Effectiveness of Adult-Plant Resistance in Reducing Grain Yield Loss to Powdery Mildew in Winter Wheat

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ABSTRACT

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We studied the effectiveness of adult-plant resistance (APR) in protecting grain yields in winter wheat grown in Virginia under varying levels of intensity of powdery mildew (caused by *Blumeria graminis* f. sp. *tritici*) obtained with different fungicide treatments in field experiments in two crop years. Mildew severity was assessed at three to four plant growth stages, and the data were used to calculate mean mildew severity (MMS) and area under the mildew disease progress curve. The susceptible cultivar Saluda had an average MMS of 5.3%. MMS and grain yield for Saluda were significantly negatively correlated in both years, and yield loss averaged 13.4% in untreated plots relative to full-season control plots. Both early- and late-season mildew control were important in protecting grain yield in Saluda. Knox 62 had an average MMS of 2.1%, and disease progress for this cultivar was greater than for other APR cultivars. Grain yields of Knox 62 without fungicides were equivalent to those obtained with full-season control in both years. Untreated plots of the APR cultivars Massey, Redcoat, and Houser had MMS values lower than 1% in both years, and genetic resistance in these cultivars was sufficiently high in most cases to negate any additional benefit from fungicides in reducing mildew development. APR is effective under conditions that favor mildew epidemics, and incorporation of APR into semidwarf wheats with high yield potential should result in cultivars with more durable resistance.

Powdery mildew, caused by *Blumeria graminis* (DC.) E. O. Speer f. sp. *tritici* Em. Marchal, is a destructive disease of wheat (*Triticum aestivum* L. em. Thell) in the mid-Atlantic states in most years (6,15,18). In Virginia, yield losses from 12 to 20% have been observed in susceptible cultivars (26–28).

Although fungicide treatment is effective in controlling powdery mildew (4,6,15,17), the most economical and environmentally safe means of control is the use of resistant cultivars. Genes that confer a hypersensitive type of resistance have been used in most cases in wheat (2), but this resistance has been ephemeral (19,22) because *B. graminis* populations with virulence matching these genes build up rapidly in response to selection pressure exerted by the resistant cultivars. Virulence already exists in the southeastern United States to the 10 genes most widely used for resistance to powdery mildew in wheat (16).

Resistance that retards infection by and growth and reproduction of the powdery mildew pathogen in adult plants, but not in seedlings, has been termed "slow mildewing" or "adult-plant resistance" (APR) (8) and has been identified in wheat (2), barley (*Hordeum vulgare* L.) (10), and oats (*Avena sativa* L.) (11). APR to powdery mildew is more durable than hypersensitive resistance. APR remained effective in the winter wheat cultivar Knox and its derivatives during the 20 yr in which these cultivars were grown commercially (23).

Shaner and his colleagues (8,22–25) have clearly described the effect of APR in Knox wheat and its derivatives on powdery mildew development, defined the rate-reducing components involved, and outlined methods for evaluating and characterizing this type of resistance. Shaner (23) concluded that the APR of Knox should provide stable, practical disease control and that this resistance should be effective under conditions that favor mildew epidemics (25).

However, the effectiveness of APR has not been evaluated in the mid-Atlantic region, where powdery mildew becomes established on winter wheat in the fall and epidemics occur yearly (4,7,15). APR is quantitative in nature, disease severity increases over time, and environment can affect the expression of resistance (25). Currently recommended management practices (1,13) that incorporate more nitrogen fertilizer produce microenvironments that are conducive to mildew development (5) and therefore may modify the effectiveness of APR (25).

Although APR has been shown to reduce mildew development (23), studies documenting its effectiveness in lowering grain yield loss to the disease have not been reported. Seedlings of APR cultivars are susceptible, and yield reduction caused by early-season mildew infection of lower leaves before stem elongation in the spring, when expression of resistance becomes apparent (24), has been reported (4,14,15,21). Fungicide seed treatments control powdery mildew throughout the fall and early spring (6). Therefore, fungicide seed treatment combined with APR should provide full-season control of powdery mildew (12).

