Race-Specific Adult-Plant Resistance in Winter Wheat to Stripe Rust and Characterization of Pathogen Virulence Patterns

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ABSTRACT

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Stripe rust, caused by *Puccinia striiformis* f. sp. *tritici*, is an important disease of wheat in the Great Plains and southeastern United States. Growing resistant cultivars is the preferred means for managing stripe rust, but new virulence in the pathogen population overcomes some of the resistance. The objectives of this study were to characterize the stripe rust resistance in contemporary soft and hard red winter wheat cultivars, to characterize the virulence of *P. striiformis* f. sp. *tritici* isolates based on the resistances found in the cultivars, and to determine wheat breeders' perceptions on the importance and methods for achieving stripe rust resistance. Seedlings of cultivars were susceptible to recent isolates, indicating they lacked effective all-stage resistance. However, adult-plants

were resistant or susceptible depending on the isolate, indicating they had race-specific adult-plant resistance. Using isolates collected from 1990 to 2013, six major virulence patterns were identified on adult plants of twelve cultivars that were selected as adult-plant differentials. Race-specific adult-plant resistance appears to be the only effective type of resistance protecting wheat from stripe rust in eastern United States. Among wheat breeders, the importance of incorporating stripe rust resistance into cultivars ranged from high to low depending on the frequency of epidemics in their region, and most sources of stripe rust resistance were either unknown or already overcome by virulence in the pathogen population. Breeders with a high priority for stripe rust resistance made most of their selections based on adult-plant reactions in the field, whereas breeders with a low priority for resistance based selections on molecular markers for major all-stage resistance genes.

Since a new strain of the pathogen emerged in 2000 (Markell and Milus 2008), stripe rust, caused by *Puccinia striiformis* f. sp. *tritici*, has been the most important foliar disease of soft red winter wheat (SRWW) in southeastern United States and hard red winter wheat (HRWW) in the Great Plains (Basnet et al. 2014, Sthapit et al. 2012). The new strain had new virulence on all-stage resistance genes *Yr8* and *Yr9* (Chen et al. 2002) and was more aggressive and adapted to warmer temperatures than the old strain (Milus et al. 2006, 2009). Growing resistant cultivars is the most efficient means for managing stripe rust (Chen 2005). The two major types of resistance to stripe rust are all-stage and adult-plant. All-stage resistance (also known as seedling resistance) provides a high level of resistance from the seedling stage through maturity but is usually overcome by new races of the pathogen (Chen 2005). With adult-plant resistance (APR), seedlings are susceptible and plants become resistant as they mature (Vanderplank 1982). Different types of APR have been described. Cromei (1992), Ma and Singh (1996) and Park and Rees (1989) found two types of APR. One type expressed as early as tillering stage, was associated with a hypersensitive infection type (IT) on flag leaves, and provided a high level of resistance in the field. Another type developed later, was associated with intermediate ITs, and provided slow-rusting in the field. Hovmøller (2007) found that APR was common in European wheat cultivars with levels of effectiveness ranging from low to high. Resistance genes *Yr11*, *12*, *13*, and *14* conferred a high level of APR with a hypersensitive IT to some isolates but were

overcome by other isolates (McIntosh et al. 1995). Qayoum and Line (1985) described high-temperature adult-plant resistance (HTAP) that requires a combination of maturity and warm temperatures for expression. HTAP resistance (Chen 2005) and APR conferred by *Yr18* (Ma and Singh, 1996) were considered to be durable because they remained effective for a long time when deployed across a large area with high disease pressure.

Sthapit et al. (2012) evaluated 18 SRWW lines that were susceptible as seedlings to races PST-3 (representative of the old strain) and PST-78 (representative of the new strain) plus 26R61 that had all-stage resistance to PST-3 (due to *Yr9*) for APR to these races at low (10 to 18°C) and high (12 to 28°C) gradually changing temperature regimes. Nine lines had race-specific APR to PST-78 but were susceptible to PST-3, nine lines had APR to both races, and 26R61 had APR to PST-78. Furthermore, only one line seemed to express a higher level of APR at the high temperature regime than at the low temperature regime, indicating that the APR found in these lines was different from HTAP resistance. These results indicated that APR was ubiquitous among the lines evaluated and that the APR in half of the lines was race-specific.

According to Zadoks (1961), German scientists in the 1930s were the first to discover APR and race-specific APR to stripe rust. In the 1940s, Manners (1950) conducted experiments to determine the types of stripe rust resistance present in wheat cultivars grown in Great Britain. He found that (i) cultivars resistant to particular isolates at the seedling stage (i.e., cultivars had all-stage resistance) were always resistant to those isolates at the adult stage, (ii) cultivars not fully susceptible to particular isolates at the seedling stage were likely to have useful levels of resistance to those isolates at the adult stage, and (iii) cultivars fully susceptible to particular isolates at the seedling stage could be either resistant or susceptible at the adult stage depending on the isolate.

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Zadoks (1961) investigated resistance to wheat stripe rust and physiologic specialization of *P. striiformis* f. sp. *tritici* in Europe during the 1950s. He found that mature plant resistance (i.e., APR) was more important for managing stripe rust than overall resistance (i.e., all-stage resistance) and that “field races” based on the reaction of adult plants in the field explained major epidemics better than “greenhouse races” based on seedling reactions in the greenhouse. He found that several greenhouse races could be split into two or more field races and that some greenhouse races could be combined into one field race.

Da Silva (1958) discussed the need for better integration of race identification of cereal rust fungi with efforts to breed resistant cultivars. The major problem was that race identification based on a standard set of differentials identified many races that were not important to breeding programs but did not identify subraces capable of attacking contemporary cultivars. This problem was addressed by adding supplemental differentials particular to different regions that contained the resistances used within a region. From a practical breeding standpoint, the supplemental differentials needed to be continuously updated as regional cultivars changed over time, and important races in the field were most likely to be differentiated on the supplemental differentials rather than the standard differentials.

