 3.8% reduction in grain yield (220 kg ha^{-1}), but it varied significantly across genotypes and environments. The *Lr47* introgression also affected several quality parameters. Lines with the alien *Lr47* segment showed consistent increases in grain and flour protein concentration (4 to 5 g kg^{-1}, $P < 0.01$) but also highly significant decreases in flour yield (21.8 g kg^{-1}, $P < 0.001$) and increases in flour ash (0.14 g kg^{-1}, $P < 0.01$). This information will help wheat breeders make informed decisions about the deployment of *Lr47* in their breeding programs. An additional round of homeologous recombination will be necessary to determine if the detrimental effects on milling parameters are pleiotropic effects of *Lr47* or the result of linked genes.

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Abbreviations: BABS, bread-baking water absorption; BC, backcross; FPC, flour protein concentration; GPC, grain protein concentration; HRS, hard red spring; *Lr*, leaf rust; MABS, mixograph water absorption; NIL, near-isogenic line; SK, single kernel.

Wheat leaf rust caused by *Puccinia triticina* Eriksson (formerly *Puccinia recondita* f. sp. *tritici*) is one of the most important diseases limiting global production of hexaploid or common wheat (*Triticum aestivum* L.). In the last decade (1997–2006), annual losses in the United States due to this pathogen have averaged 575,000 t for winter wheat and 202,000 t for spring wheat (Long, 2007). Therefore, the deployment of leaf rust (*Lr*) resistance genes into commercial cultivars is still an important objective of most wheat breeding programs. In addition, the incorporation of genetic resistance reduces the need for fungicide applications, decreasing production costs and environmental pollution.

Wild Triticeae species have been extensively used to expand the pool of resistance genes in cultivated wheat and account for approximately half of the 55 named *Lr* resistance genes (Friebe et al., 1996; Knott, 1989; McIntosh et al., 2003, 2006). The efforts to expand the number of *Lr* resistance genes are offset by the continuous evolution of new races of the pathogen. New *P. triticina* races virulent on resistance genes *Lr9*, *Lr16*, *Lr17*, *Lr24*, and *Lr26*

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have been detected in recent years in U.S. wheat production areas (Kolmer et al., 2005). The evolution of virulent strains makes the discovery and introgression of new *Lr* resistance genes an urgent task (Rommens and Kishore, 2000).

The transfer of alien resistance genes into cultivated wheat generally involves the introgression of large chromosome segments, which carry numerous alien genes with unpredictable effects on agronomic performance or quality traits. Unfortunately, studies to quantify these effects are infrequent compared to those aimed at discovering and transferring these alien genes (Labuschagne et al., 2002). The effects on quality are particularly relevant given the increasing complexity of the wheat markets and the demand for highly specific grain quality parameters (Labuschagne et al., 2002; Maghirang et al., 2006).

One of these alien resistance genes is *Lr47*, which is located on the short arm of *T. speltoides* chromosome 7S#1. The origin of chromosome 7S#1 is not clear, but it likely originated from a population obtained by irradiation of the hybrid CI15092/*T. speltoides*//'Fletcher'/3/5*'Centurk' with fast neutrons (Wells et al., 1982). An interstitial segment of chromosome 7S#1 was then transferred to chromosome 7A of hexaploid wheat using homeologous recombination induced by the *ph1b* mutation (Dubcovsky et al., 1998). This interstitial segment was backcrossed three generations into 'Pavon' and deposited in the Small Grain Collection as accession PI 603918 (Lukaszewski et al., 2000). Dubcovsky et al. (1998) determined that the translocated segment was located 2 to 10 cM from the centromere and estimated its genetic length between 20 and 30 cM. In the presence of the functional *Ph1* gene, the 7S translocated segment does not recombine with its wheat homologous chromosomes and is transmitted as a single linkage block (Helguera et al., 2000). This limitation applies to most of the alien introgressions, excluding only those from the direct donors of the wheat genomes.

It is currently unknown whether the introgression of the alien chromosome segment encompassing *Lr47* is associated with detrimental effects on agronomic traits under disease-free conditions or if it has any negative effect on milling or baking-quality characteristics. This can be the result of linked genes (linkage drag) or of pleiotropic effects of the resistance gene. Linkage drag has restricted the incorporation of a number of alien resistance genes into successful wheat cultivars (Zeven et al., 1983). A classical example of linkage drag is the transfer of *Lr19* from *Thinopyrum ponticum* (Podp.) Barkworth & D.R. Dewey to hexaploid wheat. Its use in bread-making cultivars has been limited by its linkage to the yellow pigment gene *Y*, which confers an unwanted yellow color to the flour (Knott, 1980). The negative impact of an alien gene can be also associated with pleiotropic effects (or "cost") of the resistance gene. For instance, the powdery mildew resistance gene *mlo* of barley (*Hordeum vulgare* L.) has been consistently associated with a 4% grain yield reduction (Kjær et al., 1990).

The aim of this study is to describe the effects of the introgression of the *T. speltoides* chromosome segment carrying leaf rust resistance gene *Lr47* on agronomic, milling, and bread-baking quality characteristics of hexaploid wheat to help breeders making informed decisions about deployment of *Lr47* in breeding programs.

MATERIALS AND METHODS

Plant Materials

Bread wheat line T7AS-7S#1S-7AS·7AL carrying the *T. speltoides* 7S interstitial translocation in chromosome 7AS (PI 603918, Lukaszewski et al., 2000) was used as a source of the leaf rust resistance gene *Lr47*. Recurrent hard red spring (HRS) cultivars Express (PI 573003; WestBred, LLC; Bozeman, MT), Kern (PI 612142; University of California, Davis), RSI5 (Tadinia/Probrand 775//23IBWSN#76; Resource Seeds, Inc., Gilroy, CA), Yecora Rojo (CItr 17414; Qualset et al., 1985), and breeding line UC1041 (Yecora Rojo/Tadinia) were crossed with the PI 603918 translocation line. The F_1 plants were backcrossed six times with their respective recurrent parent, and plants heterozygous for *Lr47* were selected in each generation. BC_6 plants heterozygous for *Lr47* were self-pollinated to obtain BC_6F_2 homozygous lines, which are theoretically expected to be more than 99% identical to the recurrent parent. The isogenic *Lr47* lines of Yecora Rojo and Kern have been deposited in the National Small Grain Collection as accessions PI 638738 and PI 638739, respectively (Chicaiza et al., 2006). Plants carrying the *Lr47* translocation were selected in each generation using the polymerase chain reaction markers developed by Helguera et al. (2000). Hereafter, the BC_6F_2 near-isogenic lines (NILs) carrying the *Lr47* introgression will be referred to as *Lr47* lines, and the recurrent parents will be referred as control lines.

