Identification and Selection of F_6 and F_7 Families of Wheat for High-Temperature, Adult-Plant Resistance to Stripe Rust Using Hillplots

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ABSTRACT

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F_6 and F_7 populations of winter wheat (*Triticum aestivum*) from nine crosses among the high-temperature adult-plant (HTAP) resistant cultivars, Gaines, Nugaines, Luke, Daws, and Stephens, and a susceptible line, PS279, were evaluated for resistance to *Puccinia striiformis*. Initial selection among F_6 families of each cross was done using rowplots at Mt. Vernon, WA, in 1986, and subsequent identification and selection among and within F_7 families was done using hillplots at Pullman, WA, in 1987. Stripe rust development in the hillplots was sufficient to observe significant disease differences among families of each cross. Significantly different phenotypes for disease expression were observed among and within families, indicating that it is possible to select for increased HTAP resistance at the F_7 generation. Transgressive segregation for both increased resistance and increased susceptibility was more frequently observed within families than among families. The additional space required to evaluate breeding lines at the subfamily level is much less when using hillplots than with other designs. The hillplot design is a practical and effective method for evaluating late-generation families for HTAP resistance to stripe rust.

Additional keywords: durable resistance, nonspecific resistance

Since 1961, the most effective control for stripe rust of wheat (*Triticum aestivum* L.), caused by *Puccinia striiformis* Westend., in the United States has been to grow cultivars with high-temperature, adult-plant (HTAP) resistance (5). HTAP resistance is a unique type of resistance to stripe rust that is currently incorporated into most cultivars grown where stripe rust occurs in the United States. HTAP resistance is expressed in plants at early jointing or later (adult) stages of growth at higher temperatures (10). Adult plants are resistant at diurnal temperatures of 10–30 C but are susceptible at diurnal temperatures of 6–21 C. Seedlings are susceptible at both temperature ranges. Upper leaves, especially flag leaves, are more resistant than lower leaves (10). HTAP resistance shows no differential reaction to races of *P. striiformis* and has remained durable for more than 30 yr of extensive use in the Pacific Northwest.

The soft white winter wheat cultivars Gaines (CI 13448), released in 1961; Nugaines (CI 13968), released in 1965; Luke (CI 14586), released in 1970; Daws (CI 17419), released in 1976; and Stephens (CI 17596), released in 1977, all have HTAP resistance to stripe rust (5). Milus and Line (6,7), using early generations of crosses between Gaines, Nugaines, Luke, and a susceptible parent, reported that this resistance is controlled by at least two or three recessive genes and that gene action is mostly additive. They also reported that the genes for HTAP resistance in Nugaines and Luke are different. The inheritance of HTAP resistance in Daws and Stephens has not been investigated. Selection of lines with recessive or additive types of stripe rust resistance has been successful in previous studies (4,9).

Most disease and yield data for small grains is obtained using rowplots. The size of the rowplots, although a good estimator of yield, limits the number of plots that can be practically evaluated. Hillplots can be an alternative for determining both stripe rust resistance and the effect of stripe rust on components of yield, especially when land and seed resources are limited. Hillplots have been used to estimate resistance to crown rust of oats (13) and stem rust in wheat (15) and to measure components of yield, such as number of kernels per spike, kernel weight, and spike weight (2,8), but to our knowledge have not been used to study the genetics of stripe rust resistance in wheat.

The following experiments were conducted in 1986 and 1987 using F_6 and F_7 families from nine crosses of winter wheat cultivars with different levels of HTAP resistance to stripe rust. Our objectives were to determine if differences in this resistance could still be detected and selected from within F_6 and F_7 lines and to determine if hillplots could be used to evaluate stripe rust resistance among and within families of these different crosses.

MATERIALS AND METHODS

F_6 and F_7 populations from nine winter wheat crosses, which included Gaines/PS279, Nugaines/PS279, Luke/PS279, Daws/PS279, Stephens/PS279, Gaines/Nugaines, Gaines/Luke, Nugaines/Luke, and Nugaines/HR-Luke, were evaluated for HTAP resistance. PS279 is a club wheat line from R. E. Allan, USDA, Pullman, WA, that is susceptible to all known races of *P. striiformis* in the northwestern United States (6). HR-Luke is a highly resistant selection within the cultivar Luke (6). For each cross, 100 families, each descended from a single F_2 plant, were maintained through the F_6 generation without any selection for stripe rust resistance. F_6 seed from 100 families of each cross were planted in a completely random design, using rows 1.8 m long and 0.46 m apart, at Mt. Vernon, WA, in October, 1985. Rows of each parent were replicated nine times.