In the 1970s, Priestley and Doodson (1976) determined that it was critical to describe races of *P. striiformis* f. sp. *tritici* in the United Kingdom based on adult-plant reactions because all widely grown wheat cultivars were susceptible to contemporary isolates at the seedling stage. They planted replicate tussocks (hill plots) of commercially important cultivars in each of several polyethylene tunnels, inoculated plants in each tunnel with a different isolate, and were able to identify five races based on adult-plant reactions. Priestley et al. (1984) proposed a dynamic system utilizing a set of cultivars representing the range of effective resistances and contemporary isolates representing the range of virulence found in the field for efficiently evaluating currently important cultivars for both all-stage and adult-plant resistances to stripe rust. This system with some modifications is still being used in the United Kingdom. In 2012 for example, Hubbard and Bayles (2013) tested five isolates in individual inoculated field nurseries consisting of replicated plots of 51 cultivars. The isolates were obtained from cultivars that had been rated as highly resistant in the field but later developed low levels of stripe rust. All of the isolates were virulent on seedlings of the cultivar from which they were obtained. Stripe rust intensity was evaluated eight times between flag leaf emergence and early milk stages. The mean intensity was used as a measure of virulence on adult plants, allowing gradual transitions (Zadoks 1961) or progressive increases (McIntosh et al. 1995) in virulence to be quantified and confirming virulence on five cultivars that had been rated as highly resistant in the field. In the United States, there appears to have been no reports of race-specific APR to stripe rust before 2002 (Line 2002), and races of *P. striiformis* f. sp. *tritici* are identified on seedlings of 20 differential lines (Chen et al. 2002, Wan and Chen 2012) with no known attempts to identify races based on adult-plant reactions.

The objectives of this study were to characterize the stripe rust resistance in contemporary SRWW and HRWW cultivars, to characterize the virulence of *P. striiformis* f. sp. *tritici* isolates based on the resistances found in the cultivars, and to determine wheat breeders’ perceptions on the importance and methods for achieving stripe rust resistance.

MATERIALS AND METHODS

Characterization of resistance. The 96 entries in the 2013 Arkansas Wheat Cultivar Performance Test (Mason et al. 2013) were evaluated for resistance to stripe rust at four field locations where stripe rust occurred naturally. Resistance was evaluated by estimating the percentage of total leaf area with sporulating stripe rust lesions at soft dough stage in four replicate plots (approximately 1.5 m wide ×

6 m long) of each cultivar in a randomized complete block design at each location. Sixteen of these entries were considered commonly grown SRWW cultivars and also were evaluated for all-stage resistance to eight single-lesion *P. striiformis* f. sp. *tritici* isolates collected from five locations in Arkansas during 2013. All-stage resistance was evaluated on seedlings at a 5 to 18°C gradually changing temperature regime as described previously (Sthapit et al. 2012), except that inoculum (10 mg spores per gram talc) was applied with a powder blower (Sunrise Medical HHG Inc., Somerset, PA) and ITs were recorded separately on first and second leaves.

Eight HRWW lines and seven SRWW lines containing *Yr17* that were susceptible at the seedling stage to races PSTv-37 from Arkansas and PST-127 from Washington (provided by X. Chen) and that had a range of resistance levels at two field locations with PSTv-37 (Milus et al. 2015) were evaluated for APR under controlled conditions compared with a susceptible check. The lines were vernalized in a growth chamber and grown in a greenhouse as described by Sthapit et al. (2012). To synchronize heading among plants of the 16 lines, the first plants to have emerging flag leaves were moved to a growth chamber programmed to gradually change from 10 to 15°C with a 14-h photoperiod to slow development. Plants in the chamber were returned to the greenhouse at least 48 h before inoculation. At early heading stage when expression of APR should be high (Sthapit et al. 2012), a flag leaf on three plants of each line was inoculated with race PSTv-37, and a flag leaf on another three plants of each line was inoculated with race PST-127. Inoculations were done using a powder blower to apply spores mixed with talc (30 mg g⁻¹). After approximately 24 h in a dew chamber at 12°C, plants were kept in a growth chamber programmed to gradually change from 10 to 18°C with a 14-h photoperiod. Light intensity in the 400 to 700 nm range was 430 to 470 μmol m⁻² s⁻¹ at the flag leaf level as measured using an Apogee Quantum meter, model 200 (Apogee Instruments, Inc., Logan, UT). The IT and disease intensity on flag leaves were recorded at 14, 17, and 20 dai as described previously (Sthapit et al. 2012). The experimental design was a split-plot with two repetitions of the experiment as the whole plot and a factorial of two pathogen isolates and 16 wheat lines with three replications as the split-plot. Area under disease progress curve (AUDPC) was calculated based on the three estimates of disease intensity and analyzed using Proc MIXED, SAS version 9.1.3 (SAS Institute, Cary, NC). Race and line were considered fixed effects, and experimental run and replication were considered random effects. Because AUDPC values could not be calculated for two experimental units due to premature plant death, least-squares means were compared using a protected least significant difference (LSD) at *P* = 0.05 based on the number of observations for each mean.

To compare the levels of APR among wheat lines based on the AUDPC values under controlled conditions as described above with levels of APR observed in the field, relative AUDPC values for race PSTv-37 were compared with relative stripe rust intensity values for the lines in five location-years in which PSTv-37 was the predominant race (Milus et al. 2015). Relative values were calculated by dividing the AUDPC and intensity values of each line by the corresponding AUDPC and intensity values for the susceptible check, Croplan Genetics 514W.