Field Experiments

Field experiments were conducted at two locations, Davis and Corcoran, CA, during three consecutive seasons (2002–2004). The Davis site corresponded to the Experimental Field Station of the University of California at Davis (38°32′ N, 121°46′ W), and the Corcoran site corresponded to the Hansen Ranch (36°6′ N, 119°38′ W). In 2002 the experiments were arranged as a randomized complete block design with four blocks and three pairs of isogenic lines in common wheat cultivars Express, RSI5, and Yecora Rojo. Experimental units consisted of plots of 5 m^2 at both locations. In 2003 and 2004, isogenic *Lr47* lines in Kern and UC1041 were added to the previous three, and the five pairs were grown at each location (with the exception of Yecora Rojo at Davis in 2003 due to limited seed supply) (Table 1). The 2003 and 2004 experiments were arranged in a split-plot design with four randomized complete blocks in which the main plot corresponded to the different cultivars and 5-m^2 subplots to the presence or absence of the *Lr47* introgression. In this split-plot design, the isogenic line pairs within each block were grown in close proximity to each other, maximizing the sensitivity of the experiment to detect differences between them.

Table 1. Description of wheat cultivars, previous crop, rain, and cultural management at each experimental site, Davis, CA (D), and Corcoran, CA (C).

Year	Location	Cultivars	Previous crop	Planting date	Fertilization	Irrigation	Rain
					kg ha^{-1}	—mm—	
2002	D	Express RSI5 Yecora Rojo	Fallow	11/08/2001	Preplant 75 N + 45 P_2O_5 Jointing topdress 45 N Anthesis topdress 35 N	Flood 1X, 15.2	37.3
	C	Express RSI5 Yecora Rojo	Cotton	12/06/2001	Preplant 185 N + 70 P_2O_5 Tillering topdress 100 N	Flood 3X, 40.6 total	13.5
2003	D	Express Kern RSI5 UC1041	Fallow	11/05/2002	Preplant 110 N + 45 P_2O_5 Tillering topdress 110 N	Flood 1X, 15.2	51.1
	C	Express Kern RSI5 UC1041 Yecora Rojo	Cotton	12/12/2002	Preplant 180 N + 45 P_2O_5 Tillering topdress 100 N	Flood 3X, 40.6 total	13.9
2004	D	Express Kern RSI5 UC1041 Yecora Rojo	Fallow	11/12/2003	Preplant 110 N + 45 P_2O_5 Tillering topdress 110 N	Flood 2X, 30.5 total	49.3
	C	Express Kern RSI5 UC1041 Yecora Rojo	Cotton	12/09/2003	Preplant 225 N (cow manure) Preplant 10 N + 55 P_2O_5 Tillering topdress 100 N	Flood 4X, 76.2 total	15.2

In the Davis experiment, the lines were sown in early November in a Yolo loam soil (fine-silty, mixed, superactive, nonacid, thermic Mollic Xerofluvents). Total N fertilization consisted of 155 kg ha^{-1} N in 2002, and 220 kg ha^{-1} N in 2003 and 2004. In the Corcoran experiment, the lines were planted in early December in a Tulare clay soil (fine, smectitic, calcareous, thermic Fluvaquentic Vertic Endoaquolls) (2002 and 2003) and a Goldberg loam soil (fine, smectitic, thermic Typic Natraquolls) (2004). At this site, N fertilization was 280 kg ha^{-1} N in 2002 and 2003 and 335 kg ha^{-1} N in 2004. All sites were flood irrigated as described in Table 1. Descriptions of cultivars, previous crop, planting date, fertilization, and irrigation are also detailed in Table 1. The plots were machine harvested at maturity, and the seed was weighed to estimate yield. Wheat samples were cleaned on a Carter dockage tester (Simon-Carter Co., Minneapolis, MN) before quality analysis.

Disease Presence

The presence of leaf rust and stripe rust (*Puccinia striiformis* Westend. f. sp. *tritici* Erikson) was recorded each year. Disease severity was assessed at Feekes stage 9.0 (Large, 1954) by visually estimating the flag leaf area covered by the disease on a 0 to 100% scale.

Quality Analyses

Grain samples (600 g) were sent to the Western Wheat Quality Laboratory, Pullman, WA, for complete milling and bread-baking quality analysis. In 2002 and 2003, the four replications of each isogenic pair from each location were analyzed separately. In 2004 only two replications from each isogenic pair and location were analyzed. Wheat samples were measured for test weight and then scoured in a Cyclone Grain Scourer (model 6, Forster and Son, Ada, OK). The parameters analyzed in this study included grain protein concentration (GPC), flour protein concentration (FPC), flour yield, break flour yield, flour ash, milling score, mixograph water absorption (MABS), bread-baking water absorption (BABS), bread dough mixing time, and loaf volume. The percentage of flour ash was measured from a 4-g flour sample ignited and heated at 550°C for 15 h in a muffle furnace. Grain samples were milled on a Brabender Quadrumat laboratory mill to estimate straight-grade white flour yield, break flour yield (the percentage by weight of the total products recovered as flour off the break rolls), and milling score (Jeffers and Rubenthaler, 1979). Straight-dough bread-baking analyses evaluated the optimum absorption and mixing parameters in a 90-min fermentation method using 100 g flour. Single kernel (SK) analysis was performed using 300 kernels individually analyzed using a SK Characterization System Model 4100 (Perten Instruments, Springfield, IL) which measures SK size, weight, and hardness. Protein concentration in the grain and flour was determined by near-infrared spectroscopy using an Inframatic grain and flour analyzers (Perten Instruments, Springfield, IL), calibrated using Dumas combustion nitrogen (Leco FP-528). All the methodologies for analysis are standardized and described by American Association of Cereal Chemists (2000).