Data on stripe rust intensity were recorded for the plants in each row (family) the following spring and summer on 22 May (mid-jointing), 4 June (early heading), and 30 June (soft dough). Rust intensities were recorded as the total percentage of leaf area covered with rust using a modified scale of Milus and Line (6), where the following values were used: 0, 1, 5, 10, 20, 30, 40, 50, 60, 70, 80, 90, and 99%. Data for each cross were recorded within a 24-hr period. Multiple recordings of rust intensity data were transformed to area under the disease progress curve (AUDPC) using the following formula: $AUDPC = {}_{i=1-3} \Sigma ((X_i + X_i+1)/2)t_i$ where X_i is the rust intensity at date i and t_i is the time in

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days between date i and $i+1$ when data were recorded.

These data, in addition to stripe rust intensity data recorded in 1985 at the F_5 generation on the same families grown at Mt. Vernon, were evaluated and used to select eight F_6 families that best represented the range of stripe rust resistance for each of the crosses. In addition, from each of the eight families, a single spike was harvested randomly from six different plants and individually threshed in order to determine within-family (subfamily) differences in stripe rust resistance during the following year. Ten F_7 seeds from each of the six plants were planted as hillplots 0.5 m apart at Pullman, WA, on 22 and 23 September 1986. Each of the 50 entries (eight families and six subfamilies, plus two parents per cross) was replicated three times using a randomized complete block design. To provide sufficient inoculum during the following spring, the plots were uniformly dusted with urediospores of *P. striiformis* race CDL-20 mixed in talc on 30 April (early jointing) after a rain shower. Race CDL-20, collected from Stephens wheat and identified in 1975, is virulent on seedlings of all the parents. The plants were irrigated by overhead sprinklers twice in June and once in early July to provide additional moisture for disease development and to improve plant vigor. Rust intensities were recorded on 23 and 24 June, when plants were at the boot stage of growth, and on 7 and 8 July, when plants were heading. Data for each replicate were recorded within a single 24-hr period. Rust intensity data were transformed into AUDPC for analyses. Analysis of variance and Duncan's multiple range tests were used to determine differences in rust intensity among and within families of each cross using the Statistical Analysis System GLM procedure (11).

RESULTS

In 1986, the cool spring and summer at Mt. Vernon was favorable for stripe rust development. When plants were at the mid-jointing stage (22 May), rust intensities ranged from 5 to 60% for the most resistant crosses to 50 to 80% for the most susceptible crosses (Table 1). By the soft dough stage (30 June), stripe rust intensities ranged from 5 to 90%, which made it easy to differentiate and select low, moderate, and highly resistant families among the crosses for experiments the following year. Large differences were observed for the ratio of low, moderate, and highly resistant families among the crosses (Table 2). The relative performance of these selected families was similar at Pullman the following year. At Pullman, rust intensities at the boot stage (22 June) ranged from 0 to 80% (Table 3). By heading (9 July), rust intensities had increased and ranged from 0 to 90%. AUDPC values for parents were both lower (Stephens) and higher (PS279) than those of the crosses (Table 3). Among crosses, the mean AUDPC values ranged from 196 to 784 (Table 3).

Within each cross the number of significantly different disease phenotypes observed among families ranged from two for the Gaines/Nugaines cross to six for the Nugaines/HR-Luke cross (Table 4). The number of significantly different disease phenotypes observed within families also ranged from two for the Gaines/Nugaines cross to six for the Luke/PS279 and Nugaines/HR-Luke crosses (Table 4). Significantly different phenotypes for stripe rust expression existed within most (56 of 72) of the families that were tested. For example, out of eight families that were tested in the Luke/PS279 cross, four were significantly different for rust intensity with AUDPC values ranging from 205 to 821 (Table 4). Analysis of AUDPC among families revealed transgressive segregation for increased susceptibility or increased resistance to stripe rust in the Gaines/Luke, Nugaines/Luke, and Nugaines/HR-Luke crosses. However, observations within families revealed transgressive segregation for increased susceptibility and/or increased resistance in six of the nine crosses (Table 4). If transgressive segregation was observed among families of a cross, it was always observed within families of the cross but not vice versa.