The objective of this study was to determine the potential breeding value of APR to powdery mildew in areas like the mid-Atlantic region, where mildew epidemics occur yearly. The APR of Knox has been transmitted to many of its progeny and is easily detected in conventional progeny-row tests under heavy mildew pressure (19,23). Specifically, we attempted to determine the effectiveness of APR in reducing grain yield loss under varying disease severity conditions obtained with different fungicide treatments and to assess the effect of integration of APR with fungicide seed treatment in controlling powdery mildew in wheat.

MATERIALS AND METHODS

Experiments were conducted over 2 yr on Suffolk soils (fine-loamy, siliceous, thermic Typic Hapludult) in the Coastal Plain region of Virginia. Four APR cultivars—Houser (CI17736), Redcoat (CI13170), Massey (CI17953), and Knox 62 (CI13701)—and one susceptible cultivar—Saluda (PI480474)—were tested each year. Seedlings of Massey (C. A. Griffey, *unpublished*) and Red-

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coat (20) give a hypersensitive reaction to some *B. graminis* isolates, and therefore these cultivars probably possess major gene resistance in addition to APR. On the other hand, these major genes also may condition APR in these cultivars. Hypersensitive resistance has not been observed in seedlings of Knox 62 (23) or Houser (C. A. Griffey, *unpublished*).

Plots were seeded at 78 kg/ha (66 seeds per meter of row) on 24 October 1989 and 163 kg/ha (79 seeds per meter of row) on 16 October 1990. Fertilizer (33.6 kg of nitrogen and 89.6 kg of both phosphorus and potassium per hectare) was applied in the fall when the land was prepared. Soil pH was within the range recommended for cereal production. Nitrogen fertilizer was top-dressed in early March at a rate of 95.2 kg/ha.

Experiments were split-plot designs, with cultivars as the main-plot factor and fungicide treatments as the subplot factor, with three replications in 1990 and six in 1991. In 1990, each experimental unit (subplot) consisted of three 2.48-m-long rows with 0.3 m between rows (2.2 m^2). In 1991, each experimental unit had six 2.78-m-long rows with 0.18 m between rows (3.0 m^2). The lower seeding rates and smaller subplots in 1990 were due to the limited availability of seed of some cultivars. Border plots of the susceptible cultivar Becker, equivalent in size to the experimental units, were planted between experimental units in 1990 and in three of the six replications in 1991 to increase and sustain inoculum pressure. The moderately resistant cultivar Coker 983 was used as a border in the other three replications in the 1991 study to assess the influence of interplot interference and inoculum load on treatment effects.

We used four fungicide treatments to modify the intensity of epidemics of powdery mildew: 1) a standard seed treatment with carboxin plus thiram (17% + 17%) at 0.87 g a.i./kg of seed, which we identified as "untreated" because carboxin plus thiram does not affect powdery mildew development; 2) seed treatment with triadimenol at 0.22 g a.i./kg; 3) two foliar sprays with triadimefon at 140 g a.i./ha; and 4) treatments 2 and 3 combined. These treatments were applied to assess the effectiveness of APR alone and in combination with fungicides and to evaluate the effect of early- and late-season mildew development on grain yield in APR cultivars.

Foliar sprays were applied at the same time to all cultivars when mildew reached threshold levels (29) on the susceptible cultivar Saluda. Foliar sprays were applied on 7 and 26 April 1990, when Saluda was at Zadoks (30) growth stage (GS) 38 and 50, respectively, and on 3 April and 1 May 1991, when Saluda was at GS 40 and 59, respectively.

Powdery mildew epidemics developed naturally both years. Mildew severity was assessed with the James disease assessment key (9). Five randomly selected tillers from different locations in each plot were rated, and the mean rating was used as an estimate of disease severity for the plot. Mildew severity was recorded on the flag leaf and the first (F-1), second (F-2), and third (F-3) leaves below the flag leaf. Because the five cultivars differed in time of leaf emergence and senescence, not all leaves were assessed on each date. Severity was assessed in 1990 on 5 April (GS 32–41), 25 April (GS 39–57), and 18 May (GS 83–85) and in 1991 on 10 April (GS 34–39), 24 April (GS 38–59), 8 May (GS 59–71), and 22 May (GS 75–85).