Reactions of *P. striiformis* f. sp. *tritici* isolates on adult-plant differentials. A susceptible check (Croplan Genetics 514W), seven SRWW cultivars (Progeny 166, Arcadia, Mason, AGS 2035, LA 821, 26R61, and VA07W-415), and four HRWW cultivars (Jagger, Everest, TAM 111, and Pete) were selected as adult-plant differentials based on reactions in the field that suggested they might differentiate isolates at adult-plant stages. Seven of these cultivars are known to have all-stage *Yr* genes that are effective against certain isolates. 26R61 has *Yr9* (Sthapit et al. 2012), LA 821, Jagger, and VA07W-415 have *Yr17* (Milus et al. 2015), TAM 111 has *QYr.tam-2BL* (Basnet et al. 2014), and AGS 2015 has *Yr9* (J. Johnson, *personal communication*). The remaining cultivars are not suspected of having any all-stage *Yr* genes. The APR gene *YrR61* is

present in 26R61 (Hao et al. 2011) and AGS 2035 (J. Johnson, *personal communication*). Single-lesion isolates were selected to represent isolates from Arkansas in 2013 and the range of adult-plant virulence found in tests with a preliminary set of 10 adult-plant differentials. Isolates were stored at -80°C and grown on seedlings of 'Florida 302' for at least two generations as described previously (Sthapit et al. 2012) before being used in experiments. Seedlings and adult plants were grown and vernalized as described above. Differentials were inoculated at the two-leaf seedling stage to determine the level of all-stage resistance on first and second leaves and at boot stage to determine the level of APR on flag leaves. Urediniospores were diluted with talc (10 mg g^{-1}) and applied with a powder blower. Dew chamber and growth chamber conditions were as described above. Two replicates of the differentials were inoculated in each seedling or adult-plant experiment, and each isolate was tested in at least two experiments at each growth stage. Ratings for IT and disease intensity at 18 to 21 dai were as described above. Reactions with ITs ≤ 3 were considered resistant. Reactions were considered intermediate for ITs 4 to 6 or for higher ITs with intensities less than half that of the susceptible check. Reactions with ITs ≥ 7 and intensities similar to the susceptible check were considered susceptible. Isolates used in this study have been deposited in collections managed by X. Chen and M. Hvømler.

Breeders' perceptions of stripe rust resistance and how to achieve it. A survey was e-mailed to all known public and private SRWW and HRWW breeders in the United States. The questions were as follows: (i) What is your priority for incorporating stripe rust resistance into your cultivars – high, moderate, or low? (ii) What percentage of your selection effort for stripe rust resistance is based on seedling inoculations, adult plants in the field, and molecular markers? (iii) What percentage of your sources of stripe rust resistance are specific genes or markers, specific cultivars or lines, and unknown sources?

RESULTS

Characterization of resistance. The 16 commonly grown SRWW cultivars had high ITs similar to the susceptible check on both first and second seedling leaves after inoculation with each of the eight isolates from 2013 (Table 1). However, all cultivars except Progeny 185 had low stripe rust intensities at soft dough stage across

the four field locations. Of the 96 entries in the 2013 Arkansas Wheat Cultivar Performance Test that were evaluated for resistance in the field, the number of entries with stripe rust intensities not significantly greater than 0 (one-tailed LSD test at $P = 0.025$) were 92, 94, 75, and 81 at Keiser, Kibler, Newport, and Rohwer, respectively (data not shown), indicating that most of the entries had a high level of resistance to isolates that were prevalent in 2013.

Statistical analysis of AUDPC on flag leaves of SRWW and HRWW lines with *Yr17* under controlled conditions showed that there was a significant ($P < 0.0001$) race–line interaction. Comparison of the race–line interaction means (Table 2) indicated that this interaction was due to significantly higher AUDPC values with race PSTv-37 than race PST-127 on eight of the 16 lines used in the experiment. The other eight lines had similar AUDPC values with both races. Although Jagger and LA01139D-56-1-C had significantly lower AUDPC values than the susceptible check (Croplan Genetics 514W) when inoculated with PSTv-37, these lines had AUDPC values similar to the susceptible check when inoculated with PST-127. HV9W05-1125, NE05426, NE06545, and TAM401 had low AUDPC values with both races. Differences in IT among lines inoculated with the two races (Table 2) generally agreed with the differences described above for AUDPC. However, AGS2060 gave mixed results in that it had high ITs to both races in run 1 and low ITs to both races in run 2.

Characterization of virulence patterns on seedlings and adult plants of the APR differentials. Adult-plant virulence pattern (APVP) 1 is represented by isolates AR90-01 and AR97-01 of the old *P. striiformis* f. sp. *tritici* strain (Table 3). Croplan Genetics 514W (susceptible check), Progeny 166, Arcadia, Mason, and Pete had high ITs on all leaves and high intensities on flag leaves. AGS 2035, LA 821, 26R61, VA07W-415, Jagger, and TAM 111 had low or predominantly low ITs on both seedling leaves and no signs or symptoms on flag leaves. Everest had intermediate to high and high ITs on the first and second seedling leaves and high intensities with intermediate to high ITs on flag leaves.

APVP 2 is represented by isolates AR00-05 and AR03-33 of the new *P. striiformis* f. sp. *tritici* strain (Table 4). Croplan Genetics 514W (susceptible check) was the only line that had high ITs on all leaves and high intensities on flag leaves. Progeny 166, Arcadia, Mason, and 26R61 had mostly high ITs on both seedling leaves but low intensities and ITs on flag leaves. AGS 2035, LA 821, Jagger,

TABLE 1. Stripe rust infection type (IT) on first and second leaves of seedlings inoculated with eight isolates^a of *Puccinia striiformis* f. sp. *tritici* from Arkansas in 2013 and stripe rust intensity at soft dough stage in the field at four locations in Arkansas during 2013 for 16 commonly grown cultivars of soft red winter wheat

