Yield Improvement in Eastern Soft Red Winter Wheat from 1919 to 2009

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ABSTRACT

Periodic evaluation of improvements in yield and disease resistance is necessary to assess breeding progress over time, and the elucidation of underlying traits responsible for yield gains can help direct future breeding. Objectives of this study were: 1) to determine the rate and magnitude of yield progress in eastern soft red winter (SRW) wheat (*Triticum aestivum, L.)* cultivars released from 1950 to 2009 relative to a historical cultivar Red May (1919) and; 2) to determine effects of leaf rust (*Puccinia triticina* f. sp. *tritici*) and powdery mildew [*Blumeria graminis* (DC.) E.O. Speer f. sp. *tritici* Em. Marchal] on grain yield components and agronomic traits. Replicated yield trials were grown at Warsaw, VA in 2010 and 2011, and at Holland and Blacksburg, VA in 2011. For objective 1, the genetic progress experiment: flag leaf angle, kernel weight, spikes m^{-2}, lodging, flowering date and harvest index collectively explained the most yield variation in multiple environments on the basis of linear regression analysis. Rate of genetic yield improvement ranged from 0.56% yr^{-1} at Holland in 2011 to 1.4% yr^{-1} at Blacksburg in 2011. For objective 2, the disease loss experiment: yield losses ranged from 1% at Holland in 2011 to 21% at Warsaw in 2011. Losses primarily due to powdery mildew and leaf rust were as high as 14% and 33%, respectively. Powdery mildew had the largest negative correlation with harvest index and seeds $spike^{-1}$, while leaf rust had the largest negative correlation with plant biomass and harvest index.

Dedication

This thesis is dedicated to the memory of my grandfather, Carl Eugene Green. Without his love of the outdoors and helping me discover my passion for agriculture, I might never have found what truly makes me happy. Thanks for getting me in a greenhouse early, Grandpa.

I would also like to dedicate this thesis to my parents, Rick and Mary Green. Without your completely unselfish love and support for Molly and I both throughout the years I would not be the man that I am today and for that I will always be grateful.

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Chapter I

Genetic Yield Improvement in Soft Red Winter Wheat in the Eastern United States from 1919 to 2009.

ABSTRACT

Periodic evaluation of breeding progress is necessary to assess genetic gains over time, and the underlying agronomic and morphological traits responsible for yield gains can help direct future breeding efforts. This study was conducted to determine the rate and magnitude of yield progress in eastern soft red winter (SRW) wheat (*Triticum aestivum, L.*) cultivars released from 1950 to 2009 relative to a historical cultivar Red May (1919). The effects of agronomic, morphological and yield component traits on grain yield were studied in 50 widely grown historic and current cultivars in replicated yield trials at Warsaw, VA in 2010 and 2011, and at Holland and Blacksburg, VA in 2011. Seed treatments with triadimenol, captan and imidacloprid were applied to all cultivars to limit insect damage and control diseases in seedlings and early growth stages. Foliar fungicides propiconazole and prothioconazole+tebuconazole also were applied to control subsequent foliar and spike diseases. Tests at all locations except for Blacksburg were treated with growth regulator (Trinexapac-ethyl) to minimize lodging. Genotype by environment interactions were significant ($p < 0.01$) for most traits. Linear regression models for yield were constructed for each environment, with r^2 values ranging from 0.62 to 0.76 among environments. The traits flag leaf angle, kernel weight, spikes m^{-2}, lodging, flowering date, harvest index, Normalized Difference Vegetative Index (NDVI) at Zadoks growth stage 25 and green leaf retention, respectively, explained the most yield variation in multiple environments. The rate of genetic yield improvement ranged from 0.56% yr^{-1} at Holland in 2011 to 1.4% yr^{-1} at Blacksburg in 2011. Traits which consistently increased in magnitude over time were spikes m^{-2}, erect flag leaf angle, harvest index, seeds $spike^{-1}$, seeds

spikelet^{-1} and yield. Traits which decreased over the time period studied were flowering date and plant height. Continuing on past advancements as well as improvement of traits found to significantly contribute to yield should guide breeding and selection to maximize future yield gains.

INTRODUCTION

Improvement in grain yield is a primary objective of all wheat breeding programs, with notable progress being made since the transition from selection-based breeding efforts in the early 20th century. Periodic evaluation of breeding progress allows for quantification of the magnitude and rate of genetic change that has been accomplished by breeders over a given period. Yield components, as well as agronomic and morphological traits, that are known to influence yield should be periodically analyzed to evaluate breeding progress and to determine which traits confer the greatest contribution to yield.

Wheat is one of the most important food crops in the world, along with maize (*Zea mays*, L.) and rice (*Oryza sativa*, L.). With increasing world populations, higher yields will be necessary to feed the growing population. Increases in genetic yield potential have been responsible for roughly half of yield gains in the USA, and genetic improvements are likely to drive yield gains in high output environments where technology is not limiting (Feyerherm et al., 1984).

Genetic yield gains have historically been estimated using two principal approaches. First, analysis of yields in uniform regional nurseries can be used to evaluate breeding progress, as these nurseries contain the best material in breeding programs at the time of their testing. Relative genetic gains over time can be estimated by comparing yield of long term checks with new experimental lines (Graybosch and Peterson, 2009). Schmidt (1984) and Peterson et al. (1989) reported annual rates of yield improvement between 0.75% and 1.5% yr^{-1} in two wheat nurseries. Graybosch and Peterson (2009) reported a wheat yield gain of 1.3% yr^{-1} in the Southern Plains Regional Nursery (SPRN) and 0.79% yr^{-1} for all entries in the SPRN plus the Northern Plains Regional Nursery (NPRN). Limitations in these studies include inconsistency in cultural practices used by cooperators and lack of pathogen control in the nurseries which may confound true genetic differences due to varying levels of resistance among genotypes and disease pressure among environments.

An alternative approach is to grow all cultivars released over a given time period in a common environment under uniform cultural practices. This method was used by Cox et al. (1988) by which a 1.0% yr^{-1} gain in yield was realized among 37 hard winter wheat cultivars relative to the historical benchmark cultivar Turkey. However, this study did not use chemical control to minimize the confounding effects of disease and lodging. Fufa et al. (2005) demonstrated a 0.48% yr^{-1} yield increase in the Nebraska wheat breeding program without disease control. Donmez et al. (2001) determined yield gains among 13 hard winter wheat cultivars to be 0.44% yr^{-1} relative to Turkey in a split-plot experiment where leaf rust (*Puccina triticina* f sp. *tritici*) and lodging were controlled with chemicals. A similar approach was used by Khalil et al. (1995) in which a yield gain of more than 4.0% yr^{-1} was estimated in the Oklahoma State University breeding program. Each of these studies analyzed different agronomic and morphological traits that affected yield components relevant to the region where the study was conducted.

Schmidt (1984) noted that gains in the SPRN and NPRN during the evaluated time period were minimal and suggested that yield gains in wheat were at or nearing a plateau. Most subsequent genetic progress studies have sought to either confirm or refute this assumption and the asymptotic nature of the genetic progress curve for yield in wheat, which could hinder future ability to develop high yielding cultivars given the current genetic base and traditional breeding methods.

Many factors have led to the higher yielding wheat crops of today. Breeders have consciously selected for many agronomic traits including traits directly or indirectly associated with yield and adaptation. Many studies have reported correlations between yield and other agronomic, morphological, phenological, and physiological traits. Among those, increasing number of spikes m^2 has been associated with higher yields (Sedgley, 1991; Reynolds et al., 1999; Wang et al., 2002). Despite the environmental effect on tiller density in response to management, newer cultivars may genetically produce more tillers in a modern management program versus older cultivars because they were selected from populations grown using narrower row spacing (Reynolds et al., 1999). Increasing seeds $spike^{-1}$ has also been reported to increase yield (McNeal, 1960; Nass, 1973; Hucl and Baker, 1987; Feil, 1992; Calderini et al., 1995; Wang et al., 2002). Other studies have reported a positive association between seeds $spikelet^{-1}$ and yield (McNeal, 1960; Siddique et al., 1989; Feil, 1992). Although often thought to be negatively correlated with increased number of seeds per unit area, kernel weight has also been reported to be highly associated with yield (McNeal, 1960; McNeal et al., 1978; Hucl and Baker, 1987; Wang et al., 2002).

Increasing grain yield can be achieved by either increasing the total biomass of a plant or by increasing the efficiency of partitioning photosynthetic assimilates into grain (Richards, 2000). An increase in overall biomass over time has not been observed in most wheat studies (Austin, 1980; Waddington et al., 1986). Rather, harvest index has increased over time and has been found to be highly associated with higher yields (Nass, 1973; Austin, 1980; Hucl and Baker, 1987; Siddique et al., 1989; Slafer, 1990; Feil, 1992; Reynolds et al., 1994; Sayre, 1997; Wang et al., 2002). Increased number of kernels, both per m^2 and per spike, is an important component of yield that has been affected by harvest index increases (Austin, 1980; Calderini, 1995; Sayre, 1997). The current harvest index for most modern high yielding wheat cultivars is reported to be around 50% (Richards, 2000). Austin (1980) estimated that the biological upper limit for harvest index in wheat is around 60%; however, there are concerns that lodging may limit it if the overall biomass of the culm does not increase to support a larger spike or more spikes per area.

In addition to traditional components of yield, several leaf morphological characteristics have been associated with yield, including posture (Sedgley, 1991; Hansen et al., 2005). The posture of the flag leaf can be curved, planophile or erectophile and directly affects the interception of solar radiation (Borojevic, 1986). Development of cultivars having more erectophile leaves has led to dramatic yield improvements in maize (Duvick and Cassman, 1999). However, some studies did not find a significant relationship between leaf posture and yield in wheat (Austin et al., 1976; Davidson and Sayre, 1988; Monneveux et al., 2004). Inconclusiveness of these results may have been due to confounding environmental factors such as temperature or precipitation causing differences in results and conclusions among studies. Indeed, flag leaf posture of a genotype was found to differ slightly between environments and particularly at different growth stages during the growing season in a study conducted on Yugoslavian germplasm (Borojevic and Dencic, 1986).

Post-heading chlorophyll retention in wheat has been studied extensively. For example, Borojevic (1986) found that long green leaf duration after spike emergence was the single most important green area parameter associated with higher wheat yields. Numerous studies on this trait and association with yield have been conducted in both spring and winter wheat in the USA and Europe. Hansen et al. (2005) studied 20 spring wheat cultivars and found that modern cultivars tended to have higher yields and later-senescing flag leaves. Blake et al. (2007) also reported that prolonged photosynthesis in the flag leaf increased yield in a population of recombinant inbred lines (RIL). The green leaf retention trait is one visual estimate of prolonged chlorophyll retention, which has been reported to be correlated with a longer grain-filling period and higher yields (Reynolds et al., 1994; Wang et al. 2002).

To date, nearly all of the studies on genetic yield progress in United States wheat germplasm have been conducted with hard winter wheat cultivars. The objectives of this study were to analyze historically significant and modern cultivars of soft red winter wheat in common and controlled environments in order to document genetic progress by public and private wheat breeders in the eastern United States, and to analyze the agronomic, morphological, and yield component traits which are responsible for the variation in yield over time. Evaluation of breeding progress is an appropriate measure to demonstrate historical progress, as well as to identify beneficial traits which can be selected via traditional or marker assisted breeding.