Statistical Analyses

Analysis of variance was performed using SAS version 9.1 (SAS Institute, Inc., Cary, NC). Since we were interested in the effect of the *Lr47* introgression within each NIL pair, as well as the interactions of the gene segment with the genetic background (cultivar) and location, we used the general lineal model (PROC GLM) to analyze the data. The data set from each year was analyzed separately, including data from both locations, resulting in a three-way factorial with two gene

levels (with and without the *Lr47*–carrying segment), three to five genotypes, and two locations. Location was included as a fixed factor, and blocks were nested within location. When the effect of the gene segment was consistent across locations and cultivars (nonsignificant interactions), the results were summarized by year. Parameters showing significant gene × cultivar interactions were analyzed by cultivar. When necessary, data were transformed to meet the assumptions of homogeneity of variances and normality of residuals of the ANOVA model. If a transformation was applied, graphs and tables show untransformed arithmetic means, while the significance values correspond to the results of the analysis of the transformed data. Correlations among traits were analyzed using SAS PROC CORR across cultivars and environments. Unless noted otherwise, significant correlations correspond to the results obtained from the 2003 and 2004 data sets.

RESULTS

Disease Presence

In 2002 the experiments were affected by both leaf rust and stripe rust. At Davis the control lines averaged 43% leaf rust severity, whereas the lines carrying the *Lr47* introgression were unaffected. Pairwise comparisons showed significantly ($P < 0.01$) higher leaf rust scores in the three control lines compared with the *Lr47* NILs. At Corcoran only the Yecora Rojo control had significantly higher ($P < 0.01$) leaf rust severity (47%) than its *Lr47* NIL (<5% necrotic tissue due to resistance reaction). The differences in leaf rust infection within NILs were important for the interpretation of the results from this year. During the same year, stripe rust severity scores were low and similar between the *Lr47* and control NILs (<20% severity at both locations).

In 2003 a late leaf rust infection reached low levels of severity at each location, averaging less than 20% severity in the control lines, whereas the *Lr47* NILs were unaffected. An early stripe rust infection developed at both locations but was more severe at Davis. No significant differences in stripe rust severity were detected between the *Lr47* and control NILs.

In 2004 no leaf rust was observed in Davis or Corcoran. The Davis experiment was treated with the fungicide azoxystrobin at a rate of 180 g ha^{-1} a.i. at booting stage (Feekes 10.1) to control stripe rust. Despite the fungicide application, stripe rust reached approximately 35% severity. In Corcoran the experiment was not treated, and the average stripe rust severity was approximately 60% for both *Lr47* and control lines. At each location, cultivars Kern and Yecora Rojo were the most susceptible to stripe rust.

Agronomic Traits

Lodging and Shattering

The 2002 trial at Davis was affected by severe lodging and strong winds during grain filling that caused an unusually high level of shattering. Interestingly, consistent differences in lodging were observed across all replications between two of the three isogenic pairs included in this study (Fig. 1A). A significantly lower level of lodging ($P < 0.01$) was observed in the *Lr47* NILs of cultivars Express and RSI5 (5% average lodging) relative to the corresponding control lines (23% average lodging) (Fig. 1B). Significant lodging was not observed in any of the other field experiments, precluding the validation of the differences in lodging observed at Davis in 2002. Therefore, the association between the presence of the *Lr47 T. speltoides* segment and the improved resistance to lodging should be considered as a preliminary result.

We also observed a significant difference in shattering between the isogenic lines (Fig. 1C). Given the significant negative correlation ($r = -0.5$, $P < 0.05$) between lodging and shattering phenotypic scores, we hypothesize that the differences in shattering may be a consequence of the differences in lodging. The *Lr47* NILs of Express and RSI5, which stood the strong winds, exhibited greater shattering (51% average shattering) than the lodged control lines (21% average shattering, $P < 0.01$, Fig. 1C). As expected, yield was negatively correlated with shattering ($r = -0.82$, $P < 0.001$). The Yecora Rojo NILs did not show differences in lodging or shattering in the 2002 Davis experiment.

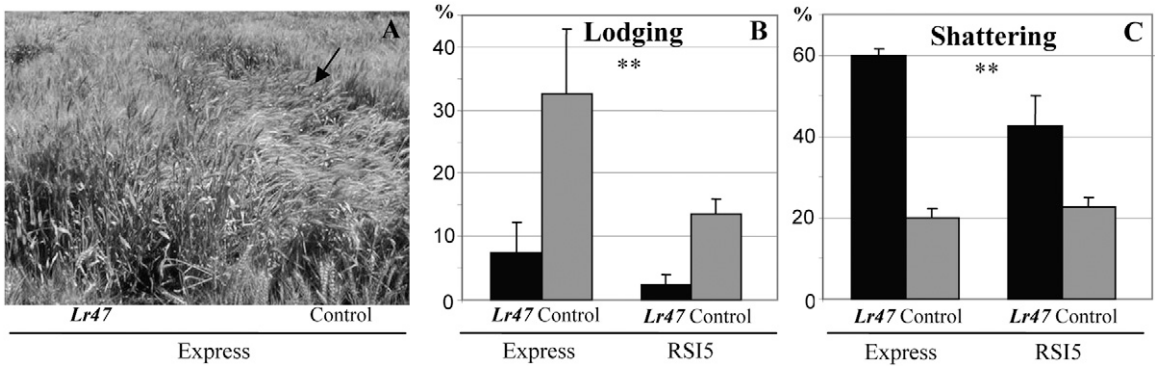

Figure 1. Effect of *Lr47* chromosome segment on (A–B) lodging and (C) shattering in hard red spring wheat cultivars Express and RSI5 in the 2002 Davis, CA, experiment. The photo (A) shows the greater resistance to lodging of the *Lr47* NIL (left) compared with the recurrent parent Express (right, arrow). Values are arithmetic means of untransformed data and error bars are SEs of the means. Asterisks indicate significant differences across cultivars ($P < 0.01$).