Table 1. Stripe rust intensity at three growth stages and area under the disease progress curve (AUDPC) for parents and F_6 families of nine crosses of winter wheat grown at Mt. Vernon, WA, in 1986

	Rust intensity (%)[a]						
	Mid-jointing[b]		Early heading		Soft dough		
Parent or cross	Mean	Range	Mean	Range	Mean	Range	AUDPC
Gaines	63	50–70	39	30–40	41	40–50	1,704
Nugaines	51	40–60	34	20–40	41	30–50	1,546
Luke	17	10–20	8	5–10	16	5–20	462
Daws	16	10–20	11	10–20	12	5–20	469
Stephens	24	10–30	14	10–20	20	10–30	700
PS279	69	60–80	79	70–90	88	80–90	3,127
Gaines/PS279	66	50–80	54	20–70	64	30–90	2,308
Nugaines/PS279	69	50–80	56	40–80	59	30–80	2,308
Luke/PS279	50	30–70	49	30–70	51	30–70	1,942
Daws/PS279	29	5–60	31	10–70	34	10–70	1,160
Stephens/PS279	26	10–60	30	10–50	30	10–50	1,146
Gaines/Nugaines	55	40–70	39	30–40	43	30–50	1,666
Gaines/Luke	32	10–50	28	10–50	29	5–50	1,129
Nugaines/Luke	41	20–70	39	30–50	38	20–50	1,511
Nugaines/HR-Luke	40	20–70	30	20–50	35	20–60	1,300

[a] Data are the means of 100 families per cross and nine replications of each parent.
[b] Dates for mid-joining, early heading, and soft dough were 22 May, 4 June, and 30 June, respectively.

Table 2. The number of low, moderate, and highly stripe rust resistant F_6 families from nine crosses of winter wheat grown at Mt. Vernon, WA, in 1986

	Rust resistance[a]		
Cross	Low	Moderate	High
Gaines/PS279	70	28	2
Nugaines/PS279	53	47	0
Luke/PS279	49	44	7
Daws/PS279	8	35	57
Stephens/PS279	0	39	61
Gaines/Nugaines	0	100	0
Gaines/Luke	0	44	56
Nugaines/Luke	11	73	16
Nugaines/HR-Luke	1	43	56

[a] Based on area under the disease progress curve (AUDPC) for data recorded at jointing, heading, and soft dough stages of growth for 100 families of each cross. AUDPC values for resistance classes were: 0–1,235 = high resistance; 1,236–2,245 = moderate resistance; and 2,246–3,055 = low resistance.

DISCUSSION

At Mt. Vernon in 1986, stripe rust was severe enough to easily determine low, moderate, and high levels of HTAP resistance in the F_6 families. These data were valuable in selecting representative groups from each cross for a more detailed within-family evaluation in the F_7 generation. A detailed evaluation of all 100 families from each cross was not possible.

At Pullman in 1987, stripe rust intensity at the boot stage of growth was low in the hillplots, but later in the season rust intensity increased (Table 3). The plots were irrigated twice in June, when rainfall was infrequent, and once in July. The temperatures were 4 C above normal in June, and the additional irrigation in June may have had a cooling effect. The reduced temperature and added moisture were conducive for stripe rust development. Rust increased the fastest during this period. Subsequently, the range of stripe rust intensity for the selected families was large enough at Pullman in 1987 to easily identify different levels of stripe rust resistance.

Selection within families of self-pollinated crops usually ends at the F_5 or F_6 generation, and selection of superior plant material usually shifts from within families to among families (1). By this time, most plants are nearly homozygous and therefore very little segregation occurs, making selection among different families more desirable. Selection for HTAP resistance to stripe rust has been most successful when made from intermediate and highly resistant lines (5,7). Selection from intermediate and highly resistant lines or cultivars is recommended because this resistance is often recessive or partially recessive with additive gene action (4,7,9). Therefore, selection for increased resistance can be effective in later generations (F_4 to F_6). Krupinsky and Sharp (4) reported transgressive segregation for increased resistance in F_5 and F_6 progeny from crosses using both spring and winter wheat cultivars with additive types of stripe rust resistance that lacked resistance in the F_2 and F_3 generations. Sharp (12) reported that segregation for greater stripe rust resistance continued to occur in the F_6 generation. Milus and Line (7) reported transgressive segregation for both increased resistance and susceptibility in F_4 progeny of crosses between Gaines, Nugaines, and Luke. In this experiment, when families of each cross were compared to their parents, some families of the Nugaines/HR-Luke cross had significantly greater AUDPC values than the most susceptible parent (Nugaines), indicating transgressive segregation for increased susceptibility. Also, some F_7 families of the Gaines/Luke and Nugaines/Luke crosses had significantly lower values for stripe rust than their most resistant parent, indicating transgressive segregation for increased resistance. This was not surprising since the genes for HTAP resistance in Luke are reported to be different than those in Gaines and Nugaines (6). Further, when subfamilies were compared with their parents, transgressive segregation for both greater resistance and/or greater susceptibility were observed in progeny of six of the nine crosses (Table 4). This also supports the conclusion of Milus and Line (6) that genes for resistance in these cultivars are different. However, it is also significant that greater resistance was observed in three resistant/susceptible crosses. This suggests that there are genes in the very susceptible parent PS279 that contribute to resistance. Wallwork and Johnson (14) reported transgressive segregation for increased adult-plant resistance to stripe rust in F_5 progeny of winter wheat and observed transgressive segregation in both resistant/resistant and susceptible/susceptible crosses. They concluded that transgressive segregation should be observed among many crosses and is not just an occasional phenomenon. Pope (9) also reported transgressive segregation for increased resistance to stripe rust among progeny from crosses using seven cultivars that he considered to be susceptible. Certain progeny from crosses using these susceptible parents expressed moderate to large increases in resistance to stripe rust. More work needs to done to identify the resistance factors in these susceptible wheats.