MATERIALS AND METHODS

Experimental

The experiment was planted at the Eastern Virginia Agricultural Research and Extension Center near Warsaw, VA (Kempsville loam, 37° 59’N, 76° 46’ W, 40.5m elevation) during the 2009-10 and 2010-11 growing seasons, and also at the Tidewater Agricultural Research and Extension Center near Holland, VA, (Eunola loamy fine sand, 36° 68' N, 76° 77'

W, 18.9 m elevation) and the Kentland Farm, near Blacksburg, VA (Guernsey silt loam, 37° 12'N, 80° 34'W, 531.5m elevation) during the 2010-11 growing season. The experiments each included 49 soft red winter wheat cultivars released from 1950 to 2009 (Table 1) and one historical SRW wheat cultivar, Red May (1919). The cultivars were chosen to represent a sample of the most historically significant cultivars grown in Virginia and the mid-Atlantic region during the period, according to seed certification records of the Virginia Crop Improvement Association (David Whitt, personal communication, 2009).

Replicated plots were planted on 23 October 2009 and 17 October 2010 at Warsaw, on 2 November 2010 at Holland and on 27 September 2010 at Blacksburg. Each experimental unit consisted of a seven-row yield plot, 2.7 m in length with 15.2 cm (Warsaw and Blacksburg) or 17.8 cm (Holland) spacing between rows. The harvested plot area was 2.9 m^2 (Warsaw and Blacksburg) or 3.4 m^2 (Holland). Plots were seeded at a density of 520 seeds m^{-2}, based on kernel weight of the seed source. Seed was treated with Baytan® fungicide (triadimenol, Bayer Crop Science) at a rate of 13.6 mL a.i. per 45.4 kg, Captan 400® fungicide (Captan, Bayer Crop Science] at a rate of 57.8 mL a.i. per 45.4 kg, and Gaucho® XT insecticide (Imidacloprid, Bayer Crop Science) at a rate of 16.9 mL a.i. per 45.4 kg to control seedling pests and diseases.

Fall nutrient management and spring nitrogen (N) applications were based on standard local management practices (Brann et al. 2000) and recommendations from the Virginia Cooperative Extension Soil Testing Laboratory. At Warsaw during both years and Holland, all plots were treated with growth regulator (Trinexipac-ethyl) between growth stage (GS) 25 and GS 30 (Zadoks et al. 1974) at a rate of 42.6 g a.i. ha^{-1} (Warsaw 2010) and 49.7 g a.i. ha^{-1} (Warsaw and Holland 2011) to minimize lodging. Growth regulator was not applied to the test at Blacksburg due to unfavorable weather and wet field conditions that prevented application at the recommended time. Weed control was achieved via herbicide Finesse® (DuPont) at Warsaw in 2010 and Harmony-Extra SG® (DuPont) at all locations in 2011 at rates recommended by Virginia Cooperative Extension (Hagood and Herbert, 2010).

All plots received Tilt® (Propiconazole, Syngenta) foliar fungicide between GS 31 and GS 45 to control foliar diseases, primarily powdery mildew [*Blumeria graminis* (DC.) E.O. Speer f. sp. *tritici* Em. Marchal; syn *Erysiphe graminis* f. sp. *tritici*]. Plots in Warsaw 2010 were treated at a rate of 58.5 g a.i. ha^{-1} on April 2 and April 15. In 2011, plots were treated at a rate of 117 g a.i. ha^{-1} on April 14 (Warsaw) and April 21 (Holland and Blacksburg). Prosaro® (Prothioconazole, Tebuconazole, Bayer Crop Science) was applied at spike emergence (GS 50) to control leaf rust (*Puccina triticina* f. sp. *tritici*) and fusarium head blight (*Fusarium graminearum*). All plots at all locations were treated at a rate of 212.8 g a.i. ha^{-1}.

Plant Trait Assessments

The total number of seedlings present in one 0.305 m sample from each of the three center rows, at staggered sites throughout each plot, was counted at the two-leaf stage (GS 12) at the Warsaw and Blacksburg locations. Seedling field emergence percentage was calculated as a ratio of seedlings at GS 12 and maximum number of seedlings, determined by the seeding rate. The NDVI was used to estimate tillers m^{-2} at GS 25 as described in Phillips et al. (2004) using a Greenseeker® optical sensor (NTech Industries, Trimble Agriculture, Sunnyvale, CA).

Anthesis date was recorded as the Julian date when 50% of the spikes in a plot had extruded anthers. Ripening date or physiological maturity was recorded at Warsaw during both years as the Julian date when 50% of the plants in a plot had yellow upper peduncles at the point of spike attachment, indicating that grain-fill was complete (GS 90). Flag leaf angle was visually estimated and recorded on a 1 to 5 scale (1, completely relaxed, 5, completely erect) during the grain-fill period (GS 70 to 89). Green flag leaf retention was visually estimated as a percentage of total flag leaf area of all plants in a plot that retained green color. This rating was made as each plot approached physiological maturity (GS 90) and conducted at 48-hr intervals until the plot reached harvest maturity (GS 92) at Warsaw in both years and once at Holland during grain-fill.

At GS 90, one 0.305 m sample was cut at ground level from each of three center rows at staggered sites in each plot. These samples were stored for 1 to 2 weeks in paper sacks and allowed to air dry. Mass of each sack was recorded to obtain a biomass for each sample. The number of spikes per sample was counted and used to derive an estimate of spikes m^{-2}. Five representative heads were retained from each plot for yield component and spike characteristic assessments. Spike characteristics studied were: seeds $spikelet^{-1}$, spikelets $spike^{-1}$, and floret fertility. Seeds $spike^{-1}$ was also obtained for yield component analysis. Three representative plants were chosen from each plot to measure peduncle and spike lengths. These samples were then threshed in a Vogel style nursery thresher (Almaco, Ames, IA). Thresher settings were optimized to recover all seeds as far as possible. Mass weight of the seed obtained from each sample was recorded and harvest index of each plot was calculated as the ratio of seed mass to total biomass.

Plant height was recorded from two places in each plot at harvest maturity (GS 92). Lodging was recorded on a 0 to 9 scale (0, no lodging, and 9, completely lodged) at the same time. Whole plots were harvested at Warsaw and Blacksburg using a plot combine. Grain yield was calculated from total mass of grain harvested from the plot area remaining after pre-harvest sampling, and was adjusted to uniform moisture of 13.5%. Spike characteristic data were obtained from the five representative heads that were retained from the hand-harvested samples from each plot as described above. Spikelets spike^{-1}, florets spikelet^{-1} and seeds spike^{-1} were counted visually, and from, seeds spikelet^{-1} was derived. Floret fertility was estimated as a percentage of seeds to total florets spike^{-1}. Kernel weight was obtained from a 500-kernel subsample of harvested plot seed. Moisture and grain volume weight (test weight) of each plot were determined on subsamples using a DICKEY-john® GAC 2000 machine (DICKEY-john, Minneapolis, MN).

Protein, starch, fat, crude fiber, and ash content were estimated on subsamples from each plot on an XDS Rapid Content Analyzer (Foss NIR Systems, Inc. Laurel, MD). Single Kernel Characterization was completed on all entries from Warsaw 2009-2010 by the USDA Soft Wheat Quality Lab (Wooster, OH).

Statistical analysis

The experiment was planted as a Randomized Complete Block, with two replicates at Warsaw in 2009-2010, due to limited seed availability, and three replicates in all three environments during 2010-2011. The Glimmix procedure (proc) in SAS 9.2 (SAS Institute, Cary, NC) was used for analysis of variance, with environment and cultivar treated as fixed effects and Rep(Environment) as a random effect. Environment was defined as a year-location. Proc Reg was used for regression of traits on years of release. The stepwise and max-r options in Proc Reg were used to construct the multivariable model for yield in each environment, with a significance level of α0.05. Collinearity analysis was performed in Proc Reg to ensure that non-acceptable collinearity did not exist between independent variables in the final model for yield. Means comparisons between cultivars within environments were calculated with the Means procedure, and the critical value for Tukey's Honestly Significant Difference (HSD) (alpha=0.05) was calculated manually (Zar, 2008).

The oldest cultivar used in the study was Red May. It was in the first group of wheat cultivars registered by USDA (Clark et al. 1926) but its origin predates that report by at least 75 years. Historically there have been as many as 18 genotypes that are synonymous with Red May (Clark et al. 1923), some of which may have been grown in the mid 18th century in Virginia (Cabell, 1858). More recently, it is believed to have been a selection from around 1830 out of the English wheat *May*, grown before the Revolutionary War in Virginia (Clark, 1936). Whatever its origin, it was widely cultivated after 1845, and even in 1934 Red May occupied 8.1% of the soft wheat acreage in the United States (Clark and Quisenberry, 1948). Because of the many years that had lapsed since the introduction of Red May and the beginning of hybridization based breeding efforts, the year 1919 was chosen as the independent variable for Red May in regression analyses. The first year of a Wheat Distribution report from USDA was in 1919, which is also the entry date of the earliest Red May accession in the USDA National Small Grains Collection.

For regression of all traits on year of release, the mean value for all traits relative to Red May were divided by the difference of years of release to obtain a percentage of genetic improvement per year in a given environment. **Percent Genetic Gain Year^{-1}= $\{[(X_G-X_{RM})/X_{RM}]/Y_G-Y_{RM}*100\}$,** where (X) is the mean value of observations for a given trait, and (Y) is the year of release of each genotype (G) and Red May (RM).

RESULTS

Weather

Temperature and precipitation varied between environments, due to differences in elevation and proximity to the Atlantic coast. The varying elevations and climate between locations affected the length of the grain-fill period, which was longest at Blacksburg and shortest at Holland. This can be partially explained by the elevation at Holland (18 m) compared with Blacksburg (541 m). Additionally, the average daily maximum and minimum air temperature, as well as monthly precipitation for each environment, varied greatly and are presented in Table 2. The growing season at Blacksburg in 2011 was cool, and precipitation was abundant. Six plots were dropped from the study at this location because of damage due to prolonged standing water. At Warsaw in 2010, the grain-fill period (GS 60-90) was cut short by hot and dry conditions (Table 2). Warsaw 2011 had a more typical weather pattern for the area, with a cooler and wetter spring. At Holland in 2011, conditions were dry and very warm throughout the spring (Table 2).

Grain Yield

In the analysis of variance, yield varied significantly ($p < 0.01$) among environments and cultivars (Table 3). There was also a significant ($p < 0.01$) interaction between cultivars across environments for yield. Because of this and the high number of significant environment by cultivar interactions reported in the analysis of variance (ANOVA), each environment was analyzed separately. All cultivars yielded more than Red May in each environment, but the ranking of genotypes among environments varied considerably (Table 4). The genotype by environment interaction likely was caused by a change in rank, resulting in a crossover type interaction (Fehr, 1991). Yields at Holland in 2011 seem to be a major factor contributing to this interaction, due to the variability in cultivar rank at Holland compared to those in the other environments (Table 4). The critical value for Tukey's HSD for yield ranged between 972.7 kg ha^{-1} in Warsaw 2010 and 1420.9 kg ha^{-1} in Blacksburg 2011. This resulted in a large number of genotypes having similar yields across environments. Despite the significance of genotype by environment interaction, performance of a genotype across environments is informative to plant breeders seeking the overall highest yielding genotypes.