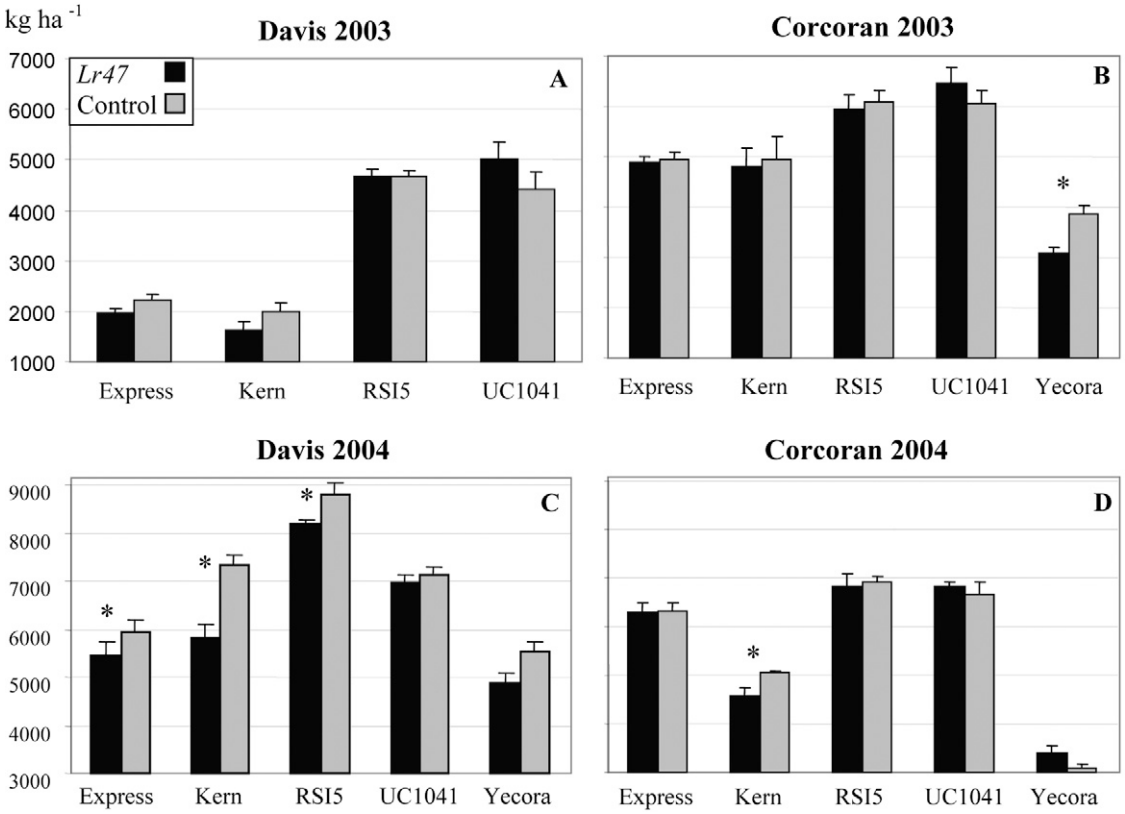

Figure 2. Effect of *Lr47* chromosome segment on grain yield of wheat cultivars in (A–B) 2003 and (C–D) 2004 at both California locations (Davis and Corcoran). Values are arithmetic means of untransformed data and error bars are SEs of the means. Asterisks indicate significant differences between *Lr47* and isogenic control lines within cultivars ($P < 0.05$). Yecora = Yecora Rojo.

Grain Yield

Grain yield data from 2002 were excluded from the analyses because of the unusually strong effects of lodging and shattering and the high level of leaf rust. Grain yield results for the 2003 and 2004 experiments are shown separately by cultivar and location (Fig. 2) due to the presence of significant gene × cultivar and gene × location interactions for this trait. Although most lines carrying the *Lr47* introgression showed yield reductions compared with their respective control line, most pairwise comparisons were not significant. In 2003 the presence of the *Lr47* introgression was associated with a nonsignificant yield reduction of 80 kg ha^{-1} (1.8%) across cultivars. Only the *Lr47* NIL of Yecora Rojo in Corcoran showed a significant yield reduction (Fig. 2A and B). In 2004 the lines carrying the *Lr47* segment showed a significant yield reduction of 5.7% ($P < 0.001$) across locations equivalent to 360 kg ha^{-1}. This negative effect was more significant in Davis than in Corcoran (Fig. 2C and D). The *Lr47* NILs of the cultivars Express, Kern, and RSI5 in Davis and cultivar Kern in Corcoran showed significant yield reductions when comparisons were analyzed by cultivar. Near-isogenic lines of UC1041 exhibited a contrasting response in yield. The *Lr47* NIL of UC1041 showed a significant ($P < 0.05$) yield increase of 518 kg ha^{-1} (nearly 10%) across locations in 2003 relative to the control lines, whereas in 2004 the yield was practically the same between UC1041 NILs. Grain yield was positively correlated with SK weight, SK size, and test weight ($P < 0.0001$, Table 2).

Grain Size

Kernel size, which corresponds to grain diameter in a SK Characterization System, was significantly larger ($P < 0.01$) in the *Lr47* lines than in the control lines both in 2002 and 2004 (~0.1 mm or ~4% increase) (Fig. 3A). During these 2 yr, the effect of the *Lr47* segment was consistent across cultivars and locations (no significant gene by environment or gene by genotype interactions). The results from 2003 showed the same trend, with a 2% increase in SK size for the *Lr47* NILs compared with the control lines. However, these differences were not significant, likely the result of some heterogeneity among cultivars as reflected by a significant gene by cultivar interaction ($P < 0.01$).

Interestingly, SK size was not significantly correlated ($r = 0.08$, not significant) with SK weight, a parameter that showed more variable results. In 2003 the *Lr47* lines showed a significant decrease ($P < 0.001$) in kernel weight across genotypes and locations, equivalent to 0.5 mg (1.3%) relative to the control lines. A significant gene by cultivar interaction ($P < 0.01$) indicated that the effect of the introgression was not homogeneous across cultivars (Fig. 3C). In 2002 and 2004, average SK weight values across cultivars and locations were slightly higher (<1%) in the *Lr47* NILs compared with the control lines, but the differences

Table 2. Correlations among main agronomic and quality traits (*r*) for the 2003 and 2004 data sets followed by the level of statistical significance.

Trait†	GY	SKS	SKW	TW	GPC	FP	FY	BFY	FASH	MS	SKH	MABS
GY	–											
SKS	0.54‡	–										
SKW	0.65‡	0.08 NS§	–									
TW	0.84‡	0.27**	0.76‡	–								
GPC	–0.08 NS	0.08 NS	–0.17 NS	–0.23*	–							
FPC	0.03 NS	0.26*	–0.17 NS	–0.15 NS	0.91‡	–						
FY	0.83‡	0.41‡	0.63‡	0.89‡	–0.15 NS	–0.06 NS	–					
BFY	0.75‡	0.41‡	0.45‡	0.76‡	–0.32**	–0.22*	0.90‡	–				
FASH	–0.60‡	–0.19 NS	–0.45‡	–0.60‡	0.24*	0.19 NS	–0.65‡	–0.71‡	–			
MS	0.81‡	0.36***	0.62‡	0.85‡	–0.20 NS	–0.12 NS	0.95‡	0.91‡	–0.85‡	–		
SKH	–0.69‡	–0.58‡	–0.69‡	–0.68‡	0.33**	0.24*	–0.69‡	–0.72‡	0.53‡	–0.69‡	–	
MABS	–0.35***	–0.21*	–0.49‡	–0.51‡	0.70‡	0.68‡	–0.41‡	–0.42‡	0.25*	–0.38***	0.63‡	–
LV	–0.12 NS	0.09 NS	–0.16 NS	–0.18 NS	0.60‡	0.69‡	–0.07 NS	–0.11 NS	0.01 NS	–0.05 NS	0.14 NS	0.64‡

†GY, grain yield; SKS, single kernel size; SKW, single kernel weight; TW, test weight; GP, grain protein concentration; FP, flour protein concentration; FY, flour yield; BFY, break flour yield; FASH, flour ash; MS, milling score; SKH, single kernel hardness; MABS, mixograph water absorption; LV, loaf volume.