Mean mildew severity (MMS) for each cultivar was calculated by averaging the severity ratings taken at each assessment. Thus, the MMS value represents early mildew that developed on lower leaves as well as late mildew that developed on the flag leaf. The disease severity assessments also were used to calculate the area under the mildew progress curve (AUMPC), as described by Bjarko and Line (3). The AUMPC value of a genotype measures the severity of disease as well as the rate of disease development for that genotype. In the 1990 experiment, it was possible to calculate AUMPC only for the F-1 leaf for the cultivars Saluda and Massey. In the 1991 experiment, AUMPC was calculated for the F-2 leaf from the first three disease severity assessments and for the F-1 leaf from the last three assessments for all five cultivars.

At maturity, the center row of each plot was harvested by hand in the 1990 test. In 1991, the four center rows of each plot were harvested with a small-plot combine. Grain yield and test weight were then recorded. In addition, a 1-m section from each plot was harvested by hand each year to assess the following yield components: number of tillers per meter of row, 1,000-kernel weight, and number of kernels per head. The number of kernels per head was determined as the mean number of kernels from 10 randomly selected heads from the meter row. Analysis of variance (ANOVA) was performed on AUMPC, MMS, grain yield, and the yield components.

RESULTS

Powdery mildew was severe both years, and conditions were favorable for disease development from the first to the last assessment. Mildew severity for F-1 leaves of the susceptible border cultivar Becker at the final reading in untreated plots was 30.5% in 1990 and 26.7% in 1991.

Disease progress over time was slower in untreated plots of the APR cultivars than in untreated plots of the susceptible cultivar Saluda (Fig. 1). Among the APR cultivars, disease progress was greatest for Knox 62 (Fig. 1B and C). Disease progress of Houser and Redcoat was intermediate between those of Knox 62 and Massey; however, considering that

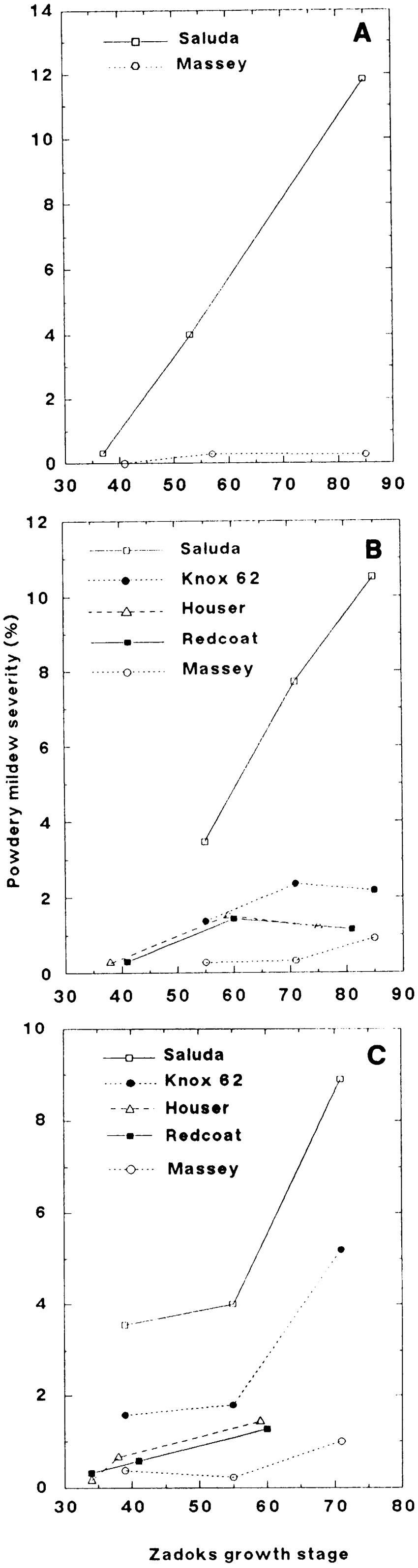

Fig. 1. Powdery mildew severity on F-1 leaves **(A and C)** and F-2 leaves **(B)** of selected wheat cultivars at three growth stages in untreated plots in 1990 **(A)** and 1991 **(B and C)**. Cultivar Saluda is susceptible to powdery mildew, and cultivars Massey, Knox 62, Houser, and Redcoat have adult-plant resistance to powdery mildew.

the former cultivars mature later and thus were probably exposed to greater disease pressure than Massey, it is doubtful whether they differ significantly from Massey with respect to disease progress.