Cultivar	Seedling IT (0 to 9) to 8 isolates		Stripe rust intensity in field (% leaf area diseased) ^b			
	Leaf 1	Leaf 2	Keiser	Kibler	Newport	Rohwer
Jamestown	7, 8, or 9	8 or 9	0	0	0	0
Havoc	7, 8, or 9	8 or 9	0	0	0	0
Octane	7, 8, or 9	8 or 9	0	0	0	0
McAlister	7, 8, or 9	8 or 9	0	0	0	0
Xtreme	7, 8, or 9	8 or 9	0	0	0	0
26R10	7, 8, or 9	8 or 9	0	0	0	0
26R41	7, 8, or 9	8 or 9	0	0	0	0
Coker 9553	7, 8, or 9	8 or 9	0	0	0	0
Harrison	7, 8, or 9	8 or 9	0	0	0	0
Oakes	7, 8, or 9	8 or 9	0	0	1	4
Terral TV8861	7, 8, or 9	8 or 9	0	0	1	0
Vandal	7, 8, or 9	8 or 9	1	0	0	2
Ricochet	7, 8, or 9	8 or 9	5	0	1	1
26R20	7, 8, or 9	8 or 9	5	0	11	1
Progeny 357	7, 8, or 9	8 or 9	7	0	4	0
Progeny 185	7, 8, or 9	8 or 9	50	70	43	78
Croplan Genetics 514W (susceptible check)	8 or 9	8 or 9	...	...	...	...
Croplan Genetics 554W (susceptible check)	...	...	30	9	58	89
USG 3993 (susceptible check)	...	...	57	46	70	89

^a AR13-01 from Lonoke; AR13-06 from North Little Rock; AR13-07, AR13-09, AR13-10 from Rohwer; AR13-12, AR13-14 from Newport, and AR13-15 from Kibler.

^b Mean across four replicates of the Arkansas Wheat Cultivar Performance Test at each location in 2013.

Everest, TAM 111, and Pete had low or predominantly low ITs on first seedling leaves, intermediate or high ITs on second seedling leaves, and low intensities and ITs on flag leaves, except for Pete that had intermediate to high ITs on flag leaves. VA07W-415 had higher ITs and intensity with AR03-33 than with AR00-05. APVP 3 is represented by isolates AR10-04 and AR 12-19 (Table 5) and was similar to APVP 2 except for higher ITs and severities on LA 821, VA07W-415, and Jagger that have *Yr17*.

APVP 4 is represented by isolate AR12-25 (Table 6). Both seedling leaves of all lines had mostly high ITs. On flag leaves, intensities and ITs were high except on Mason that had a low intensity and IT, Jagger that had an intermediate intensity and IT, and AGS 2035 that had an intermediate intensity.

APVP 5 is represented by AR13-06 and AR13-10 (Table 7) and four additional isolates from 2013 (data not shown). Both seedling leaves of all lines had high ITs. On flag leaves, intensities and ITs were high except on Arcadia and Mason that had low intensities and ITs, Everest that had low intensities and intermediate ITs, Jagger and VA07W-415 that had intermediate intensities and intermediate

to high ITs, and AGS 2035 that had intermediate intensities and high ITs.

APVP 6 is represented by the type isolate of race PST-127 (Table 8). Both seedling leaves of all lines had high ITs. On flag leaves, intensities and ITs were high except on Mason and VA07W-415 that had low intensities and ITs, Arcadia, LA 821, Everest, and TAM 111 that had high intensities and intermediate ITs, and AGS 2035 that had an intermediate intensity and intermediate to high ITs.

The reactions of the six APVPs on flag leaves of the 12 differentials are summarized in Figure 1. Based on these reactions, all of the APR was race-specific.

Breeders' perceptions of stripe rust resistance and how to achieve it. Ten SRWW and seven HRWW breeders responded to the survey, and their responses are summarized in Table 9. SRWW breeders were about evenly distributed for their priority for incorporating stripe rust resistance into their cultivars, whereas most HRWW breeders considered it a high priority. Regardless of wheat market class, most selection for stripe rust resistance was based on evaluating adult plants in the field. All but one breeder

TABLE 2. Area under the disease progress curve (AUDPC) averaged across two runs of the experiment and infection type (IT) on flag leaves of 16 wheat lines in *Yr17* inoculated at heading stage with isolate AR10-04 (race PSTv-37^a) and the type isolate of race PST-127^b (both virulent on *Yr9* and *17*) of *Puccinia striiformis* f. sp. *tritici* and incubated at a 10 to 18°C gradually changing temperature regime with a 14-h photoperiod

Line	AUDPC ^c		IT (0 to 9)			
			Run 1		Run 2	
	AR10-04	PST-127	AR10-04	PST-127	AR10-04	PST-127
Croplan Genetics 514W	578	471	9	8	9	8
HV9W03-1596R	520* ^d	227	7	2–5	6	2–4
VA07W-415	510*	239	9	2–5	9	2–4
VA06HRW-108	493*	207	9	2–5	6	2–5
LA 821	463*	155	9	2–7	9	2–4
HV9W04-1594R	458*	118	9	2–5	9	2–4
SS8641	413*	88	7	3	7	2–4
Jagger	408	450	8	9	9	7
VA08MAS-412	377*	146	9	2–5	8	2–4
LA01139D-56-1-C	341	416	8	2–4	7	2–4
AGS 2026	306	205	4	4	3	2–4
AGS 2060	301	329	8	7	2–4	2–4
HV9W05-1125	215*	69	6	4	7	2–3
NE05426	203	136	7	4	8	2–4
NE06545	169	101	3	3–6	2	2–4
TAM401	122	41	4	3	4	2–4

^a Since 2010, races were determined on a new set of differentials described by Chen (2014).

^b Before 2010, races were determined on a set of differentials described by Chen et al. (2002).

^c Least significant difference (LSD) ($P = 0.05$) = 117 for comparing any pair of AUDPC values except as follows where there were missing values. For comparing NE05426 inoculated with AR10-04 or VA06HRW-108 inoculated with PST-127 to any other mean, the LSD ($P = 0.05$) = 123.

^d * Indicates a significantly higher value for AR10-04 than PST-127.