*$P < 0.05$.

**$P < 0.01$.

***$P < 0.001$.

‡$P < 0.0001$.

§NS, not significant at $P > 0.05$.

were not statistically significant. When pairwise comparisons were considered for 2002 and 2004, only the cultivar Express in 2002 showed a significant increase in kernel weight in the *Lr47* lines (Fig. 3B and D).

Both SK size and SK weight were positively correlated with flour yield, break flour yield, and milling score and negatively correlated with SK hardness and water absorption ($P < 0.05$, Table 2).

Test Weight

The effects of the *Lr47* segment on test weight were small but significant. The NILs carrying the *Lr47* translocation had overall lower average test weight (809.1 ± 3.6 kg m^{-3}) compared with the lines without the translocation (813.9 ± 3.2 kg m^{-3}). Differences were significant both in 2003 (8 kg m^{-3} or 1% difference, $P < 0.001$) and 2004 (5.9 kg m^{-3} or 0.7% difference, $P < 0.05$). Despite the significant decrease in test weight observed across cultivars in 2004, all *Lr47* NILs showed a nonsignificant decrease in test weight when pairwise comparisons were analyzed. In 2002 there was no difference in test weight between the *Lr47* lines and the recurrent parent lines.

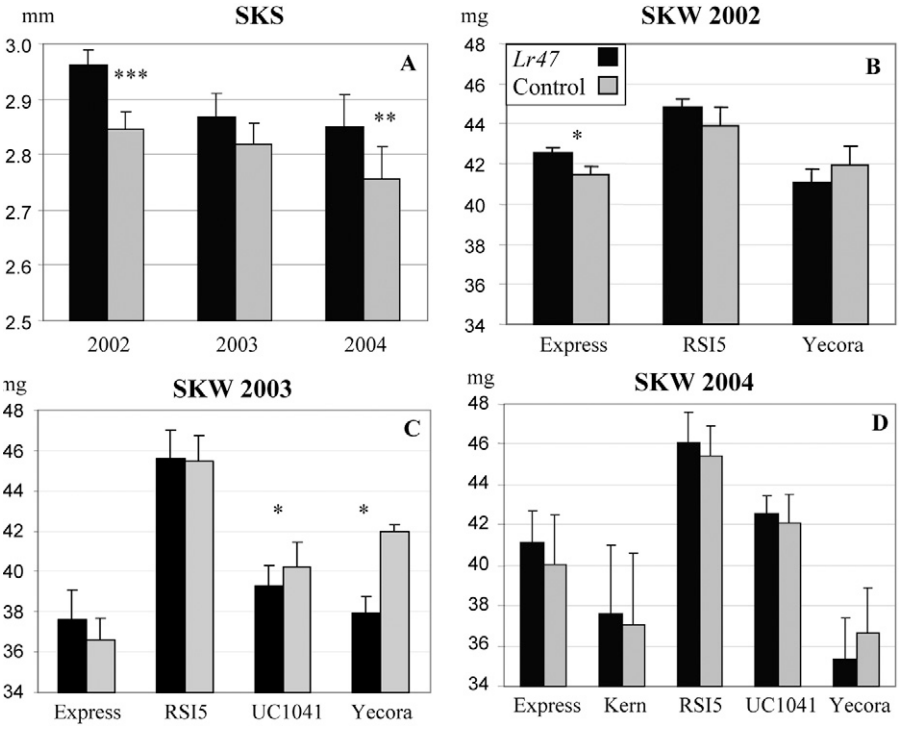

Figure 3. Effect of *Lr47* chromosome segment on (A) single kernel size (SKS) and (B–D) single kernel weight (SKW) across wheat cultivars and locations between 2002 and 2004. Values are arithmetic means of untransformed data and error bars are SEs of the means. Asterisks indicate significant differences between the *Lr47* lines and the control lines within years. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$. Yecora = Yecora Rojo.

Phenological and Morphological Traits

We observed no evident phenological (flowering and maturity dates) or morphological (plant height and spike morphology) differences between the *Lr47* and control NILs. The only exception was the presence of anthocyanin pigments in the stem of all *Lr47* NILs but not in the control NILs. This was not surprising since the purple culm genes *Pc1* and *Pc2* are known to be located on the

syntenic chromosome arms 7BS and 7DS, respectively (McIntosh et al., 2003). The presence of stem anthocyanin pigments in the *Lr47* NILs was clearer at the borders of the plots but was strongly affected by the environment. When present, the purple stems can be used as a simple phenotypic marker for the presence of the *Lr47* gene.

Milling Quality Traits

Grain and Flour Protein

The presence of *Lr47* was consistently associated with higher protein concentration in the grain and flour. Overall, the increments in GPC were highly significant ($P < 0.01$) all 3 yr (Fig. 4A). The *Lr47* lines showed an average increase in grain protein of 7.5 g kg^{-1} (6%) in 2002, 4.1 g kg^{-1} (3.2%) in 2003, and 2.6 g kg^{-1} (1.9%) in 2004. As expected, a highly significant effect ($P < 0.001$) of the *Lr47* introgression was also observed for FPC (Fig. 4B), a parameter highly correlated with GPC ($r = 0.91$, $P < 0.0001$). Increases in FPC associated with the presence of the *Lr47* chromosome segment ranged from 3.1 g kg^{-1} (2.8%) in 2003 to 7 g kg^{-1} (6.8%) in 2002. Both GPC and FPC exhibited strong and positive correlations with water absorption and loaf volume ($r > 0.60$, $P < 0.0001$; Table 2).