ANOVA revealed significant ($P \leq 0.05$ except where noted otherwise) effects of cultivar and treatment on MMS and grain yield and a significant cultivar-by-treatment interaction for MMS in 1990 (Table 1). Significant variation among cultivars was observed for all yield components studied in 1990 (*data not presented*). However, significant treatment effects were observed only for 1,000-kernel weight and test weight. None of the yield components was significantly affected by the cultivar-by-treatment interaction.

Table 1. Analysis of variance of mean mildew severity (MMS), area under the powdery mildew progress curve (AUMPC), and grain yield for five wheat cultivars in 1990 and 1991

		Mean squares[a]			
			AUMPC		
Source	**df**	**MMS**	**F-2[b]**	**F-1[c]**	**Grain yield**
		1990			
Replication (R)	2	0.01			9,640
Cultivar (C)	4	13.18**			6,398,582**
Error A (R × C)	8	0.29			713,182
Treatment (T)	3	8.69**			2,332,608**
C × T	12	2.10**			364,158
Error B	30	0.40			179,918
		1991			
Replication (R)	5	0.09	382	111	744,312**
Cultivar (C)	4	20.26**	38,021**	15,297**	27,274,035**
Error A (R × C)	20	0.17	220	268	193,049
Treatment (T)	3	17.99**	26,381**	17,707**	894,476**
C × T	12	3.37**	6,538**	3,670**	79,905
Error B	75	0.17	398	236	78,936

[a] Asterisks denote significance at $P < 0.05$ (*) and $P < 0.01$ (**).

[b] Second leaf below the flag leaf.

[c] First leaf below the flag leaf.

Table 2. Mean mildew severity (MMS), area under the powdery mildew progress curve (AUMPC), and grain yield for five fungicide-treated and untreated wheat cultivars in 1990 and 1991[x]

	1990			1991			
					AUMPC		
Cultivar Treatment	**MMS (%)**	**AUMPC F-1[y]**	**Grain yield (kg/ha)**	**MMS (%)**	**F-2[z]**	**F-1[y]**	**Grain yield (kg/ha)**
Saluda							
Untreated	5.8 a	225 a	5,577 b	4.84 a	206 a	143 a	5,288 c
Triadimenol	2.1 b	99 b	6,136 ab	3.34 b	144 b	93 b	5,445 bc
Triadimefon	2.7 b	63 bc	5,748 b	0.87 c	41 c	14 c	5,755 ab
Triadimenol + triadimefon	0.6 c	10 c	6,590 a	0.61 c	21 c	11 c	5,962 a
Knox 62							
Untreated	2.1 a		4,497 b	2.02 a	58 a	73 a	3,344 a
Triadimenol	0.6 b		4,800 ab	1.33 b	43 a	46 b	3,628 a
Triadimefon	1.4 ab		5,356 a	0.27 c	7 b	10 c	3,492 a
Triadimenol + triadimefon	0.2 b		4,475 b	0.20 c	5 b	5 c	3,654 a
Massey							
Untreated	0.4 a	9 a	5,864 c	0.34 a	11 a	13 a	5,356 ab
Triadimenol	0.1 a	5 a	6,108 bc	0.29 a	11 a	11 a	5,283 b
Triadimefon	0.2 a	3 a	6,770 ab	0.04 a	0.2 a	2 a	5,548 ab
Triadimenol + triadimefon	0.1 a	2 a	7,134 a	0.02 a	0.9 a	1 a	5,639 a
Redcoat							
Untreated	1.0 a		4,327 b	0.84 a	30 a	19 a	3,027 b
Triadimenol	0.7 a		5,004 ab	0.48 ab	21 ab	11 a	3,392 a
Triadimefon	0.6 a		4,984 ab	0.06 b	5 b	0.9 a	3,323 ab
Triadimenol + triadimefon	0.2 a		5,100 a	0.05 b	2 b	1.4 a	3,506 a
Houser							
Untreated	0.9 a		4,595 b	0.86 a	32 a	20 a	4,136 a
Triadimenol	0.4 a		5,681 a	0.60 a	24 ab	17 ab	4,149 a
Triadimefon	0.6 a		6,028 a	0.04 b	1.9 b	0.6 b	4,257 a
Triadimenol + triadimefon	0.1 a		5,884 a	0.02 b	1.6 b	0.2 b	4,448 a
$LSD_{(0.05)}$	1.1	65	707	0.47	23	18	323

[x] Numbers within a column for each cultivar followed by different letters are significantly different.