TABLE 3. Infection type (IT, 0 to 9 scale) on first and second leaves of seedlings and stripe rust intensity (percentage of leaf area diseased) and IT on flag leaves of differential wheat lines inoculated with *Puccinia striiformis* f. sp. *tritici* isolates AR90-01 and AR97-01 (both race PST-3^a) that have adult-plant virulence pattern 1

Differential	AR90-01				AR97-01			
	Seedling IT ^b		Flag leaf		Seedling IT ^b		Flag leaf	
	Leaf 1	Leaf 2	Intensity ^c	IT ^b	Leaf 1	Leaf 2	Intensity ^c	IT ^b
Croplan Genetics 514W	8	8	84	9	8–7	8–9	90	9
Progeny 166	8	8	64	9–8	8–6	8–9	78	9
Arcadia	8	8	43	9–8	8–6	8–9	71	9–8
Mason	8	8	79	9	8	8	77	9
AGS 2035	1	1	0	0	1	1	0	0
LA 821	1–2	3–6	0	0	2	2–4	0	0
26R61	1	1	0	0	1	1	0	0
VA07W-415	2–4	2–5	0	0	2	2	0	0
Jagger	2–4	2–6	0	0	2	2	0	0
Everest	5–8	8	45	6–9	5–7	8–6	75	6–8
TAM 111	2	2	0	0	2	2	0	0
Pete	8–5	8	74	8–9	8–6	8	71	8–9

^a Race designation based on the U.S. standard set of differentials before 2010 (Chen et al. 2002).

^b A dash (–) indicates a range of ITs with the predominant IT listed first across two repetitions of the experiment with two replications each.

^c Averaged across two repetitions of the experiment with two replications each.

reported using molecular markers for stripe rust resistance, and two breeders relied completely on markers for incorporating stripe rust resistance. One SRWW and four HRWW breeders used seedling inoculations for a small portion of their selection effort. Regardless of market class, breeders considered most of their sources of stripe rust resistance as unknown. Among the specific *Yr* genes and sources being used, *Yr17* (seven responses) and 26R61 (four responses) were the most frequently listed. Among the all-stage genes that are effective in eastern United States, *Yr 5*, *10*, and *15* were the most frequently used by breeders who utilize molecular markers (two responses for each).

DISCUSSION

The results of this study indicate that there was no effective all-stage resistance to isolates of *P. striiformis* f. sp. *tritici* collected in 2013 among the 16 commonly grown SRWW cultivars or the 12 APR differential lines selected for this study. Likewise, there was no effective all-stage resistance to PSTv-37 or PST-127 among the eight HRWW and seven SRWW lines with *Yr17*. Given these results, race identification on seedling differentials cannot explain differences in virulence that are important to wheat growers or breeders in eastern United States. As discussed by McIntosh (2010)

and da Silva (1958), virulence data are most useful when they accurately predict what will happen in farmers' fields. To be most useful, differentials should include the resistances used in regional cultivars and advanced breeding lines.

APR was identified in all of the HRWW and SRWW cultivars and lines evaluated except for the susceptible check (Croplan Genetics 514W) and Progeny 185. This is similar to the situation in the United Kingdom in the early 1970s that made assaying *P. striiformis* f. sp. *tritici* virulence on adult-plant differentials a common practice (Priestley and Doodson 1976). Furthermore, the APR in all the APR differential lines and in 10 of 15 lines with *Yr17* was shown to be race-specific. This agrees with previous reports of race-specific APR to stripe rust in winter wheat cultivars from eastern United States (Sthapit et al. 2012, Markell et al. 2009), Europe (Hovmøller 2007, Hubbard and Bayles 2013, Zadoks 1961) and with the conclusion of Danial et al. (1995) that resistances conferring a hypersensitive reactions are likely race-specific. However, these results are contrary to those from western United States where race-specific APR has never been reported and all APR has been classified as HTAP that is effective against all races (Line 2002, Chen 2007).

Based on the major patterns of stripe rust intensity and IT on flag leaves of the APR differentials, isolates were classified into one of

TABLE 4. Infection type (IT, 0 to 9 scale) on first and second leaves of seedlings and stripe rust intensity (percentage of leaf area diseased) and IT on flag leaves of differential wheat lines inoculated with *Puccinia striiformis* f. sp. *tritici* isolates AR00-05 (race PST-78^a) and AR03-33 (race PST-100^a) that have adult-plant virulence pattern 2

Differential	AR00-05				AR03-33			
	Seedling IT ^b		Flag leaf		Seedling IT ^b		Flag leaf	
	Leaf 1	Leaf 2	Intensity ^c	IT ^b	Leaf 1	Leaf 2	Intensity ^c	IT ^b
Croplan Genetics 514W	8–7	8	41	9	8	8	40	9
Progeny 166	8–7	8–9	15	2–5	8	8	21	2–6
Arcadia	8–6	8	2	2	8	8	2	0–3
Mason	8–6	8	6	2–4	8	8	6	2–3
AGS 2035	2–5	8–7	3	3–0	3–5	8–6	1	0–3
LA 821	2	4–8	1	0–4	3–5	7–6	9	5–2
26R61	8–6	8	1	0–3	8–5	8	9	2–5
VA07W-415	4–2	8–7	2	0–3	8–7	8	19	6–5
Jagger	2–4	5–7	1	0–2	3–6	7–4	4	2–5
Everest	3–4	8–7	1	0–5	4–5	8	2	0–3
TAM 111	2–3	4–7	0	0–2	2–4	5–4	8	2–4
Pete	3–6	7–8	6	6–8	4–6	8	15	4–7

^a Race designation based on the U.S. standard set of differentials before 2010 (Chen et al. 2002).

^b A dash (–) indicates a range of ITs with the predominant IT listed first across two repetitions of the experiment with two replications each.

^c Averaged across two repetitions of the experiment with two replications each.