Thirteen cultivars that were in the top yielding group of genotypes in every environment are shown in Table 5. These represent the most productive cultivars across all environments and were not statistically different from each other in any environment as determined by Tukey's HSD.

Analysis of variance for plant traits

An analysis of variance for yield and select traits is presented in Table 3. All traits were significantly different among environments except spikes m^{-2}, and all traits except GS 25 tiller number were significantly different among cultivars. For the interaction between cultivar and environment, all traits were significant except for GS 25 tiller number, spikes m^{-2}, biomass and seeds $spike^{-1}$. Given the complexity of the traits studied and compensation among yield components and spike characteristics in diverse environments, significance of genotype by environment interactions is not surprising.

Linear regression for yield

All evaluated traits were regressed on yield, and significant ($p < 0.05$) traits for each environment were included in models for yield that explained a maximum possible amount of yield variation. The models, which contain all significant traits and the coefficient estimating their effect on yield in each environment, are presented in Table 6. An eight-variable model explaining 72% of yield variation was fitted for Warsaw 2010, while seven traits explained 76% of yield variation in Warsaw 2011. The best yield models for Blacksburg 2011 and Holland 2011 explained 75% and 62% of the variation and contained nine and six trait variables, respectively. The traditional yield components were all found to contribute to yield variation, with spikes m^{-2} being highly significant ($p < 0.01$) and 500 kernel weight significant ($p < 0.05$) in three of four environments. Seeds $spike^{-1}$ was highly significant ($p < 0.01$) at Warsaw 2010. Additionally, erect flag leaf angle and lodging were also highly significant ($p < 0.01$in three of four environments. Flowering date and harvest index were highly significant variables ($p < 0.01$) in two environments, and NDVI was significant ($p < 0.05$) in two environments. Green leaf retention, assessed throughout grain-fill, significantly affected yield at Warsaw and Holland in 2011, but at different growth stages in the two environments, and was affected by the differing maturity dates of the cultivars Spike characteristics differed significantly in explaining overall yield differences between environments. Seeds $spikelet^{-1}$ and spikelets $spike^{-1}$ each significantly ($p < 0.01$) explained a portion of yield variation in one environment each. Starch content had a positive effect on yield in two environments. Interestingly, protein content also positively contributed to yield in two environments. This is contrary to the traditional understanding of yield and protein content being inversely related, although protein quantity is less important than protein quality in soft wheat cultivar development.

Genetic change over time

In each environment, the annual percentage of genetic gain relative to Red May was calculated for several traits of interest. A simple regression of yield on year of release is presented in Figure 1. The highest estimates for annual yield increase were noted in Blacksburg 2011 and Warsaw 2011, with the slope of the best fit line showing increases of 49.7 and 46.7 kg year^{-1}, respectively. The lowest estimate for annual genetic yield improvement was in Holland 2011, where the slope of the best fit line for the regression estimated annual gains of 24.9 kg year^{-1}. Similar slopes for rate of improvement were observed for Holland 2011 and Warsaw 2010, the two environments with the hottest grain fill periods and similar mean yields. Averaged across all environments, the overall regression of yield on year of release showed an increase of 37 kg yr^{-1} with an r^2 of 0.84. Mean percentage gain for each trait relative to Red May represents the average annual change on a percentage basis for all 50 cultivars in each environment (Table 7). The average annual rate of improvement for yield varied by environment and ranged between 0.56% per year at Holland in 2011 and 1.41% per year at Blacksburg in 2011. The r^2 for regression of yield over time ranged from 0.57 to 0.80. These rates of genetic yield improvement are slightly higher than, but still consistent with, those in previous studies with wheat (Cox et al., 1988; Donmez et al., 2001; Fufa et al., 2005).

All traits analyzed showed consistent trends, although the magnitude of improvement rates differed greatly between environments. This is expected due to the varying environmental conditions and is consistent with ANOVA results for these traits (Table 3). Aboveground biomass, spikelets spike^{-1} and kernel weight changed negligibly over time, with inconsistent estimates between the four environments and r^2 values near zero in each case. Spikelets spike^{-1} and 500-kernel weight differed significantly between cultivars in the ANOVA; thus, these traits could be affected more by environment than genetic factors. In addition to yield, other traits that increased over time included spikes m^{-2}, erect flag leaf angle, harvest index, seeds spikelet^{-1} and seeds spike^{-1}. These traits represent the most significant traits that explain yield progress made during the time period considered in this study. Spikes m^{-2}, erect flag leaf angle and harvest index were also three of the most consistently significant traits from the linear regression for yield. Traits that decreased in magnitude over time were flowering date, spike length and plant height. Later flowering date also consistently had a negative impact on yield in two environments in the linear regression (Table 6). A reduction in plant height among cultivars over time was expected with the transition from standard height to semi-dwarf cultivars, but the trend of continued height reductions throughout the entire time period was surprising.

DISCUSSION

Genotype by environment interaction was significant for grain yield prohibiting analysis of data across environments. As such, individual regression models for yield were derived for each of the four environments (Table 6). However, results from the diverse environments in which the 50 cultivars were tested provide important information about maximum yield potential of cultivars among environments. The yield components spikes m^{-2} and 500 kernel weight both accounted for yield variation in three of the four environments. Spike characteristics also were different among environments, and different single spike characteristics contributed most significantly to yield variation in three of the four environments in the regression analysis. The most significant spike characteristics and yield components in each environment was likely impacted by the overall response of cultivars to varying environmental conditions. It is a well known fact that compensation and negative intercomponent correlations occur among yield components in wheat (McNeal et al., 1978), thus it is reasonable that the significance of spike characteristics, as well as the yield component seeds $spike^{-1}$ was different across locations.

The highest mean yields were obtained at Warsaw in 2011, suggesting that it was the least limiting environment for discerning true genetic yield potential. Yet, neither seeds $spike^{-1}$ nor any single spike characteristic contributed predominantly to yield variation in this environment in the regression for yield. This does not infer that spike related yield components did not contribute to yield in this environment; rather that other traits (Table 6) explained more of the variation in yield. The regression model for yield at Warsaw in 2011 explained more yield variability (r^2=0.76) with fewer traits (seven) than in other environments. Each significant trait in the Warsaw 2011 model also was significant in at least one other environment. Because yields in the other three environments were lower than Warsaw 2011, significance of individual spike characteristics in these environments may indicate those components were most important in overcoming specific abiotic stresses which limited yield in those environments.

The wide range in estimates for mean annual percentage of genetic gain for grain yield can be explained by the fact that gains for each cultivar were calculated relative to Red May. The yield of Red May among environments varied and therefore affected the estimated genetic gains. Red May was the lowest yielding cultivar in all environments, but at Blacksburg and Warsaw in 2011, the range between the highest yielding cultivar and Red May was almost twice that of Warsaw in 2010 and Holland in 2011. Evaluation of a set of cultivars in a common environment provides the least biased estimates for genetic gain; however, it is important to consider that all estimates for genetic progress over time are only relevant to the given set of cultivars and the environment in which they were tested due to variability in adaptation among cultivars. While the 50 cultivars were grown under intensive management conditions for semi-dwarf wheat, such intensive management practices may have been more advantageous to the newer cultivars.

Because biomass of the 50 cultivars did not change over time, the progress in yield gains over time must have been accompanied by an increase in harvest index, which was confirmed in this study. The spike characteristic and yield component traits that concurrently increased with harvest index over time were seeds spikelet^{-1} and seeds spike^{-1} (Table 7). Results of the genetic change over time analysis indicate that the major improvements achieved in the given time period include shorter plants with earlier flowering dates, more erect flag leaf angle, higher harvest index and increased number of spikes m^{-2}. While spike length tended to have been shortened slightly, the r^2 values for this trait were inconsistent. Interestingly, for the time period studied, spikelets spike^{-1} did not change over time. If spikes have shortened, and they contain the same number of spikelets, these more compact spikes must produce more seeds spikelet^{-1} and thus more seeds spike^{-1}, which was supported by this study. It is understood that yield gains have likely been achieved by simultaneous increases in source (photosynthetic capacity) and sink (grain partitioning) (Reynolds et al., 1999), which was confirmed by this study.

The thirteen cultivars in Table 5 which represent the top yielding genotypes across each environment possess different strengths in terms of yield contributing traits identified in the yield regression analyses. In defining the ideotype for yield, there is not a single "perfect" phenotype which possesses all beneficial yield-contributing traits identified in this study.

The high yielding cultivar Sisson did not differ from the mean for most traits, yet a high harvest index and high number of seeds spike^{-1} likely contributed to its overall performance. Traits contributing to yield in Pioneer '26R15' included a higher than average kernel weight, a high number of seeds spike^{-1} and seeds spikelet^{-1}. In some cultivars only one yield component was noted as being higher than the overall mean, such as spikes m^{-2} in 'USG 3555' and seeds spike^{-1} in cultivar MPV 57. Because of the compensation between yield components in successful cultivars, future gains in wheat yield may best be achieved by breeding cultivars which contain favorable combinations of agronomic, yield component and spike characteristics traits that have been shown to significantly contribute to yield.

CONCLUSIONS

For the set of SRW wheat cultivars included in this study, the most consistent yield related improvements over time were an increase in spikes m^{-2} and increasing harvest index by increasing seeds $spikelet^{-1}$ and seeds $spike^{-1}$. High yielding wheat cultivars in this study also had earlier flowering dates and more erect flag leaf angles. In addition, cultivars were consistently shortened in height over the period studied, although further reductions in height, particularly when considering use of double dwarfs, likely will not result in further yield gains. Increasing the number of seeds per unit area, through selection for increased spike number should be a target of future efforts, as that trait was stable across environments and significantly contributed to yield variation. Considering the tradeoff between other components of yield particularly within spike components, direct selection for yield will likely result in favorable combinations of yield contributing traits for future breeding efforts to maximize yield potential. Development of molecular markers for yield related traits may result in more efficient breeding, although the quantitative nature of most important yield traits will make this difficult.

Table 1. State of origin, year of release and dwarfing genes for 50 soft red winter wheat cultivars used in the study.

Cultivar	State of Origin	Year of Release	Dwarfing Gene†	Cultivar	State of Origin	Year of Release	Dwarfing Gene
Red May	Unknown	1919	none	Pioneer 2580	SC	1993	Rht2
Seneca	OH	1950	none	Pioneer 2643	IN	1993	Rht2
Wakeland	NC	1959	het- Rht8	Florida 302	FL	1994	Rht2
Redcoat	IN	1960	none	Coker 9663	AR	1997	none
Blueboy	NC	1966	Rht1	Pioneer 26R24	IN	1999	Rht2
Arthur	IN	1968	Rht1	Roane	VA	1999	Rht2
Coker 68-15	SC	1971	Rht2	USG 3209	VA	1999	het-Rht1/Rht2
Potomac	MD/VA	1975	Rht1	AGS 2000	GA	2000	Rht2
Coker 747	SC	1976	Rht2	Sisson	VA	2000	Rht2
Coker 916	SC	1980	Rht1	SS 520	VA	2000	Rht2
Tyler	VA	1980	Rht1	SS 560	VA	2001	Rht1, Rht8
Wheeler	VA	1980	none	Tribute	VA	2002	Rht2
Massey	VA	1981	Rht1	Pioneer 25R47	IN	2003	Rht2
Saluda	VA	1983	Rht2	Pioneer 26R15	IN	2003	Rht1
Coker 983	SC	1983	Rht2	Coker 9436	AR	2004	Rht2
Pioneer 2555	IN	1986	Rht2	Branson	IN	2004	Rht1
Pioneer 2548	IN	1988	het-Rht1/2	MPV 57	VA	2005	none
Coker 9803	AR	1990	Rht2	Pioneer 26R31	IN	2005	Rht2
Coker 9835	AR	1990	Rht2	Dominion	VA	2005	Rht2
Madison	VA	1990	Rht1	Panola	AR	2005	Rht2
Wakefield	VA	1990	Rht1	USG 3555	VA	2007	Rht2
FFR555W	VA	1991	Rht2	SS 5205	VA	2008	Rht2
Coker 9134	AR	1992	Rht2	Shirley	VA	2008	Rht1
Pioneer 2684	SC	1992	Rht2	Oakes	AR	2009	Rht2
Jackson	VA	1993	Rht2	Merl	VA	2009	Rht2

† Source: USDA Genotyping Lab, Raleigh, NC het=heterozygous

Table 2. Mean daily minimum and maximum air temperature and mean precipitation by month for four environments.