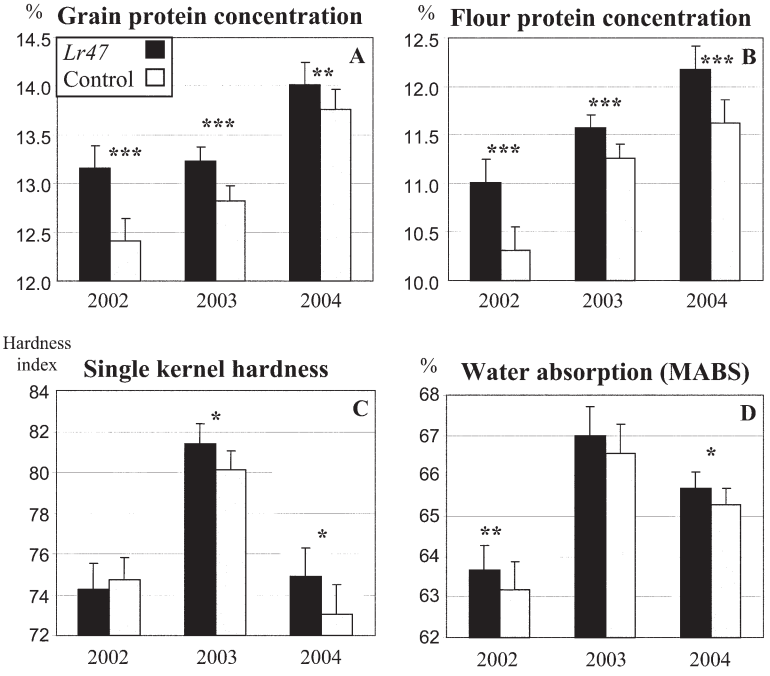

Figure 4. Effect of *Lr47* chromosome segment on (A) grain protein concentration (GPC), (B) flour protein concentration (FPC), (C) single kernel hardness, and (D) mixograph water absorption (MABS) across wheat cultivars and locations between 2002 and 2004. Values are arithmetic means of untransformed data and error bars are SEs of the means. Asterisks indicate significant differences across cultivars. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Protein yield, defined as grain yield × GPC, was affected more by differences in yield than by differences in GPC, as reflected by a higher correlation with yield ($r = 0.98$, $P < 0.0001$) than with GPC ($r = 0.13$, not significant). In 2003 no significant differences were found between the *Lr47* NILs and the control lines when protein yield was analyzed across cultivars (data not shown). However, pairwise comparisons during the same year showed variable results. The *Lr47* NIL for UC1041 had significantly higher protein yield than the control line ($P < 0.01$), whereas the Yecora Rojo NILs showed the opposite effect ($P < 0.05$). In 2004 the *Lr47* introgression was associated with a significant reduction in protein yield ($P < 0.01$) equivalent to 28.6 kg ha^{-1} protein, or a 3.5% decrease relative to the protein yield exhibited by the control lines. This likely reflects the negative impact of the *Lr47* segment on grain yield in 2004. The interactions observed that year between grain yield and the *Lr47* segment were reflected in a highly significant ($P < 0.01$) gene by cultivar interaction for protein yield. Although in 2004 all *Lr47* NILs except UC1041 showed an absolute decrease in protein yield relative to their controls, the difference was significant only for Kern ($P < 0.01$).

Flour Yield, Flour Ash, and Milling Score

The *Lr47* NILs exhibited a highly significant reduction ($P < 0.001$) in flour yield relative to the control lines over the 3-yr study. On average, the presence of the *Lr47* segment decreased flour yield by 21.8 g kg^{-1} (3.5%), ranging from 19.8 g kg^{-1} in 2004 to 25.3 g kg^{-1} in 2003 (Fig. 5A). Break flour yield, which is the percentage of flour obtained from break rolls by weight of the total products, was affected in the same way by the *Lr47* introgression. Its presence was associated with a significant decrease ($P < 0.001$) in break flour yield of 20.6 g kg^{-1} on average (5.9%, Fig. 5B).

An additional negative effect associated with the *Lr47* introgression was a highly significant increase ($P < 0.01$) in flour ash across cultivars (Fig. 5C). The *Lr47* lines showed a 6% increase in 2003 (0.25 g kg^{-1}) and a 2.6% increase in 2004 (0.11 g kg^{-1}) relative to the flour ash content in the control lines. In 2002 the increase in flour ash was smaller and not significant ($P > 0.05$).

The calculation of the milling score includes flour yield and flour ash. Since both parameters were negatively affected by the *Lr47* introgression, the milling score was significantly smaller ($P < 0.001$) in the *Lr47* than in the control lines (Fig. 5D). The results were consistent across years, locations, and cultivars.

Single Kernel Hardness

The *Lr47* introgression was associated with small but significant increases in SK hardness. Across cultivars, the *Lr47* lines exhibited significant ($P < 0.05$) increments in 2003 (1.6%) and 2004 (2.6%) (Fig. 4C), but no significant differences were observed in 2002. Single kernel hardness values showed a strong ($P < 0.0001$) negative correlation with flour yield ($r = -0.69$) and break flour yield ($r = -0.72$) and

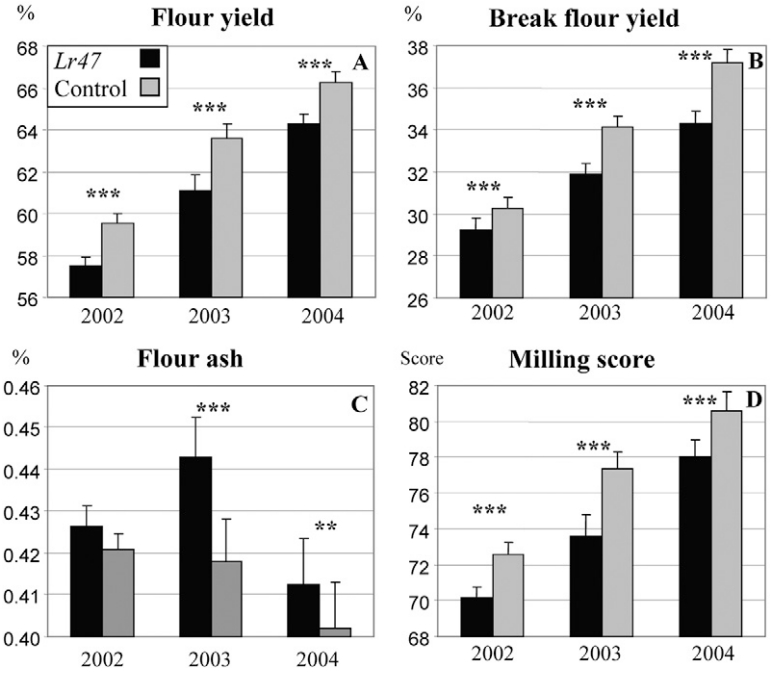

Figure 5. Negative effect of *Lr47* chromosome segment on (A) flour yield, (B) break flour yield, (C) flour ash, and (D) milling score across wheat cultivars and locations between 2002 and 2004. Values are arithmetic means of untransformed data and error bars are standard errors of the means. Asterisks indicate significant differences between the *Lr47* lines and the control lines within years. $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