TABLE 5. Infection type (IT, 0 to 9 scale) on first and second leaves of seedlings and stripe rust intensity (percentage of leaf area diseased) and IT on flag leaves of differential wheat lines inoculated with *Puccinia striiformis* f. sp. *tritici* isolates AR10-04 (race PSTv-37^a) and AR12-19 (race PSTv-34^a) that have adult-plant virulence pattern 3

Differential	AR10-04				AR12-19			
	Seedling IT ^b		Flag leaf		Seedling IT ^b		Flag leaf	
	Leaf 1	Leaf 2	Intensity ^c	IT ^b	Leaf 1	Leaf 2	Intensity ^c	IT ^b
Croplan Genetics 514	7–8	8–9	78	9	8	8	97	9
Progeny 166	8	8	6	2–3	8	8	21	2–5
Arcadia	5–8	8	8	0–4	8	8	1	1–2
Mason	8–6	8	6	0–2	8	8	6	2–3
AGS 2035	2–6	7–5	6	5–6	2–4	7–8	10	5–7
LA 821	4–6	8	19	8	8	8	66	8–9
26R61	8	8	4	0–2	8	8–9	19	2
VA07W-415	8–7	8–9	57	9–8	8–7	8–9	82	9
Jagger	6–2	8–7	25	6–8	8–7	8–9	64	9–8
Everest	8	8	2	0–2	8	8	6	2–3
TAM 111	2–5	6–8	2	1	3–2	7–8	6	1–2
Pete	7–3	8–6	29	6–7	8–5	8	50	7–5

^a Race designation based on the new U.S. standard set of differentials since 2010 (Chen 2014).

^b A dash (–) indicates a range of ITs with the predominant IT listed first across two repetitions of the experiment with two replications each.

^c Averaged across two repetitions of the experiment with two replications each.

six APVPs. This term was chosen rather than “adult-plant race” because races are described on a standard set of differentials (Roelfs 1984, Zadoks 1961), and there was no intention of proposing the differentials used in this study as a standard set. On the contrary, adult-plant differentials need to be flexible and should be chosen from among important contemporary cultivars and advanced breeding lines that are susceptible to contemporary isolates at the seedling stage but have been resistant in the field as described by da Silva (1958) and Zadoks (1961) and put into practice in the United Kingdom (Priestley et al. 1984, Hubbard and Bayles 2013).

The expression of stripe rust resistance is often different under different environmental conditions (Boyd 2005, Zadoks 1961). The results of our study were based on a monocyclic infection of flag leaves under high inoculum density and arbitrary environmental conditions in a growth chamber that may be favorable for the expression of some resistance genes but unfavorable for the expression of others. Relative AUDPC values (i.e., relative to the susceptible check) for the 15 wheat lines inoculated with race PSTv-37 under controlled conditions at a gradually changing 10 to 18°C temperature regime ranged from 0.21 to 0.90 and averaged

0.61 (calculated from data in Table 2). Relative stripe rust intensities for the same 15 lines at soft dough stage in the field averaged 0.08, 0.13, 0.15, 0.18, and 0.34 in five location-years in which PSTv-37 was the predominant race (calculated from data in Milus et al. 2015). AUDPC values under controlled conditions underestimated the resistance in the field except for line VA07W-415 at Fayetteville in 2011. The 10 to 18°C temperature regime is representative of temperatures in the field during the early spring in Arkansas and is favorable for stripe rust development, whereas warmer temperatures that occur later in the growing season are more favorable for the expression of some resistances and less favorable for stripe rust development (Zadoks 1961). Quantification of APR levels in field nurseries based on polycyclic infection cycles under natural conditions and with multiple evaluations during the epidemic as done in the United Kingdom (Hubbard and Bayles 2013) and Denmark (Hovmøller 2007) is likely the most accurate method for evaluating APR of wheat lines and adult-plant virulence of *P. striiformis* f. sp. *tritici* isolates.

TABLE 6. Infection type (IT, 0 to 9 scale) on first and second leaves of seedlings and stripe rust intensity (percentage of leaf area diseased) and IT on flag leaves of differential wheat lines inoculated with *Puccinia striiformis* f. sp. *tritici* isolate AR12-25 (PSTv-39^a) that has adult-plant virulence pattern 4

Differential	AR12-25			
	Seedling IT ^b		Flag leaf	
	Leaf 1	Leaf 2	Intensity ^c	IT ^b
Croplan Genetics 514	8	8–9	80	9
Progeny 166	8	8–9	75	9
Arcadia	8	8	75	8–7
Mason	8	8–9	6	1
AGS 2035	8	8–9	35	9–8
LA 821	8	8–9	65	9–8
26R61	8	8–9	70	9
VA07W-415	8–5	8–9	56	7–8
Jagger	5–8	8–6	35	6–3
Everest	8	8	70	8–9
TAM 111	8	8–9	80	9
Pete	8	8	72	9–8

^a Race designation based on the new U.S. standard set of differentials since 2010 (Chen 2014).

^b A dash (–) indicates a range of ITs with the predominant IT listed first across two repetitions of the experiment with two replications each.

^c Averaged across two repetitions of the experiment with two replications each.

TABLE 8. Infection type (IT, 0 to 9 scale) on first and second leaves of seedlings and stripe rust intensity (percentage of leaf area diseased) and IT on flag leaves of differential wheat lines inoculated with the type isolate of *Puccinia striiformis* f. sp. *tritici* race PST-127^a that has adult-plant virulence pattern 6

Differential	PST-127			
	Seedling IT (0 to 9) ^b		Flag leaf	
	Leaf 1	Leaf 2	Intensity ^c (%)	IT ^b
Croplan Genetics 514	8	8	95	9
Progeny 166	8	8	90	9
Arcadia	8	8	77	3–6
Mason	8	8–9	7	1
AGS 2035	8	8	31	6–8
LA 821	8	8	55	2–5
26R61	8	8	75	9
VA07W-415	8	8	21	1–3
Jagger	8	8	54	9–8
Everest	8	8	57	6–5
TAM 111	8	8–9	85	4–5
Pete	8	8–9	81	9–8

^a Isolate obtained from X. Chen and race designation based on the U.S. standard set of differentials before 2010 (Chen et al. 2002).