Blacksburg 2011				Holland 2011				Warsaw 2010				Warsaw 2011			
Month	Max	Min	Precip	Month	Max	Min	Precip	Month	Max	Min	Precip	Month	Max	Min	Precip
	°C		mm		°C		mm		°C		mm		°C		mm
Sept (n[†]=3)	18.3	11.2	33	-	-	-	-	-	-	-	-	-	-	-	-
Oct	20.8	5.3	56	Oct (n=5)	24.2	10.0	39	Oct (n=8)	21.6	11.9	71	Oct (n=15)	22.3	10.3	40
Nov	14.3	-0.7	55	Nov	17.4	2.0	18	Nov	16.8	6.8	241	Nov	16.3	3.7	35
Dec	1.6	-6.2	51	Dec	6.4	-5.1	70	Dec	8.6	-0.7	199	Dec	5.4	-4.0	51
Jan	4.1	-5.3	12	Jan	7.8	-3.9	68	Jan	8.2	-2.7	93	Jan	5.0	-3.3	52
Feb	10.8	-3.2	66	Feb	14.4	-0.9	15	Feb	6.0	-4.2	99	Feb	13.2	0.2	25
March	12.2	0.4	117	March	16.3	2.5	74	March	17.2	4.3	137	March	15.1	3.2	108
April	20.7	5.4	128	April	24.0	9.5	51	April	24.9	8.9	47	April	22.9	10.4	87
May	23.7	10.8	161	May	28.0	13.0	57	May	27.9	14.7	40	May	25.2	19.0	64
June (n=27)	28.8	14.9	0	June (n=7)	32.1	15.6	11	June (n=10)	30.8	19.1	20	June (n=10)	32.5	17.9	10

[†] n = number of days included, varying due to planting and harvest date.

Table 3. Analysis of variance and F-values for select traits for 50 wheat cultivars across four environments.

Source	Error d.f.†	Yield	GS 25 Tillers	Flowering Date	Erect FLA‡	Spikes m^{-2}	Seeds $Spike^{-1}$	500 Kernel Weight	Spike Length	Biomass	Harvest Index	Seeds $Spikelet^{-1}$	Spikelets $Spike^{-1}$
Environment (Env)	3	22.63**	7191.77**	223.44**	42.04**	1.1^{NS}	7.12*	267.54**	4527.33**	13.18**	11.36**	11.21**	35.82**
Rep(Env)	7	-	-	-	-	-	-	-	-	-	-	-	-
Cultivar (Cult)	49	35.2**	1.04^{NS}	17.08**	33.03**	8.47**	10.99**	33.92**	17.78**	2.13**	29.48**	8.76**	9.98**
Env*Cult	147	2.42**	0.86^{NS}	2.64**	3.02**	1.10^{NS}	1.17^{NS}	2.6**	2.45**	1.11^{NS}	1.72**	1.28*	1.3*
Residual	335	-	-	-	-	-	-	-	-	-	-	-	-
Total	542												

†Degrees of freedom

‡Flag Leaf Angle

**, * Significant at the 0.01 and 0.05 probability levels, respectively, ^{NS} Not Significant

Table 4. Mean yields and ranks of 50 wheat cultivars for four environments and mean yield over environments.

Cultivar	**Year of Release**	**Blacksburg 2011**		**Holland 2011**		**Warsaw 2010**		**Warsaw 2011**		**Mean Yield Across Environments**
		Yield kg ha^{-1}	Rank	Yield kg ha^{-1}	Rank	Yield kg ha^{-1}	Rank	Yield kg ha^{-1}	Rank	—— kg ha^{-1}——
Sisson	2000	**7434**[†]	5	**6352**	11	**6248**	1	**8347**	4	7095
Pioneer 26R24	1999	**6902**	14	**7051**	1	**5833**	5	**8365**	3	7038
Pioneer 25R47	2003	**7444**	4	**6809**	3	**6006**	2	**7890**	18	7037
Pioneer 26R15	2003	**7771**	1	**5904**	32	**5885**	4	**8178**	5	6934
SS 520	2000	**6993**	13	**6192**	19	**5885**	3	**8657**	1	6932
SS 560	2001	**7082**	11	**6709**	4	**5652**	7	**8167**	7	6903
USG 3209	1999	**7345**	6	**6427**	9	**5455**	15	**8144**	8	6843
MPV 57	2005	**7541**	3	**5820**	35	**5645**	8	**8130**	9	6784
USG 3555	2007	**7590**	2	**5842**	33	**5295**	20	**8394**	2	6780
SS 5205	2008	**6694**	18	**6984**	2	**5438**	17	**7967**	14	6771
Oakes	2009	**7243**	8	**6448**	8	**5500**	12	**7835**	21	6757
Branson	2004	**7145**	9	**6352**	10	**5454**	16	**7996**	13	6737
Merl	2009	**7016**	12	**6075**	24	**5566**	10	**8178**	6	6709
Shirley	2008	**7332**	7	**6340**	12	**5611**	9	7319	33	6651
AGS 2000	2000	**6447**	21	**6702**	5	**5457**	14	**7960**	15	6641
Wakefield	1990	**6779**	16	**6167**	20	**5491**	13	**8004**	12	6610
Pioneer 26R31	2005	**6379**	25	**6204**	16	**5751**	6	**7865**	19	6550
Dominion	2005	**6738**	17	**5948**	29	**5302**	19	**8067**	10	6514
Pioneer 2555	1986	**7099**	10	**6039**	26	4970	35	**7945**	17	6513
Tribute	2002	**6880**	15	**6192**	18	**5340**	18	**7631**	25	6511
Coker 9134	1992	6301	28	**6478**	7	5263	24	**7771**	23	6453
FFR 555W	1991	**6435**	22	**5908**	31	**5281**	23	**8043**	11	6417
Pioneer 2580	1993	6231	30	**6160**	21	**5512**	11	**7734**	24	6409
Jackson	1993	**6610**	19	**6304**	14	5237	26	7305	35	6364
Coker 9835	1990	**6448**	20	**6595**	6	5080	29	7269	37	6348
Coker 9803	1990	5969	37	**6274**	15	5112	28	**7824**	22	6295
Coker 9663	1997	6205	32	**6196**	17	**5285**	21	**7483**	29	6292
Pioneer 2684	1992	6257	29	**5774**	37	5238	25	**7842**	20	6278
Saluda	1983	**6360**	26	**5969**	27	5123	27	**7620**	26	6268
Panola	2005	5967	38	**5714**	40	**5282**	22	**7954**	16	6229
Pioneer 2548	1988	**6430**	23	**6317**	13	4782	41	7314	34	6211
Coker 9436	2004	6103	34	**6149**	22	5062	30	7270	36	6146
Florida 302	1994	6108	33	**5961**	28	4893	37	**7544**	27	6126
Roane	1999	**6388**	24	5635	41	5022	33	7370	31	6104
Tyler	1980	5971	36	**6046**	25	4913	43	7429	30	6090
Pioneer 2643	1993	6220	31	5496	42	4976	34	**7539**	28	6058
Madison	1990	**6355**	27	**5750**	38	5033	32	6992	39	6032
Coker 916	1980	5633	41	**6118**	23	4806	40	7339	32	5974
Coker 983	1983	6030	35	**5736**	39	4898	36	7070	38	5934
Massey	1981	5933	39	5438	43	**5336**	31	6807	43	5878
Coker 68-15	1971	5795	40	**5840**	34	4822	38	6946	41	5851
Potomac	1975	5355	44	**5930**	30	4814	39	6902	42	5750
Wheeler	1980	5408	43	5388	44	4681	42	6988	40	5616
Blueboy	1966	5597	42	**5802**	36	4231	47	6270	46	5475
Arthur	1968	5241	45	5179	46	4601	44	6648	44	5417
Coker 747	1976	5093	46	5269	45	4434	45	6389	45	5296
Wakeland	1959	4182	47	5023	47	4258	46	5743	47	4801
Redcoat	1960	4072	48	4899	48	4172	48	4870	49	4503
Seneca	1950	3932	49	4437	49	3783	49	5015	48	4292
Red May	1919	3123	50	4267	50	3490	50	4161	50	3760
Mean		**6272**		**5972**		**5144**		**7410**		
HSD (0.05)		**1421**		**1374**		**973**		**1192**		
C.V. (%)		**17.7**		**11.3**		**12.6**		**13.1**		

[†]Bold yield values indicate top yield within environment, as determined by Tukey's means separation ($p < 0.05$).

Table 5. Mean yield and select traits associated with yield for thirteen top yielding wheat cultivars across all four environments.

Cultivar	Year of Release	Mean Yield	Flag Leaf Angle[†]	Harvest Index	Flowering Date	Spikes m^{-2}	500 Kernel Weight	Seeds $Spike^{-1}$	Seeds $Spikelet^{-1}$
		$kg\ ha^{-1}$	(1-5)	%	Julian		g		
Sisson	2000	7095	4	44.4	125	789	40.6	33.5	2.2
Pioneer 26R24	1999	7038	4	43.1	125	881	40.6	30.8	2.2
Pioneer 25R47	2003	7037	3	43.5	126	772	42.8	31.1	2.3
Pioneer 26R15	2003	6934	4	42.6	125	794	43.3	34.5	2.4
SS 520	2000	6932	4	45.5	125	794	39.8	31.6	2.3
SS 560	2001	6903	4	46.0	124	749	42.0	34.6	2.2
USG 3209	1999	6843	3	42.2	125	772	42.5	28.6	2.0
MPV 57	2005	6784	4	43.1	126	708	40.5	33.4	2.0
USG 3555	2007	6780	4	43.7	125	921	43.5	24.6	2.0
SS 5205	2008	6771	5	44.8	127	864	38.9	36.7	2.2
Oakes	2009	6757	3	42.2	125	827	38.4	33.5	2.3
Branson	2004	6737	3	46.5	125	768	42.9	33.8	2.4
Merl	2009	6709	3	45.1	125	798	42.4	32.4	2.3
Mean (n=50)		6299	3	40	126	787	40.9	29	2.1
Minimum		2940	1	21	117	387	30.2	14	1.2
Median		6287	3	41	125	832	41.0	29	2.1
Maximum		8960	5	62	142	1249	49.2	42	3.0

[†] 1= completely relaxed, 5=completely erect

Table 6. Linear regression of select traits observed on grain yield of 50 wheat cultivars, with coefficient of determination (r^2), for four environments.