a positive correlation with flour ash ($r = 0.53$, $P < 0.0001$). All traits associated with kernel morphology (SK size, SK weight, and test weight) showed highly significant negative correlations with SK hardness ($P < 0.0001$, Table 2).

Bread-Baking Quality Traits

Water Absorption

The lines carrying the *Lr47* introgression showed an increase in MABS (Fig. 4D). Although each year the overall increase was smaller than 5 g kg^{-1} (<1%) relative to the MABS values of the control lines, the differences were significant in 2002 ($P < 0.01$) and 2004 ($P < 0.05$).

The related parameter BABS, which defines the amount of water needed to make dough of proper consistency for bread making using a full bread formula as opposed to only water, was not significantly affected by the *Lr47* introgression across cultivars (data not shown). However, the results for BABS followed a similar pattern as those observed for MABS, with an average increase associated with the *Lr47* introgression ranging from 3.2 g kg^{-1} (0.5%) in 2004 to 9.7 g kg^{-1} (1.4%) in 2003. Both MABS and BABS were significantly ($P < 0.0001$) correlated with GPC and SK hardness ($R > 0.60$, Table 2).

Mixing Time and Loaf Volume

Less-consistent results were found for mixing time and loaf volume. Mixing time appeared to be consistently higher in the *Lr47* lines relative to the control (Table 3). However, only in 2003 was the increment (0.35 min or 12.5%) marginally significant ($P = 0.04$).

Loaf volume was significantly higher in the *Lr47* lines compared with the control lines only in 2002 (Table 3). This may be related to the larger differences in GPC and FPC observed that year between the *Lr47* and the control lines. For 2003 and 2004, loaf volume showed a positive and highly significant correlation with GPC and FPC ($r = 0.60$ and 0.69, $P < 0.0001$).

DISCUSSION

Agronomic Effects

The introgression of the *T. speltoides* segment carrying leaf rust resistance gene *Lr47* was associated with positive and negative effects on agronomic traits. Among the positive effects was the improved resistance to lodging observed in the *Lr47* NILs at Davis in 2002. Although this is a preliminary result based on a single location observation, we feel that this is worth mentioning given the limited knowledge we have today of loci affecting straw strength in wheat (Berry et al., 2003; Keller et al., 1999).

An additional effect associated with the introgression of *Lr47* was the increase in SK size (diameter), which was consistent across cultivars, sites, and years. Nevertheless, the higher SK size was not always associated with a significant increase in SK weight. In 2002 and 2004, the *Lr47* NILs showed a marginal increase in SK weight, whereas in 2003 the *Lr47* introgression was associated with a significant decrease in SK weight relative to the control lines. Although kernel morphological traits are generally correlated, some studies have shown that these traits can be independent. Breseghello and Sorrells (2007) found a low correlation between kernel length and width in two hexaploid wheat mapping populations.

The introgression of *Lr47* was also associated with some negative agronomic effects. Averaged across all cultivars and environments, NILs with the *Lr47* introgression showed a small grain yield reduction (3.8%). However, the effect of this segment on grain yield was strongly influenced by genotype and environmental interactions, suggesting that breeders may be able to select *Lr47* genotypes with limited yield penalties. The significant correlation between grain yield and kernel weight (Table 2) suggests that the latter may be one of the components contributing to differences in grain yield. In 2003 the grain yield decrease (1.8%) observed in the *Lr47* NILs was paralleled by a similar decrease in kernel weight (1.3%). However, in 2004 kernel weight was slightly higher in the NILs carrying the *Lr47* introgression, whereas grain yield was significantly reduced in the same NILs, indicating that yield components other than kernel weight might have affected grain yield that year.

Significant yield penalties associated with *Lr* resistance genes have been reported for *Lr9* (Ortelli et al., 1996) and *Lr34* (Singh and Huerta-Espino, 1997). However, it is still not clear if these detrimental effects on yield are due to pleiotropic effects of the resistance genes or to the negative effect of linked genes, a limitation that also applies to our current results for the *Lr47* segment. In a few cases, such as the barley powdery mildew resistance gene *mlo,* there is good evidence that yield reductions observed in lines carrying the resistant allele are the result of pleiotropic effects of the gene associated with necrotic leaf spotting in the absence of the disease (Brown, 2002).

Table 3. Effect of *Lr47* chromosome segment across wheat cultivars and locations on mixing time and loaf volume.

Year	*Lr47* allele	Mixing time		Loaf volume	
		Mean ± SE	Δ†	Mean ± SE	Δ
		min	%	cm^3	%
2002	(+) *Lr47*	3.58 ± 0.18	+4.0 NS‡	911.7 ± 19.2	+3.1*
	(–) *Lr47*	3.44 ± 0.23		884.4 ± 17.9	
2003	(+) *Lr47*	3.14 ± 0.13	+12.5*	862.7 ± 13.4	–0.7 ns
	(–) *Lr47*	2.79 ± 0.12		869.1 ± 13.3	
2004	(+) *Lr47*	3.32 ± 0.16	+1.8 NS	879.3 ± 22.9	–0.3 ns
	(–) *Lr47*	3.26 ± 0.19		876.5 ± 19.4	

*$P < 0.05$.

†Δ, mean change of the *Lr47* near-isogenic lines relative to the control lines.

‡NS, not significant.

Quality Effects

More consistent effects of the *T. speltoides* segment carrying *Lr47* were observed in the milling and baking data. The average 3.5% reduction in flour yield associated with the *Lr47* segment relative to the control lines represents a direct measure of its potential negative economic impact for the milling industry. Unfortunately, this negative effect on break flour yield and total flour yield was highly consistent across cultivars, years, and locations. The stronger decrease in break flour yield compared to the reduction observed in total flour yield suggests that the ease of removing the endosperm from the bran is affected from the beginning of the milling process.