^b A dash (–) indicates a range of ITs with the predominant IT listed first across two repetitions of the experiment with two replications each.

^c Averaged across two repetitions of the experiment with two replications each.

TABLE 7. Infection type (IT, 0 to 9 scale) on first and second leaves of seedlings and stripe rust intensity (percentage of leaf area diseased) and IT on flag leaves of differential wheat lines inoculated with *Puccinia striiformis* f. sp. *tritici* isolates AR13-06 and AR13-10 (both race PSTv-52^a) that have adult-plant virulence pattern 5

Differential	AR13-06				AR13-10			
	Seedling IT ^b		Flag leaf		Seedling IT ^b		Flag leaf	
	Leaf 1	Leaf 2	Intensity ^c	IT ^b	Leaf 1	Leaf 2	Intensity ^c	IT ^b
Croplan Genetics G514	8	9	64	9	8–9	9	52	9
Progeny 166	9–8	9–8	53	9–8	9–8	9	57	9
Arcadia	8	8	5	2–4	8–9	9–8	6	2–4
Mason	8–9	9	1	0–1	8	8–9	3	1
AGS 2035	8–9	9–8	29	9	9	9	23	8–9
LA 821	8–9	9	69	8–9	8–9	9	21	9–8
26R61	8–9	9	68	9–8	8	9	59	9
VA07W-415	8–6	9–8	46	5–6	7–8	8–9	12	8–3
Jagger	8–9	8–9	16	4–7	7–8	8–9	29	3–8
Everest	8	8–9	7	4–6	7–8	8–9	6	3–7
TAM 111	8–9	9–8	77	9	8–9	9–8	56	9–8
Pete	8–9	9	57	9	8–9	9	28	8–9

^a Race designation based on the new U.S. standard set of differentials since 2010 (Chen 2014).

^b A dash (–) indicates a range of ITs with the predominant IT listed first across two repetitions of the experiment with two replications each.

^c Averaged across two repetitions of the experiment with two replications each.

Fig. 1. Stripe rust infection on flag leaves of 12 winter wheat cultivars inoculated with isolates of *Puccinia striiformis* f. sp. *tritici* representative of six adult-plant virulence patterns (APVP) and their reactions on seedlings (S = susceptible = infection type [IT] ≥ 7 on first and second leaves, R = resistant = IT ≤ 4 on first and second leaves, I = intermediate = IT 5 to 6 or resistant IT on first leaf and susceptible IT on second leaf) and flag leaves (S = IT ≥ 7 and intensity similar to susceptible check, R = IT ≤ 4 , I = IT 5 to 6 or IT ≥ 7 with intensity < half that of susceptible check). CG514 = Croplan Genetics 514W (susceptible check), P166 = Progeny 166, Arc = Arcadia, Mason = Mason, 2035 = AGS 2035, LA 821 = LA 821, 26R61 = 26R61, VA415 = VA07W-415, Jagger = Jagger, Eve = Everest, T111 = TAM 111, Pete = Pete. APVP 1 = isolates AR90-01 and AR97-01 that are representative of the old *P. striiformis* f. sp. *tritici* strain that was present before 2000; APVP 2 = isolates AR00-05 and AR03-33 of the new *P. striiformis* f. sp. *tritici* strain from 2000 and 2003, respectively; APVP 3 = isolates AR10-04 and AR12-19 from 2010 and 2012, respectively; APVP 4 = AR12-25 from 2012; APVP 5 = isolates AR13-06 and AR13-10 from 2013; and APVP 6 = type isolate of race PST-127 from Washington State in 2007. Yellow shading around seedling and flag leaf reactions indicates race-specific adult-plant resistance.

The all-stage resistance conferred by *Yr9* in AGS 2035 and 26R61, by *Yr17* in LA 821, VA07W-415 and Jagger, and by *QYr.tam-2BL* in TAM 111 were easy to identify when seedlings were inoculated with isolates AR90-01 or AR97-01 (both avirulent on *Yr9*, *17* and *QYr.tam-2BL*) because both seedling leaves had low or predominantly low ITs (Table 3). When inoculated with isolates AR00-05 or AR03-33 (both virulent on *Yr9* and avirulent on *Yr17*), the resistance conferred by *Yr17* in the above three lines could be interpreted as either all-stage or adult-plant depending on which seedling leaf is considered to represent the seedling reaction (Table 4) and the IT threshold for distinguishing resistance from susceptibility as described previously by Milus et al. (2015). Likewise, AGS 2035 and TAM 111 had low to intermediate ITs on the first seedling leaf but mostly high ITs on the second seedling leaf when inoculated with AR10-04 or AR12-19 (Table 5). For these host-pathogen interactions, the IT on the first leaf was a more accurate predictor of the intensity and IT on flag leaves than the IT on the second leaf. As summarized in the companion paper (Milus et al. 2015), some stripe rust researchers consider the IT on the first leaf to represent the seedling reaction whereas other stripe rust researchers consider the IT on the second leaf to represent the seedling reaction. The results of this study support the use of the first leaf to represent the seedling reaction for wheat stripe rust as reported by Boshoff et al. (2002), Hubbard and Bayles (2013), Prashar et al. (2007), Yahyaoui et al. (2002), and Zadoks (1961) and are in agreement with Stakman et al. (1962) who used the first leaf to evaluate seedling reactions for wheat stem rust and with Roelfs et al. (1992) who recommended that the first leaf be evaluated to determine seedling reactions for leaf, stem and stripe rusts of wheat. In addition to being a better predictor of the adult-plant reaction, utilizing reactions on the first leaf would shorten the time needed to conduct seedling tests for resistance and virulence. A quick completion of seedling tests was important in earlier times when tests were done in poorly designed greenhouses in which powdery mildew was a constant problem (A. P. Roelfs, *personal communication*).