Environment	Intercept	Erect FLA†	KW‡	Spikes m^{-2}	Lodging	Flowering Date	HI§	NDVI¶	Green Leaf Retention#	Seeds $Spike^{-1}$	Spikelets $Spike^{-1}$	Seeds $Spikelet^{-1}$	PL††	Starch	Protein	Ash	Fat	r^2
Warsaw 2010	-6313.77	146.98**	46.89**	1.98**	-195.60**	-	-	851.21*	-	49.81**	-	-	-	190.76**	-	-1570.35*	-	**0.72**
Warsaw 2011	8762.74	240.35**	41.26*	0.91**	-	-75.30**	80.45**	2747.39**	5.30**	-	-	-	-	-	-	-	-	**0.76**
Blacksburg 2011	8000.89	-	77.89**	-	-80.22**	-154.12**	60.96**	-	-	-	132.72**	-	-31.07**	189.36*	228.00**	-	-657.21*	**0.75**
Holland 2011	7150.47	180.95**	-	1.00**	-168.17**	-	-	-	6.43**	-	-	626.77**	-	-	-237.47**	-	-	**0.62**

**, * Significant at the 0.01 and 0.05 probability levels, respectively
† Flag Leaf Angle
‡ 500 kernel weight
§ Harvest Index
¶ Normalized Difference Vegetative Index
# Green Leaf Retention measurements for Warsaw 2011 taken on 30 May 2011, and for Holland 2011 on 3 June 2011
†† Peduncle Length

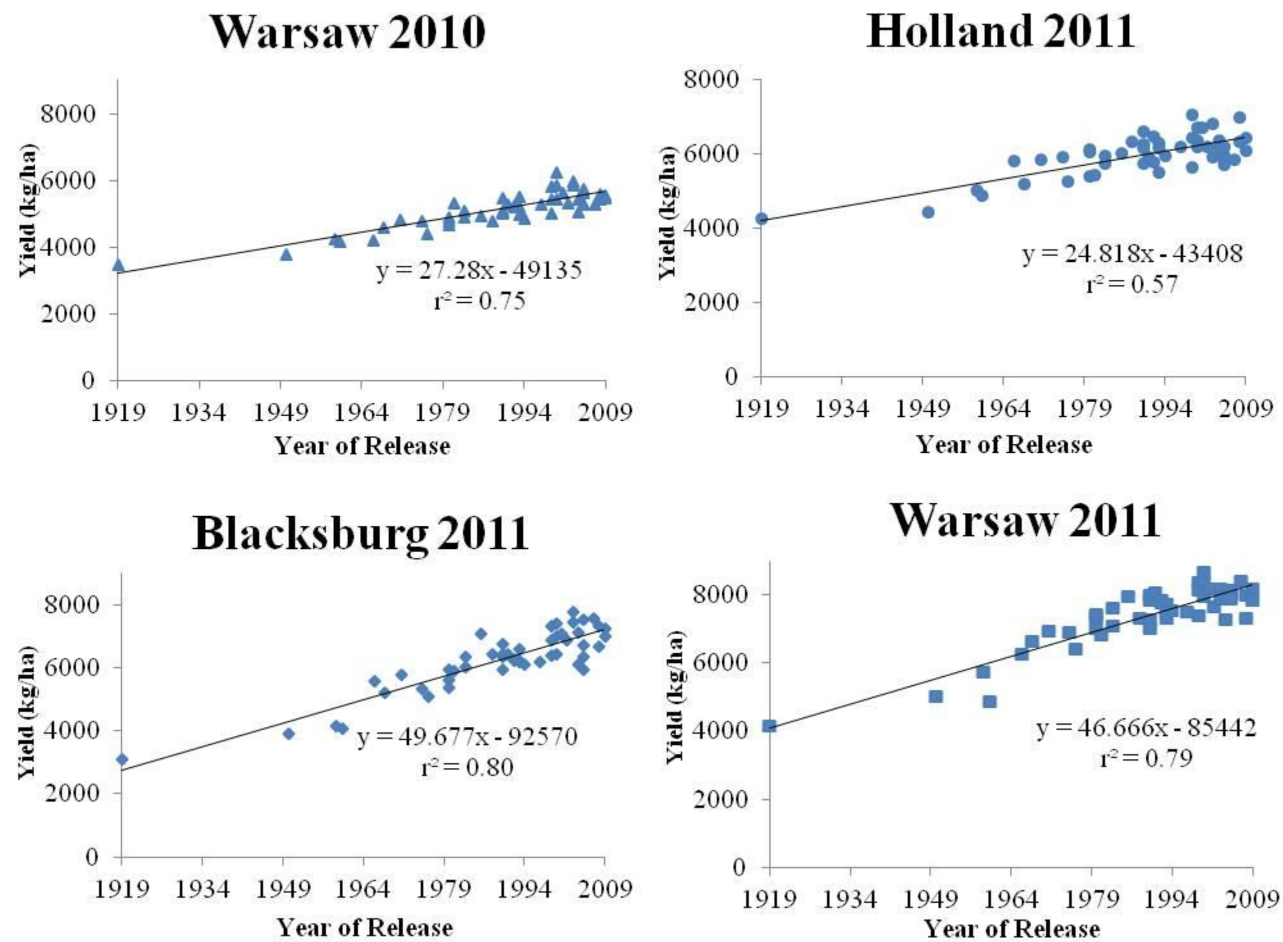

Figure 1. Linear regression of wheat yield on year of cultivar release with equation of best-fit line for four environments.

Table 7. Mean percentage gains per year relative to Red May and coefficient of determination (r^2) from linear regression of select traits on year of wheat cultivar release, for four environments.

		Yield	Biomass	Harvest Index	Flowering Date	Flag Leaf Angle	Spikes m^{-2}	Seeds $Spike^{-1}$	500 Kernel Weight	Seeds/ Spikelet	Spikelets $Spike^{-1}$	Spike Length	Plant Height
Blacksburg 2011	mean % yr^{-1}	1.408	0.124	1.257	-0.079	0.432	0.742	0.303	0.069	0.250	0.023	-0.122	-0.342
	r^2	**0.80**	**0.06**	**0.69**	**0.29**	**0.39**	**0.34**	**0.39**	**0.00**	**0.42**	**0.00**	**0.04**	**0.68**
Holland 2011	mean % yr^{-1}	0.560	-0.027	1.038	-0.019	0.283	1.020	0.147	-0.020	0.198	-0.045	-0.136	-0.485
	r^2	**0.57**	**0.01**	**0.76**	**0.09**	**0.24**	**0.08**	**0.27**	**0.00**	**0.33**	**0.00**	**0.08**	**0.72**
Warsaw 2010	mean % yr^{-1}	0.659	-0.059	0.550	-0.050	0.423	0.419	0.146	-0.030	0.107	0.017	-0.177	-0.347
	r^2	**0.75**	**0.01**	**0.51**	**0.32**	**0.21**	**0.096**	**0.17**	**0.003**	**0.16**	**0.006**	**0.14**	**0.62**
Warsaw 2011	mean % yr^{-1}	1.097	0.099	1.031	-0.001	0.006	0.008	0.001	0.000	0.003	-0.002	-0.002	-0.445
	r^2	**0.79**	**0.02**	**0.76**	**0.43**	**0.57**	**0.19**	**0.15**	**0.01**	**0.24**	**0.00**	**0.13**	**0.71**

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Chapter II

Genetic Resistance to and Effect of Leaf Rust and Powdery Mildew on Yield and its Components in 50 Soft Red Winter Wheat Cultivars

ABSTRACT

Breeding for resistance to fungal pathogens is a primary goal of most wheat (*Triticum aestivum* L.) cultivar development programs. Previous studies have reported substantial yield losses due to leaf rust (*Puccinia triticina* f. sp. *tritici*) and powdery mildew [*Blumeria graminis* (DC.) E.O. Speer f. sp. *tritici* Em. Marchal; syn *Erysiphe graminis* f. sp. *tritici*] in soft red winter (SRW) wheat. This study was conducted to determine yield losses and analyze effects of diseases on grain yield components and agronomic traits. The experiment consisted of 50 widely grown historical and current cultivars of SRW wheat released from 1919 to 2009, which were evaluated as the sub-plot factor in split-plot experiments at Warsaw, VA in 2010 and 2011 and Holland, VA in 2011. The whole plot factor was disease control with treated replications receiving seed treatments triadimenol, captan and imidacloprid and foliar applications of propiconazole and prothioconazole+tebucanazole fungicides, while non-treated replications received only tebucanazole+metalaxyl+imazalil seed treatment. Data for agronomic and yield-related traits, as well as grain yield components and spike characteristics were collected and analyzed to determine the effect of leaf rust and powdery mildew on these traits under natural field conditions. Severe leaf rust epidemics occurred at Warsaw in both years, while powdery mildew severity was highest in 2011. Powdery mildew at Holland in 2011 was significantly ($p < 0.01$) and negatively correlated with yield. Leaf rust was not observed at Holland in 2011. Prevalence or impact of other diseases and pests was negligible in the study. Yield losses as high as 54% were observed in the susceptible cultivar Red May, and average yield losses for all other cultivars ranged from 1% at Holland in 2011 to 21% at Warsaw in 2011. Yield losses primarily

due to powdery mildew were as high as 14%, and losses primarily due to leaf rust were as high as 33%. In this group of cultivars, powdery mildew had the largest negative correlation with harvest index and seeds/spike. Leaf rust had the most negative correlation with plant biomass and harvest index, with a less consistent negative relationship with kernel weight.

INTRODUCTION

Identifying and maintaining genetic resistance to diseases in cultivars has been a central focus of wheat breeding research since the beginning of organized cultivar development programs. In the mid-Atlantic and southeastern regions of the USA, the two primary pathogens of soft red winter (SRW) wheat are leaf rust and powdery mildew. While the impact of these diseases on grain yield has been well documented, their impact on yield components in common wheat is less clearly understood.

Battling the rusts of wheat has been a central campaign of breeding and pathology for several hundred years, with significant progress being made in the 20^{th} century (Mcintosh et al. 1995). Leaf rust is the most widespread of the three rusts and is prevalent nearly everywhere wheat is grown (Kolmer, 1996). In a survey of incidence and severity of leaf rust in all wheat-producing states of the USA from 1918 to 1976, Roelfs (1978) reported yield losses due to leaf rust in nearly every state surveyed, with statewide losses as high as 50% in one instance. In the southeastern USA, leaf rust can reach epidemic levels during years that favor pathogen development (Long et al., 1985; Roelfs, 1986; Subba Rao et al., 1990). In a study conducted in Mississippi, a yield-loss model was developed that estimated wheat yield losses as high as 1% for each 1% increase in disease severity at the milky ripe stage (Khan et al., 1997). Leaf rust has been reported to impact yield in several ways. Herrera-Foessel et al. (2006) reported a reduction in kernels/m^2 as the primary effect of leaf rust on yield. Many authors have reported reduction in kernel weight as a primary effect of leaf rust infection (Chester, 1946; Keed and White, 1972; Salazaar Huerta et al., 1993; Sayre et al., 1998, Singh and Huerta-Espino, 1994). Additionally, Singh and Huerta-Espino (1994) reported yield losses resulting from leaf rust due to decreased biomass, kernels/spike, test weight, and harvest index. Use of fungicides is often neither economical nor feasible in many production systems; so development of cultivars with durable resistance is the most economical and therefore the preferred method for combating leaf rust (Kolmer, 1996). Control of leaf rust using resistant cultivars has been quite successful in the northern USA and Canada; but in the southern regions of the USA, resistance to prevailing races is often lost in a few years (Kolmer, 1996). It is thought that this is primarily due to the diverse virulence in the pathogen population, due to the proximity to overwintering and over-summering areas of the fungus (Khan et al., 1997).