[y] First leaf below the flag leaf.

[z] Second leaf below the flag leaf.

In the 1991 study, mildew severity ratings on F-1 leaves of Becker and Coker 983 border plots at the final reading were 26.7 and 1.4%, respectively. In ANOVA using replications with different borders as separate environments with respect to inoculum load, no significant ($P \geq 0.05$) effect of environment on powdery mildew or interaction of environment with cultivar or with treatment was found; subsequently, data from the six replications were analyzed as a single environment. The lack of significant effects relating to the degree of resistance of border cultivars suggests that inoculum was abundant and that airborne conidia were dispersed over a wide area. These experiments were conducted in a major wheat production area, and plots were adjacent to other breeding nurseries and commercial fields.

Mean squares for MMS, AUMPC for F-2 and F-1 leaves, and grain yield for 1991 are presented in Table 1. Cultivar and treatment had significant effects on grain yield. Cultivar, treatment, and cultivar-by-treatment interaction had significant effects on MMS and AUMPC. Cultivar effects were significant for all yield components studied (*data not presented*), treatment effects were significant for 1,000-kernel weight, and cultivar-by-treatment interaction effects were significant for 1,000-kernel weight and test weight.

In both years, triadimenol seed treatment significantly reduced MMS and AUMPC for the susceptible cultivar Saluda compared to untreated plots (Table 2). Triadimenol seed treatment did not reduce MMS or AUMPC significantly for any of the APR cultivars except Knox 62. Seed-treatment plots of Knox 62 had significantly lower MMS both years and lower AUMPC for the F-1 leaf in 1991 than did untreated plots.

MMS and AUMPC for Saluda were significantly lower in triadimefon-treated plots than in untreated plots both years (Table 2). MMS did not differ significantly in untreated and triadimefon-treated plots of APR cultivars in 1990. In 1991, MMS and AUMPC for the APR cultivars Knox 62, Redcoat, and Houser were significantly lower in triadimefon-treated plots than in untreated plots. However, untreated plots of Redcoat and Houser had MMS values of less than 1%. Thus, while differences in disease severity between fungicide-treated and untreated plots of Redcoat and Houser were significant, they were small and may be attributed to the higher levels of disease pressure on these late-maturing cultivars relative to Massey.

In both years, MMS and AUMPC for Saluda were significantly lower in plots that received both triadimenol and triadimefon treatments (full-season control) than in untreated plots (Table 2).

Untreated and full-season control plots did not differ significantly in MMS in 1990 for the APR cultivars, except for Knox 62. In 1991, full-season control plots of Knox 62, Redcoat, and Houser had significantly less mildew than untreated plots. The reduction in disease severity in these APR cultivars achieved with fungicide treatments was not biologically significant compared to that observed in Saluda. MMS and AUMPC values for the cultivar Massey were similar for all treatments and in both years.

MMS and grain yield were significantly negatively correlated for the susceptible cultivar Saluda in both years (Table 3). Correlations between MMS and grain yield among APR cultivars did not generally reflect a yield response to powdery mildew severity.

In both years, grain yields of Saluda were significantly higher in full-season control plots than in untreated plots (Table 2). Grain yields of Knox 62 without fungicides and with full-season control were not significantly different either year. No consistent differences in grain yields of fungicide-treated versus untreated plots were observed over years for the other APR cultivars.

Few significant correlations between MMS and yield components were observed either year. In 1991, tillers per meter of row was significantly negatively correlated with MMS for Saluda and Knox 62, and 1,000-kernel weight was associated with MMS for Saluda (Table 3).