Isolates AR00-05 and AR03-33 (APVP 2) of the new *P. striiformis* f. sp. *tritici* strain revealed a high level of APR in Progeny 166, Arcadia, Mason, Everest and Pete that were susceptible to isolates AR90-01 and AR97-01 (APVP 1) of the old strain. Virulence overcoming the resistance in Progeny 166, Arcadia, Everest and Pete evolved by 2012 (APVP 4), but the resistance in Mason has remained effective against all isolates tested. A similar phenomenon was reported recently from Europe (Sørensen et al. 2014). An isolate of the new *P. striiformis* f. sp. *tritici* strain (*PstS2*) revealed high levels of APR in a cultivar and

several recombinant inbred lines and near-isogenic lines with different QTL for APR that were susceptible to the old *P. striiformis* f. sp. *tritici* strain. Furthermore, a new race that was first detected in 2011 was virulent on several of the wheat lines that were resistant to *PstS2*. These examples indicate that *P. striiformis* f. sp. *tritici* isolates from different epidemiological regions can differ greatly in their ability to overcome race-specific APR.

Wheat breeders in the eastern United States have been concerned with incorporating stripe rust resistance into their cultivars only since the emergence of the new *P. striiformis* f. sp. *tritici* strain in 2000 (Basnet et al. 2014). As might be expected, the breeders' survey found high priorities for incorporating stripe rust resistance in the southern SRWW region and the southern and central HRWW regions that have experienced frequent stripe rust epidemics and low priorities in the northern SRWW and HRWW regions where stripe rust rarely becomes epidemic. The high priority among most HRWW breeders also may be due to few effective sources of resistance in adapted backgrounds. However, it is easier for SRWW breeders to develop resistant cultivars because there are many sources of effective resistance, as evidenced by the large number of highly resistant entries in the 2013 Arkansas Wheat Cultivar Performance Tests. The results of the survey also indicated that most of the current selection effort for stripe rust resistance is based on evaluations of adult plants in the field. However, breeders with a low priority for incorporating stripe rust resistance because epidemics are rare in their region tended to rely most on molecular markers for specific genes, whereas breeders with a high priority for incorporating stripe rust resistance because epidemics were common in their region tended to rely most on selection in the field. Although selection in the field can be effective for both all-stage and adult plant resistances, our study found no evidence for currently effective all-stage resistance among the wheat lines evaluated. As of the 2013 season, *Yr5* and *15* were the only all-stage genes in the U.S. set of stripe rust differentials that were resistant to all isolates evaluated for virulence (Chen 2014). However, virulence on *Yr5* and *15* were reported from elsewhere more than 20 years ago before these genes were ever deployed in cultivars (McIntosh et al. 1995). Breeders listed *Yr5*, *10*, and *15* as the most frequently used all-stage resistance genes, but the probability for managing stripe rust in eastern United States with all-stage resistance seems to be low.

Unknown sources were most frequently used by both HRWW and SRWW breeders as sources of stripe rust resistance. Most of the adult-plant resistance described in this study is in this unknown category and appears to be responsible for protecting SRWW cultivars in southeastern United States and HRWW cultivars in the

TABLE 9. Summary of responses to survey questions by breeders of soft red winter wheat (SRWW) or hard red winter wheat (HRWW)

Survey question	Breeder responses by wheat market class	
	SRWW	HRWW
Priority for incorporating stripe rust resistance?		
High	3	6
Moderate	4	0
Low	3	1
Percentage of selection effort is based on?		
Seedling inoculations	Range 0 to 20%, $\bar{X}$ = 2%	Range 0 to 20%, $\bar{X}$ = 5%
Adult plants in field	Range 0 to 100%, $\bar{X}$ = 67%	Range 65 to 90%, $\bar{X}$ = 82%
Molecular markers	Range 0 to 100%, $\bar{X}$ = 31%	Range 9 to 35%, $\bar{X}$ = 13%
Sources of stripe rust resistance by percentage?		
Specific genes/markers	Range 0 to 100%, $\bar{X}$ = 38%	Range 0 to 10%, $\bar{X}$ = 5%
Specific lines/cultivars	Range 0 to 40%, $\bar{X}$ = 12%	Range 0 to 20%, $\bar{X}$ = 8%
Unknown	Range 0 to 100%, $\bar{X}$ = 50%	Range 70 to 100%, $\bar{X}$ = 87%
Specific genes/markers being used? (number of multiple responses in parentheses)	<i>Yr5</i> , <i>15</i> , <i>17</i> (6), <i>18</i>	<i>Yr5</i> , <i>10</i> (2), <i>15</i> , <i>17</i> , <i>18</i> , <i>29</i> , <i>35</i> , <i>36</i> (2), <i>38</i> , <i>42</i> , <i>45</i> , <i>52</i>
Specific sources being used? (number of multiple responses in parentheses)	26R61 (4), USG3555 (2), Jamestown, VA00W-38, LA841	TAM 111 (2), Duster, Billings, Fannin

Great Plains from stripe rust. Although this resistance appears to be race-specific and not durable, the resistance is highly effective against avirulent isolates. It also is found in diverse adapted backgrounds, easily selected in the field and likely to be simply inherited (Markell et al. 2009).

Some of the APR described in this study may be useful in other regions where stripe rust is a problem, and even susceptible cultivars from other regions may have additional race-specific APR genes that may be effective in the United States. International research efforts are needed to identify sources of race-specific APR and to survey regional *P. striiformis* f. sp. *tritici* populations for avirulence to the resistances. To prevent the introduction of exotic *P. striiformis* f. sp. *tritici* isolates, it would be best to exchange wheat lines rather than *P. striiformis* f. sp. *tritici* isolates among regions.

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