Powdery mildew is frequently the most important disease of wheat in maritime and semi-continental environments (Bennett, 1984). It has been reported to reduce wheat yields by as much as 45% in previous studies (Fried et al. 1981; Leath and Bowen, 1989; Stromberg et al., 1990). In studies with strictly natural inoculum sources, yield has been reduced by 10% to 15% (Frank and Ayers, 1986; Lipps and Madden, 1989). Yield losses have been explained by a reduction in tiller numbers and seeds/spike; however, these effects differed by environment (Bowen et al., 1991). Effects of powdery mildew on wheat quality have also been reported but were not stable across environments (Everts et al., 2001).

Leaf rust and powdery mildew have a negative and additive effect on yield when both pathogens incite disease epidemics (Bowen et al., 1991). As with leaf rust, resistant cultivars are often the most economical and efficient means of controlling powdery mildew (Griffey and Das, 1994). While adult plant resistance has been identified, mapped and characterized as being durable, hypersensitive race-specific resistance genes continue to be used widely in breeding programs. The latter type of resistance generally is not durable due to a rapid buildup of isolates in *B. graminis* populations with matching virulence genes (Griffey and Das, 1994).

Very useful information can be obtained from studies conducted in controlled environments, but studies with natural inoculum sources in field trials are needed as they are more similar to conditions under commercial production and are, therefore, important to breeding efforts. However, in order to draw definitive conclusions about the effects of disease on yield loss, comparisons of performance between healthy genotypes with those having varying levels of disease infection are required (James and Teng, 1979), as was achieved in the current study.

The objectives of this study were to examine the impact of cultivar resistance on powdery mildew and leaf rust, and the effect of these two diseases on yield, agronomic traits, spike characteristics and yield components in 50 historically significant SRW wheat cultivars.

MATERIALS AND METHODS

Experimental

Field experiments were conducted at the Eastern Virginia Agricultural Research and Extension Center near Warsaw, VA (Kempsville loam, 37° 59’N, 76° 46’ W, 40.5m elevation) during the 2009-10 and 2010-11 growing seasons and at the Tidewater Agricultural Research and Extension Center near Holland, VA (Eunola loamy fine sand, 36° 68' N, 76° 77' W, 18.9 m elevation) during the 2010-2011 growing season. The experiments each included 49 soft red winter (SRW) wheat cultivars released from 1950 to 2009 (Table 1) and one historical cultivar, Red May (1919). The cultivars represent a sample of the most historically significant cultivars grown in Virginia and the mid-Atlantic region during the period, according to the certification records of the Virginia Crop Improvement Association (David Whitt, personal communication, 2009). Replicated plots were planted on 23 October 2009 and 17 October 2010 at Warsaw and on 2 November 2010 at Holland. Each experimental unit consisted of a seven-row yield plot, 2.7 m in length with 15.2 cm (Warsaw) or 17.8 cm (Holland) spacing between rows. The harvested plot area was 2.9 m^2 (Warsaw), and 3.4 m^2 (Holland). Plots were seeded at a density of 520 seeds/m^2 based on kernel weight of the seed source.

The study was planted as a split-plot design, with disease control being the whole plot factor and cultivar being the sub-plot factor. For the disease controlled (treated) plots, seeds were treated with Baytan® fungicide (triadimenol, Bayer Crop Science) at a rate of 13.6 mL active ingredient (a.i.) / 45.4 kg, and Captan 400® fungicide (Captan, Bayer Crop Science) at a rate of 57.8 mL a.i. / 45.4 kg, and Gaucho® XT insecticide (Imidacloprid, Bayer Crop Science) at a rate of 16.9 mL a.i. / 45.4 kg to control seedling pests and diseases. For the plots not controlled for disease (untreated) plots, Raxil-MD® (Tebuconazole, Metalaxyl and Imazalil, Bayer Crop Science) at a rate of 3 mL a.i. / 45.4 kg was used as the seed treatment to control seed-borne diseases and to maximize seed germination and emergence.

Fall nutrient management and spring nitrogen (N) applications were based on standard local management practices (Brann et al. 2000) and recommendations from the Virginia Cooperative Extension Soil Testing Laboratory. All plots were treated with growth regulator (Trinexapac-ethyl) between growth stage (GS) 25 and GS 30 (Zadoks et al. 1974) at a rate of 42.6 g a.i./ha (Warsaw 2010) and 49.7 g a.i./ha (Warsaw and Holland, 2011) to minimize lodging. Weed control was achieved using herbicide Finesse (DuPont) at Warsaw in 2010 and

Harmony-Extra SG (DuPont) at all locations in 2011 at rates recommended by Virginia Cooperative Extension (Hagood and Herbert, 2010).

Fungicide treated plots received Tilt® (Propiconazole, Syngenta) between GS 31 and GS 45 to control foliar diseases, primarily powdery mildew. Plots at Warsaw 2010 were treated at a rate of 58.5 g a.i./ha on April 2 and April 15. In 2011, plots were treated at a rate of 117 g a.i./ ha on April 14 (Warsaw) and April 21 (Holland). Prosaro® (Prothioconazole, Tebuconazole, Bayer Crop Science) was applied at GS 50 (spike emergence) to control leaf rust and fusarium head blight (*Fusarium graminearum* Schwabe). All treated plots during both years were treated at a rate of 212.8 g a.i./ha. Foliar fungicide was not applied to the untreated plots. Late season leaf rust and powdery mildew were observed at very low incidence and severity in only a few plots in the treated portions of the study.

Disease ratings and plant trait assessments

Rating of disease reaction was initiated when sufficient levels of infection developed on known highly susceptible cultivars used in the study. Powdery mildew was rated three times at Warsaw in 2010, (March 31, April 20 and May 5) and three times in 2011, (April 12, April 26, and May 11). Powdery mildew ratings were initiated when sufficient levels of infection were present on the cultivars Blueboy, Tribute, and Seneca. Lower levels of powdery mildew incidence and severity occurred at Holland and plots were rated only once on 16 May when infection levels were at a maximum. Powdery mildew ratings were based on leaf coverage of the plant canopy and rated on a 0 to 9 scale (0=no disease to 9= severe infection). Plants throughout each plot were surveyed to determine a representative disease rating on a whole-plot basis.

Leaf rust was rated three times in Warsaw 2010, on May 10, May 20, and May 24. For the first two ratings, the F-1 leaf (leaf below the flag leaf) leaf was scored on a 0 to 100% scale on the basis of total leaf area coverage using a modified Cobb scale (Peterson et al., 1948). The final rating of the season was on the flag leaf, using the same scale. Leaf rust was rated twice during 2011 at Warsaw, on May 11 and May 26, using the same scale on the F-1 and flag leaf, respectively. Leaf rust ratings were initiated when sufficient levels of infection were present on susceptible cultivars Massey, Red May and Sisson. Leaf rust was not rated at Holland in 2011, as the most highly susceptible cultivars had only trace levels of visible infections.

The total number of seedlings present in one 0.305 m sample from each of the three center rows, at staggered sites throughout each plot, was counted at the two-leaf stage (GS 12) at Warsaw in both years. Field emergence percentage was calculated as a ratio of seedlings at GS 12 and maximum number of seedlings, determined by the seeding rate. The normalized difference vegetative index (NDVI) was used to estimate tillers/m^2 at GS 25 as described in Phillips et al. (2004) using the Greenseeker® sensor (NTech Industries, Trimble Agriculture, Sunnyvale, CA).

Anthesis date was recorded as the Julian date when 50% of the spikes in a plot had extruded anthers. Ripening date or physiological maturity was recorded at Warsaw during both years as the Julian date when 50% of the plants in a plot had yellow upper peduncles at the point of spike attachment, indicating that grain-fill was complete (GS 90). Flag leaf angle was visually estimated and recorded on a 1 to 5 scale (1=completely relaxed and 5=completely erect) during the grain-fill period (GS 70 to 89). Green flag leaf retention was visually estimated as a percentage of total flag leaf area of all plants in a plot which retained green color. This rating was made as each plot approached physiological maturity (GS 90) and conducted at 48 hr intervals until the plot reached harvest maturity (GS 92) at Warsaw in both years and once at Holland during grain-fill. At GS 90, one 0.305 m sample was cut at ground level from each of three center rows at staggered sites in each plot. These samples were stored for 1 to 2 weeks in paper sacks and allowed to air dry. Mass of each sack was recorded to obtain a biomass for each sample. The number of spikes per sample was counted and used to derive an estimate of spikes/ m^2. Five representative heads were retained from each plot for yield component and spike characteristic assessments. Spike characteristics studied were: seeds/spikelet, spikelets/spike, and floret fertility. Seeds/spike was also obtained for yield component analysis. Three representative plants were chosen from each plot to measure peduncle and spike lengths. These samples were then threshed in a Vogel style nursery thresher (Almaco, Ames, IA). Thresher settings were optimized to recover all seeds as far as possible. Mass weight of the seed obtained from each sample was recorded and harvest index of each plot was calculated as the ratio of seed mass to total biomass.

Plant height was recorded from two places in each plot at harvest maturity (GS 92). Lodging was recorded on a 0 to 9 scale (0=no lodging, and 9=completely lodged) at the same time. Whole plots were harvested at Warsaw and Holland using a plot combine. Grain yield was calculated from total mass of grain harvested from the plot area remaining after pre-harvest sampling, and was adjusted to uniform moisture of 13.5%. Spike characteristic data were obtained from the five representative heads that were retained from the hand-harvested samples from each plot as described above. Spikelets/spike, florets/spikelet, and seeds/spike were counted visually, and from, seeds/spikelet was derived. Floret fertility was estimated as a percentage of seeds to total florets/spike. Kernel weight was obtained from a 500 kernel subsample of harvested plot seed. Moisture and grain volume weight of each plot were determined on subsamples using a DICKEY-john® GAC 2000 machine (DICKEY-john, Minneapolis, MN).

Protein, starch, fat, crude fiber and ash content were estimated on subsamples from each plot on an XDS Rapid Content Analyzer (Foss NIR Systems, Inc. Laurel, MD). Single Kernel Characterization was completed on all entries from Warsaw 2010 by the USDA Soft Wheat Quality Lab (Wooster, OH).

Statistical analysis

The experiment was planted as a split-plot design as described above, with two replicates at Warsaw in the 2009-10 crop season, due to limited seed availability and three replicates in both environments during 2010-11. The Glimmix procedure (proc) in SAS 9.2 (SAS Institute, Cary, NC) was used for analysis of variance with disease control, cultivar, environment and all possible interactions treated as fixed effects. Rep nested within Environment [rep(environment)], the interaction of disease control and rep(environment) and the interaction of cultivar with rep(environment) were considered as random effects. Environment was defined as a test grown in a different year or location. The stepwise and max-r options in Proc Reg were used to construct multivariable models for yield, with alpha=0.05. Collinearity analysis was performed in Proc Reg to ensure that unacceptable collinearity did not exist between independent variables in the final model for yield. Proc Corr (alpha=0.05) was used to calculate Pearson correlation coefficients between disease levels and select agronomic, yield component and spike characteristic traits. Means comparison between cultivars within environments were calculated with the Means procedure, and the critical value for the Tukey's Honestly Significant Difference (HSD) (alpha=0.05) was calculated manually (Zar, 2008).