DISCUSSION

In both years, mild fall and winter conditions were conducive to early establishment and development of powdery mildew and were followed by disease epidemics in the spring that persisted through the dough stage of grain ripening. Unprotected cultivars with APR had similar MMS both years and were associated with reduced disease development even though conditions favored epidemics throughout the season. This result agrees with the findings of Shaner and Finney (25). In most cases, the APR cultivars Massey, Redcoat, and Houser had high enough levels of genetic resistance to negate any additional benefit from fungicide application in suppressing mildew development. MMS and AUMPC values for these three APR cultivars in untreated plots were lower than or equivalent to those observed for Saluda in plots that received both triadimenol seed treatment and triadimefon foliar sprays. Each of the fungicide treatments reduced MMS and AUMPC for Knox 62 both years; however, disease severity of Knox 62 in untreated plots was similar to or lower than that of Saluda with triadimenol seed treatment. Jones et al (12) observed similar results with APR to powdery mildew in oats.

Over the 2 yr, Saluda had an average yield loss of 13.4% in untreated plots compared to full-season control plots, which is similar to the yield losses of 17 and 10–18% previously found for this cultivar in North Carolina (15) and Virginia (26,28), respectively. Results from this study support those of Bowen et al (4) and suggest that both early- and late-season mildew control are often necessary for maximum protection of grain yield in susceptible cultivars such as Saluda.

The APR cultivar Knox 62 generally did not show a significant yield advantage from fungicide treatments in either year. However, the significant negative correlation between tillers per meter of row and MMS in 1991 and the significant reduction in MMS with triadimenol seed treatment in both years suggest that early-season mildew control could be economically important in Knox 62 when the incidence of mildew is high. We would expect both the resistance of Knox 62 and the efficacy of seed treatments to be higher under field conditions than in the current study, where adjacent plots of a susceptible cultivar produced conidia throughout the season.

MMS values of the APR cultivars Massey, Redcoat, and Houser were less than 1% both years, yet some yield advantage was observed with fungicide treatments in a few cases. Yield differences among treatments were not consistent for these cultivars between years. The presence of other diseases, variability in cultivar growth stage when foliar sprays were applied, and the limited area of experimental units tested for grain yield may have had confounding effects on observed yield differences among treatments. Leaf rust (caused by *Puccinia recondita* Roberge ex Desmaz. f. sp. *tritici*) was prevalent late in the 1990 season, but flag leaf severities did not exceed 1.3% (James scale). Grain yield losses in Massey were observed only in plots that did not receive triadimefon foliar sprays, which suggests that some yield loss in this rust-susceptible cultivar may be attributed to leaf rust. Grain yield in Redcoat was significantly negatively correlated with barley yellow dwarf severity in 1991. Observed differences in grain yield in fungicide-treated versus untreated plots of Redcoat may be partly attributable to barley yellow dwarf.

Mildew severity was low on the APR cultivars Massey, Redcoat, and Houser, and fungicide effects were minimal. This suggests that cultivars such as these with higher levels of APR could be grown without fungicides when powdery mildew is of primary concern. The yield potential of Saluda and other currently recommended cultivars (>6,500 kg/ha) exceeds that of most APR cultivars in this study.

In spite of the apparent value of APR, breeding programs continue to rely on the few remaining effective sources of race-specific resistance available (2). APR to powdery mildew in Knox 62, Massey, Redcoat, and Houser is governed by two to four genes, additive in nature, and moderately to highly heritable (M. K. Das and C. A. Griffey, *unpublished*). Therefore, APR in these cultivars should be readily transferable to their progeny.

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Table 3. Correlation coefficients of mean mildew severity with grain yield and yield components for five wheat cultivars in 1990 and 1991[a]

Cultivar	Grain yield	Test weight	1,000-kernel weight	Kernels/ head	Tillers/ meter of row
			1990 ($n = 12$)		
Saluda	−0.62*	−0.11	−0.01	−0.12	−0.32
Knox 62	0.10	0.36	−0.08	−0.08	0.12
Massey	−0.15	0.03	0.04	−0.01	0.38
Redcoat	−0.12	−0.07	−0.35	−0.10	0.16
Houser	−0.59*	−0.47	−0.76**	−0.51	−0.09
			1991 ($n = 24$)		
Saluda	−0.71**	0.11	−0.50**	0.16	−0.40*
Knox 62	−0.19	0.26	−0.30	−0.25	−0.55**
Massey	−0.21	−0.43*	−0.09	0.28	0.06
Redcoat	−0.48*	−0.23	−0.28	−0.19	−0.34
Houser	−0.34	−0.19	0.21	−0.19	0.08

[a] Asterisks denote significance at $P < 0.05$ (*) and $P < 0.01$ (**).

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