This is the first report of hillplots being used to study the genetics of stripe rust resistance in wheat. Because the hillplots required less area, a more detailed (within-family) test of the populations was

Table 3. Stripe rust intensity at two growth stages and area under the disease progress curve (AUDPC) for parents and F_7 families of winter wheat grown at Pullman, WA, in 1987

	Rust intensity (%)[a]				
	Boot		Heading		
Parent or cross	Mean	Range	Mean	Range	AUDPC
Gaines	20	10–30	52	40–60	502
Nugaines	22	10–30	60	40–80	571
Luke	5	1–10	19	5–40	164
Daws	3	0–10	15	0–30	125
Stephens	1	0–5	1	0–5	17
PS279	48	40–60	76	60–80	863
Gaines/PS279	43	0–80	69	0–90	784
Nugaines/PS279	36	0–70	65	0–90	710
Luke/PS279	26	0–60	53	0–90	555
Daws/PS279	20	0–60	43	0–90	440
Stephens/PS279	15	1–50	29	0–80	306
Gaines/Nugaines	27	0–40	57	0–80	588
Gaines/Luke	8	0–30	20	0–60	192
Nugaines/Luke	9	0–40	25	0–80	237
Nugaines/HR-Luke	19	1–70	41	1–90	421

[a] Data are the means of eight families per cross.

Table 4. Area under the disease progress curve (AUDPC), number of disease phenotypes, and transgressive segregants for F_7 families of winter wheat grown at Pullman, WA, in 1987

	AUDPC										Number of phenotypes[a]		Transgressive segregants[b]			
			Family by rank										Among families		Within families	
Cross (parent 1/parent 2)	Parent 1	Parent 2	1	2	3	4	5	6	7	8	Among families	Within families	Res.	Susc.	Res.	Susc.
Gaines/PS279	490	863	414	723	766	778	859	894	902	941	3	4	0	0	1	3
Nugaines/PS279	560	887	533	595	661	716	739	774	797	871	5	5	0	0	3	0
Luke/PS279	236	863	205	254	381	428	754	797	805	821	4	6	0	0	3	0
Daws/PS279	125	863	126	196	426	450	490	502	663	670	3	4	0	0	0	0
Stephens/PS279	17	840	133	164	167	181	332	438	465	560	4	5	0	0	0	0
Gaines/Nugaines	513	698	474	537	556	583	607	614	649	692	2	2	0	0	0	0
Gaines/Luke	513	107	22	115	142	179	226	228	290	333	4	4	1	0	6	0
Nugaines/Luke	490	201	90	109	174	228	240	241	355	456	5	5	2	0	9	1
Nugaines/HR-Luke	536	110	135	243	278	278	363	546	721	805	6	6	0	2	0	9

[a] Values indicate the number of significantly different phenotypic groups among eight families and 48 subfamilies (six subfamilies within each family) for each cross at $P \leq 0.05$.

[b] Transgressive segregation for res. (resistance significantly greater than the most resistant parent) or susc. (susceptibility significantly greater than the most susceptible parent) among eight families and 48 subfamilies for each cross at $P \leq 0.05$.

possible. The greater number of differences observed within families as compared to between families demonstrates the benefit of using hillplots to distinguish these differences and shows that selection within families as late as the F_6 generation can be useful for improving lines for HTAP resistance to stripe rust.

Yield in wheat is determined by both environmental and genetic factors. Families with a high yield potential can mitigate the effects of disease, so low ratings for stripe rust intensity do not necessarily identify lines with high yield potential (3). Because of this, further evaluation of HTAP resistant lines is necessary to identify lines that have high yield potential while under pressure from stripe rust. In these experiments, hillplots were useful for determining differences in HTAP resistance to stripe rust for F_7 families and provided more information about their resistance that may enhance breeding efforts using these lines. From a management perspective, hillplots offer an additional and useful method of evaluating cultivars or lines for stripe rust resistance and require a minimum amount of labor and other resources.

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