The oldest cultivar used in the study was Red May. It was in the first group of wheat cultivars registered by USDA (Clark et al. 1926) but its origin predates that report by at least 75 years. Because of the many years that had lapsed since the introduction of Red May and the beginning of hybridization-based breeding efforts, the year 1919 was chosen as the independent variable for Red May in regression analyses. The first year of a Wheat Distribution report from USDA was in 1919, which is also the entry date of the earliest Red May accession in the USDA National Small Grains Collection.

RESULTS

Weather and infection levels

The mean daily maximum and minimum air temperatures as well as monthly precipitation for each environment are presented in Table 2. At Warsaw in 2010, the late spring became suddenly hot and dry, and as a result, the grain-fill period (GS 60-90) was shortened, while in 2011, the spring was cooler with more precipitation. In 2011 at Holland, conditions were dry and very warm throughout the spring. Because pathogen development is dependent on favorable environmental conditions, weather impacted infection and disease severity levels. Leaf rust was severe at Warsaw during 2010 and 2011, while its prevalence and severity were very low at Holland in 2011 either due to lack of an early inoculum source or unfavorable environmental conditions for infection. Powdery mildew infection and severity were high at Warsaw in both years, but the disease persisted much longer in the growing season at Warsaw in 2011 due to cooler temperatures. Powdery mildew development at Holland in 2011 was substantially lower than at Warsaw in either year (Table 3). Other diseases were negligible in the three environments.

Final mean disease severities (MDS) for leaf rust and powdery mildew of all cultivars within each environment are presented in Table 3. Among cultivars, MDS for leaf rust ranged from 1% (Coker 9835) to 96.5% (Saluda) at Warsaw in 2010 and from 1% (Shirley) to 97% (Red May) in 2011. Powdery mildew MDS ranged from 0 to 4 at Holland in 2011, from 0 to 6 at

Warsaw in 2010 and from 0 to 8 at Warsaw in 2011. The study contained cultivars known to be highly susceptible to leaf rust (e.g. Massey and Sisson) and powdery mildew (e.g. Blueboy and Coker 68-15) or both (e.g. Red May and Seneca) all of which had stable MDS for leaf rust and powdery mildew across environments. However, many cultivars had MDS values that varied among environments, particularly for leaf rust. The cultivar Redcoat had a final leaf rust MDS of 28% at Warsaw in 2010 versus 3% at Warsaw in 2011. Concomitantly, MDS values for some cultivars increased from 2010 to 2011, as was the case with 'Florida 302', which had a leaf rust MDS of 43% in 2010 versus 80% in 2011. Cultivars susceptible to powdery mildew at Warsaw in 2010 were also susceptible in 2011, but MDS values were higher in 2011.

Analysis of variance

An analysis of variance (ANOVA) for yield and select traits is shown in Table 4. The treatment by cultivar by environment interaction is useful for assessing genotype by environment interactions across levels of disease control and directing further analysis. This interaction term was not significant for spike length, biomass, seeds/spikelet and seeds/spike, indicating stability across the test environments and levels of disease control. The highly significant ($p < 0.01$) interactions for this source of variation for all other traits, including yield, necessitated separate analyses for each environment, and prohibits drawing conclusions for these traits on the simple effects of treatment, environment, and cultivar.

Yield loss

Mean yields for treated and untreated cultivars in each environment are presented in Table 5, along with percentage change between mean yields in untreated versus treated plots in each environment. Yields of cultivars Shirley and USG 3555 at Warsaw in 2010 were similar in untreated and treated plots. In 2011 at Warsaw, Shirley had the lowest percentage yield difference (-1%) between untreated and treated plots, while the yield difference (-27%) in USG 3555 was notably higher than in 2010 Warsaw. The percentage yield differences of cultivars in non-controlled versus disease controlled plots ranged from 3% (Shirley) to -50% (Red May) at Warsaw in 2010, and from -1% (Shirley) to -54% (Red May) at Warsaw in 2011. The average overall yield loss was 21% at Warsaw in 2011 and 14% in 2010. This validates the disease ratings that indicated a higher degree of disease severity in 2011. The yield difference between untreated and treated plots at Holland in 2011 reflects the impact of powdery mildew on susceptible cultivars even though severity in this environment was lower than at Warsaw in either year, as determined by MDS (Table 3). A number of cultivars had similar or higher mean yields in untreated versus treated plots at Holland in 2011, which likely can be attributed to varying levels of cultivar resistance to powdery mildew and other sources of variation within the experiment.

Linear regression and Pearson correlations with yield

Data for all traits evaluated in untreated portions of the study were regressed on yield, and significant ($p < 0.05$) traits for each environment were included in models for yield explaining the maximum amount of yield variation (Table 6). Each significant term in these models is shown along with the coefficient estimating their relative impact on yield in each environment. The amount of yield variation explained (r^2) by the linear regression model was 0.84 at Warsaw in 2010, 0.88 at Warsaw in 2011, and 0.75 at Holland in 2011. Powdery mildew had a highly significant ($p < 0.01$) negative effect on yield at Warsaw in 2010 and 2011. Powdery mildew was negatively correlated with yield ($p < 0.01$) at Holland in 2011 (Table 7), although it was not a significant factor in the linear regression for yield. Leaf rust also had a highly significant negative effect on yield at Warsaw in both years (Table 6). However, the regression coefficient estimating leaf rust's impact on yield was much less than for powdery mildew.

Other traits significantly affecting yield under diseased conditions indicate which spike characteristics, yield components and agronomic traits were negatively affected by the pathogens and, simultaneously, which were responsible for higher yields in cultivars resistant to disease. Spikelets/spike had a significant effect on yield in all three environments, but other components of yield varied between environments with spikes/m^2 being significant in Warsaw 2010 and at Holland in 2011. Spike length was negatively associated with yield at Warsaw and Holland in 2011, and peduncle length was positively associated with yield at Warsaw in 2010 but negatively associated with yield at Holland in 2011. Erect flag leaf angle had a positive relationship with higher yields at Warsaw in 2010 and at Holland in 2011, while flowering date was negatively associated with yield at Warsaw in both years. Harvest index also had a significant positive impact on yield in 2011 at Warsaw and Holland. Other traits explained yield variation in single environments, suggesting that their effects were somewhat dependent on the environment in which cultivars are grown.

Pearson correlation coefficients ($\alpha=0.05$) for powdery mildew and leaf rust MDS, and yield are shown for select traits in Table 7. Yield was negatively correlated with MDS for both pathogens in all environments. Leaf rust MDS was negatively correlated ($p < 0.01$) with plant biomass, harvest index and test weight at Warsaw in both years. Leaf rust MDS also had a significant negative correlation ($p < 0.01$) with kernel weight at Warsaw in 2010 and floret fertility at Warsaw in 2011. These relationships highlight the specific plant traits that tended to be impacted most under severe leaf rust epidemics. The correlation analysis indicates that the most significant negative impact of leaf rust on yield occurred along with a decreased plant biomass, harvest index and test weight. Spikes/m^2 was negatively correlated with leaf rust MDS, but did not differ significantly between treatments in the ANOVA (Table 4), indicating that its relationship with decreased yield was not exclusive to either level of disease control.

The yield-related traits that were negatively correlated ($p < 0.01$) with powdery mildew in all three environments included harvest index, seeds/spike, spikes/m^2, and seeds/spikelet. (Table 7). The correlation analysis indicates that the largest negative impact of powdery mildew on yield occurred due to a lower harvest index and fewer seeds/spike (Table 7).

DISCUSSION

The linear regression analysis presented in Table 6 suggests that yield variation in the study was only partially attributable to leaf rust and powdery mildew development and severity in the field. However, yield, plant biomass, harvest index, seeds/spike, spikes/m^2, seeds/spikelet, spike length and kernel weight were associated with the observed yield losses due to leaf rust and powdery mildew (Table 5), helping to explain the impact that these diseases had on yield. Yield losses between treated and untreated plots were as high as 50% at Warsaw in 2010 (Red May), 54% at Warsaw in 2011 (Red May) and 15% at Holland in 2011 (Redcoat and SS 560).

Yield losses in cultivars that were primarily affected by only one pathogen can be used to estimate the relative impact of leaf rust versus powdery mildew in a given environment. For example, the cultivar Tribute is resistant to current local races of leaf rust (MDS below 3 on a 0-100 scale in both years at Warsaw) but susceptible to powdery mildew (Table 3). At Warsaw in 2010, the mean yield for untreated Tribute was 9% less than the treated, and a loss of 14% was observed at Warsaw in 2011. Because of the very low ratings for leaf rust in both environments, these losses were likely due primarily to powdery mildew.

The cultivar Massey exhibits adult-plant resistance to powdery mildew (Griffey and Das, 1994) and had low powdery mildew MDS (0 – 9) values of 2.3 at Warsaw 2011 and 0 in both other environments (Table 3). However, Massey is highly susceptible to leaf rust (Table 3), and yield losses of 33% were observed at Warsaw in 2010 and 2011 (Table 4). Massey was the only cultivar having moderate leaf rust infection at Holland in 2011 (data not shown) and had a 2% yield loss (Table 3). The cultivar Sisson is resistant to powdery mildew but highly susceptible to leaf rust (Table 3). Losses of 29% and 33% were observed at Warsaw in 2010 and 2011, respectively. The largest impacts on yield were observed in cultivars that are susceptible to both leaf rust and powdery mildew such as Blueboy, Potomac, Red May and Tyler with yield losses ranging from 10% to 54% over environments.

Durable cultivar resistance to powdery mildew and leaf rust is complex, and hypersensitive resistance to these pathogens is often easily overcome. The historical cultivars tested in the study likely contain varying levels of hypersensitive and durable resistance, some of which have remained more effective over time since their release. Considering release date, cultivars Arthur (1968), Coker 747 (1976), Coker 9835 (1990), Coker 9663 (1997), and AGS 2000 (2000) exhibited higher than expected levels of resistance to leaf rust (Table 3). This, indicates that they likely possess a combination of genes conferring effective and/or durable resistance, or that virulence to specific hypersensitive resistance genes in these cultivars is rare or has not been maintained in the pathogen population. As mentioned previously, the cultivar Massey has adult-plant resistance to powdery mildew (Griffey and Das, 1994), which it shares with its derivatives USG 3209, USG 3555, and Shirley. Other cultivars that exhibited high levels of resistance to powdery mildew included Coker 9835, Wakefield (gene *Pm1a*), Pioneer 2643, and SS 520 (Table 3). The cultivar Shirley was highly resistant to both leaf rust and powdery mildew in all environments. Further genetic analysis of the underlying resistance genes and mechanisms present in each of these cultivars would facilitate development of cultivars having more durable disease resistance in future breeding efforts.