The negative effect of the *Lr47* introgression on milling parameters was accentuated by a significant increase in flour ash, a parameter that provides an indirect measure of bran contamination. With only 20% of the minerals in the kernel contained in the endosperm and 80% in the bran (Lintas, 1988), an increase in flour ash indicates an undesirable increase in bran particles in the flour. To our knowledge, none of the studies addressing the effect of other *Lr* gene introgressions on milling quality has reported reductions in flour extraction or increases in flour ash associated with them, suggesting that the effects observed here may be the result of the presence of a detrimental *T. speltoides* gene linked to *Lr47.* However, we cannot rule out the alternative hypothesis of pleiotropic effects of the *Lr47* gene affecting these parameters.

Size and shape of the grain can affect flour extraction. Bigger, better-filled grains have a greater proportion of endosperm relative to bran, facilitating higher flour extraction relative to smaller or shrunken grains. In addition, smaller grains are generally associated with an increase in flour ash content. This seems to be the case for 2003, the only year with a significant decrease in kernel weight, which showed the highest flour yield reduction (4% decrease) and flour ash increase (6% increase) in the *Lr47* NILs compared with the control lines. Ohm et al. (1998) studied kernel characteristics of 12 hard winter wheat cultivars and found a positive correlation between kernel weight and flour yield and a negative correlation between kernel weight and flour ash content. In 2002 and 2004, the reductions in flour yield associated with the presence of the *Lr47* segment were slightly compensated by a small increase in kernel weight, but they were still significantly lower than in the control lines. These interpretations need to be considered cautiously, however, because studies on the effect of kernel morphological characteristics on milling parameters are sometimes conflicting (Breseghello and Sorrells, 2007; Campbell et al., 1999).

Another parameter related to kernel morphology that was negatively affected by the *Lr47* introgression was test weight. The NILs carrying the *Lr47* segment exhibited significantly lower test weight in 2003 and 2004 (1% decrease) compared with the recurrent parental lines. Test weight is influenced by a number of factors, such as kernel morphology, uniformity, and packing capacity (Campbell et al., 1999). In our lines, we found a strong positive relationship between test weight and traits such as kernel size, kernel weight, flour yield, break flour yield, and milling score and a significant negative correlation with flour ash (Table 2). These results suggest that the detrimental effects on milling parameters associated with the *Lr47* introgression may be in part the result of changes in kernel morphology.

Grain hardness also plays an important role in the determination of flour yield and ash content. The significant increase in SK hardness observed in the *Lr47* NILs likely contributed to the overall decrease in flour extraction and increase in flour ash. Single kernel hardness was negatively correlated with flour yield and break flour yield, and positively correlated with flour ash (Table 2). Similar correlations have been reported in other studies (Martin et al., 2001; Ohm et al., 1998).

The major positive effect associated with the *Lr47* introgression was the increase in GPC and FPC. Increases in GPC have also been found to be associated with the introgression of *Lr29*, *Lr34*, *Lr35*, and *Lr37* (Labuschagne et al., 2002), whereas increased FPC has been reported for *Lr29* and *Lr37* (Dyck and Lukow, 1988). In some cases, this can

be the result of the negative impact of the introgressed segment on yield, given the well-documented negative correlation between grain yield and GPC (Gonzalez-Hernandez et al., 2004; Groos et al., 2003; Kibite and Evans, 1984; Mesfin et al., 2000), but in our study this relationship was not significant. In addition, the variable results in kernel weight across years and genotypes did not parallel the consistent increases in GPC associated with the *Lr47* NILs.

The largest difference in GPC and flour protein between the *Lr47* lines and controls was observed in 2002. This may be a consequence of the presence of higher levels of leaf rust in the susceptible control lines during that year. Dimmock and Gooding (2002) reviewed the effect of rust on GPC and concluded that *Puccinia* infections were generally more detrimental to N than to carbon accumulation in the grain. This is consistent with the observation that applications of fungicides to control rust usually result in relative increases in GPC, contrary to the common belief that the increases in grain yield would dilute GPC. The presence of the *Lr47* segment was associated with higher GPC relative to the control lines even in locations where no leaf rust was observed, indicating that the effect of this chromosome segment on GPC was not necessarily mediated by its effect on leaf rust resistance.

The increase in GPC was expected to have a positive effect on loaf volume and water absorption, since these last parameters showed highly significant correlations with GPC (Table 2). However, differences in loaf volume were not as consistent as those observed for protein concentration. Only in 2002, the year with largest differences in protein concentration, the *Lr47* NILs showed a significant improvement in loaf volume compared with the control lines. The *Lr47* chromosome segment was also associated with improved water absorption (MABS and BABS) relative to the control NILs. This improvement may be related to parallel increases in GPC and grain hardness in the *Lr47* NILs since proteins and damaged starch granules absorb at least two times the water absorbed by undamaged starch (Bloksma and Bushuk, 1988). Harder grains result in higher starch damage during milling, explaining the positive correlation between kernel hardness and MABS (Table 2).

Despite the highly significant increase in GPC across cultivars and locations, the *Lr47* lines produced the same or less total protein per unit of area (protein yield) than the recurrent parents. The increases in GPC were offset by the decreases in grain yield associated with the *Lr47* introgression in some genetic backgrounds. The important role of grain yield in defining protein yield was also supported by the highly significant correlation between grain and protein yield (Table 2).

CONCLUSIONS

The effectiveness of leaf rust resistance gene *Lr47* against all races of wheat leaf rust pathogen tested by Dubcovsky et al. (1998) demonstrates the usefulness of this gene in breeding programs. Its detrimental effects on grain yield, milling yield, and ash content, however, may limit the adoption in wheat breeding programs. Since some of these negative effects showed significant gene × genotype interactions (e.g., yield), breeders may be able to ameliorate them through selection of adequate gene combinations. The recurrent parents for all NILs in this study represented only hard red spring cultivars, and it is possible that different effects could be observed if *Lr47* is transferred into wheat cultivars from different market classes.

We have initiated an additional round of homeologous recombination between chromosomes 7S and 7A using the *ph1b* mutation to determine whether the negatives effects on grain yield and milling parameters observed in the *Lr47* NILs are due to pleiotropic effects of the *Lr47* gene or to linkage with other alien genes.

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