CONCLUSIONS

Yield losses as high as 54% (Warsaw 2011) were observed in susceptible cultivars when both leaf rust and powdery mildew epidemics were severe. Yield losses attributable mostly to powdery mildew were as high as 14% in the cultivar Tribute at Warsaw in 2011, while the impact of leaf rust on yield reduction was as high as 33% at Warsaw in 2011 in susceptible cultivars Sisson and Massey. The higher estimates of yield loss resulting from leaf rust versus powdery mildew were primarily due to higher disease severities for leaf rust and the low number of cultivars that are resistant to one pathogen and not the other. As such, results of this study do not imply that leaf rust more adversely affects yield than powdery mildew in all cases. Among the 50 cultivars, powdery mildew had the largest negative correlation with a lowered harvest index and seeds/spike. Leaf rust had the most negative relationship with decreased biomass and harvest index, and a less consistent negative association with the yield component kernel weight. Because seeds/spike was the only yield component that was significantly different between treated and untreated portions of the study, determining the specific yield component(s) associated with the decrease in harvest index due to disease is difficult.

Table 1. State of origin, year of release and dwarfing genes for 50 soft red winter wheat cultivars in the study.

Cultivar	State of Origin	Year of Release	Dwarfing Gene†	Cultivar	State of Origin	Year of Release	Dwarfing Gene
Red May	Unknown	1919	none	Pioneer 2580	SC	1993	Rht2
Seneca	OH	1950	none	Pioneer 2643	IN	1993	Rht2
Wakeland	NC	1959	het- Rht8	Florida 302	FL	1994	Rht2
Redcoat	IN	1960	none	Coker 9663	AR	1997	none
Blueboy	NC	1966	Rht1	Pioneer 26R24	IN	1999	Rht2
Arthur	IN	1968	Rht1	Roane	VA	1999	Rht2
Coker 68-15	SC	1971	Rht2	USG 3209	VA	1999	het-Rht1/Rht2
Potomac	MD/VA	1975	Rht1	AGS 2000	GA	2000	Rht2
Coker 747	SC	1976	Rht2	Sisson	VA	2000	Rht2
Coker 916	SC	1980	Rht1	SS 520	VA	2000	Rht2
Tyler	VA	1980	Rht1	SS 560	VA	2001	Rht1, Rht8
Wheeler	VA	1980	none	Tribute	VA	2002	Rht2
Massey	VA	1981	Rht1	Pioneer 25R47	IN	2003	Rht2
Saluda	VA	1983	Rht2	Pioneer 26R15	IN	2003	Rht1
Coker 983	SC	1983	Rht2	Coker 9436	AR	2004	Rht2
Pioneer 2555	IN	1986	Rht2	Branson	IN	2004	Rht1
Pioneer 2548	IN	1988	het-Rht1/2	MPV 57	VA	2005	none
Coker 9803	AR	1990	Rht2	Pioneer 26R31	IN	2005	Rht2
Coker 9835	AR	1990	Rht2	Dominion	VA	2005	Rht2
Madison	VA	1990	Rht1	Panola	AR	2005	Rht2
Wakefield	VA	1990	Rht1	USG 3555	VA	2007	Rht2
FFR555W	VA	1991	Rht2	SS 5205	VA	2008	Rht2
Coker 9134	AR	1992	Rht2	Shirley	VA	2008	Rht1
Pioneer 2684	SC	1992	Rht2	Oakes	AR	2009	Rht2
Jackson	VA	1993	Rht2	Merl	VA	2009	Rht2

† Source: USDA Genotyping Lab, Raleigh, NC; het=heterozygous

Table 2. Mean daily minimum and maximum air temperature and mean precipitation by month for three environments.

Holland 2011				Warsaw 2010				Warsaw 2011			
Month	Max	Min	Precip	Month	Max	Min	Precip	Month	Max	Min	Precip
	°C		mm		°C		mm		°C		Mm
Oct (n[†]=5)	24.2	10.0	39	Oct (n=8)	21.6	11.9	71	Oct (n=15)	22.3	10.3	40
Nov	17.4	2.0	18	Nov	16.8	6.8	241	Nov	16.3	3.7	35
Dec	6.4	-5.1	70	Dec	8.6	-0.7	199	Dec	5.4	-4.0	51
Jan	7.8	-3.9	68	Jan	8.2	-2.7	93	Jan	5.0	-3.3	52
Feb	14.4	-0.9	15	Feb	6.0	-4.2	99	Feb	13.2	0.2	25
March	16.3	2.5	74	March	17.2	4.3	137	March	15.1	3.2	108
April	24.0	9.5	51	April	24.9	8.9	47	April	22.9	10.4	87
May	28.0	13.0	57	May	27.9	14.7	40	May	25.2	19.0	64
June (n=7)	32.1	15.6	11	June (n=10)	30.8	19.1	20	June (n=10)	32.5	17.9	10

[†]n=number of days included, varying due to planting and harvest date

Table 3. Final mean disease severity (MDS) ratings for leaf rust and powdery mildew for 50 cultivars grown at Warsaw 2010 and 2011, and Holland 2011.

		Leaf Rust† (0-100)		Powdery Mildew‡ (0-9)		
Cultivar	Year of Release	Warsaw 2010	Warsaw 2011	Holland 2011	Warsaw 2010	Warsaw 2011
Red May	1919	92.5	97.0	3.3	1.0	3.3
Seneca	1950	62.5	70.0	4.0	3.0	6.3
Wakeland	1959	21.5	58.3	1.0	0.5	4.0
Redcoat	1960	27.5	3.3	0.3	3.0	4.0
Blueboy	1966	72.5	83.3	4.0	6.0	8.3
Arthur	1968	17.5	20.0	0.3	4.0	6.0
Coker 68-15	1971	77.5	65.0	2.0	4.5	5.7
Potomac	1975	87.5	80.0	1.3	1.0	2.3
Coker 747	1976	4.0	15.0	1.3	2.0	4.0
Coker 916	1980	32.5	70.0	0.0	0.0	3.7
Tyler	1980	90.0	71.7	0.7	4.0	1.0
Wheeler	1980	17.5	23.3	2.0	3.5	5.7
Massey	1981	90.0	90.0	0.0	0.0	2.3
Saluda	1983	96.5	58.3	1.3	4.0	4.7
Coker 983	1983	70.0	68.3	0.3	2.0	2.0
Pioneer 2555	1986	37.5	45.0	0.3	1.0	2.3
Pioneer 2548	1988	82.5	70.0	0.0	1.5	2.7
Coker 9803	1990	29.0	35.0	0.0	1.5	2.7
Coker 9835	1990	1.0	20.0	0.0	1.0	1.0
Madison	1990	27.5	41.7	0.0	1.0	1.3
Wakefield	1990	77.5	28.3	0.0	2.0	0.0
FFR 555W	1991	67.5	66.7	2.0	1.5	4.3
Coker 9134	1992	24.0	55.0	0.0	1.5	3.3
Pioneer 2684	1992	17.5	50.0	0.3	1.0	3.0
Jackson	1993	85.0	68.3	0.0	1.0	4.0
Pioneer 2580	1993	62.5	65.0	0.7	1.5	0.7
Pioneer 2643	1993	20.0	25.0	0.0	0.5	0.0
Florida 302	1994	42.5	80.0	0.3	1.0	2.7
Coker 9663	1997	0.5	25.0	0.3	2.0	4.7
Pioneer 26R24	1999	20.0	36.7	0.0	0.0	1.3
Roane	1999	65.0	56.7	0.0	2.5	2.3
USG 3209	1999	92.5	83.3	0.3	0.5	1.3
AGS 2000	2000	1.5	13.3	0.0	0.5	1.3
Sisson	2000	90.0	94.3	0.7	0.5	1.3
SS 520	2000	16.0	35.0	0.0	0.0	0.3
SS 560	2001	20.0	51.7	0.0	0.0	1.7
Tribute	2002	1.0	2.3	1.7	2.5	4.0
Pioneer 25R47	2003	30.0	36.7	0.0	1.5	3.3
Pioneer 26R15	2003	37.5	35.0	0.0	0.5	0.7
Coker 9436	2004	27.5	30.0	0.0	1.5	3.3
Branson	2004	35.0	41.7	0.3	0.5	0.7
MPV 57	2005	55.0	53.3	0.0	1.0	1.7
Pioneer 26R31	2005	62.5	60.0	0.0	1.0	2.0
Dominion	2005	21.5	50.0	0.0	0.0	1.3
Panola	2005	25.0	68.3	0.0	0.0	2.0
USG 3555	2007	57.5	53.3	0.0	0.5	0.3
SS 5205	2008	3.5	5.7	0.0	0.0	2.3
Shirley	2008	2.0	1.0	0.0	0.0	0.0
Oakes	2009	47.5	28.3	0.0	2.0	3.7
Merl	2009	30.0	33.3	0.0	0.5	0.0
Mean		43.5	48.4	0.6	1.4	2.6
σ		31.8	27.2	1.1	1.5	2.1
Tukey HSD (α=0.05)		48.1	40	1.0	3.3	2.4

† 0-100% of flag leaf surface area. 0= no infection, 100=complete infection
‡ 0-9, with 0 being no infection, and 9 being severe infection

Table 4. Analysis of variance F-values for select traits in 50 wheat cultivars grown in a split-plot design at Warsaw 2010 and 2011 and Holland 2011.

	df[†]	Error df	**Yield**	**MDS PM[‡]**	**MDS LR[§]**	**Flower Date**	**FLA[¶]**	**Spikes /m2**	**Seeds/ Spike**	**KW[#]**	**SL[††]**	**Biomass**	**HI[‡‡]**	**Seeds/ Spikelet**	**Spikelets/ Spike**	**Floret Fert.**
Treatment	1	5	45.85**	13.23*	1201.3**	4.58^{NS}	4.72^{NS}	0.42^{NS}	18.35**	26.58**	2.5^{NS}	13.17*	87.29**	1.28^{NS}	3.25^{NS}	3.21^{NS}
Environment (Env)	2	5	1613.72**	88.91**	3.28^{NS}	549.00**	44.17**	1.84^{NS}	6.7*	349.92**	66.77**	47.92**	25.46**	10.5*	39.2**	0.74^{NS}
Rep(Environment)	5	-	-	-		-	-	-	-	-	-	-	-	-	-	
Cultivar (Cult)	49	243	33.87**	18.68**	21.51**	22.38**	30.37**	13.61**	17.4**	43.48**	32.92**	2.49**	63.05**	12.98**	29.28**	5.42**
Treatment*Cult	49	242	2.66**	10.08**	21.54**	0.93^{NS}	1.2*	1.10^{NS}	1.33^{NS}	2.47**	0.71^{NS}	1.43*	2.07**	1.43*	1.57*	1.22^{NS}
Treatment*Env	2	5	34.64**	16.52*	0.2119^{NS}	3.71^{NS}	0.33^{NS}	4.23^{NS}	4.88^{NS}	5.49^{NS}	0.09^{NS}	5.41^{NS}	11.08*	0.61^{NS}	2.39^{NS}	0.68^{NS}
Treatment*Rep(Env)	5	-	-	-		-	-	-	-	-	-	-	-	-	-	
Treatment*Cult*Env	196	242	5.23**	3.01**	2.79**	3.26**	2.27**	1.21^{NS}	1.09^{NS}	3.3**	0.91^{NS}	1.1^{NS}	2.04**	1.12^{NS}	1.8**	1.31*
Residual	243	-	-	-	-	-	-	-	-	-	-	-	-	-	-	

**, * Significant at the 0.01 and 0.05 probability levels, respectively. ^{NS} Non significant
† degrees of freedom
‡ final mean disease severity rating for powdery mildew
§ final mean disease severity rating for leaf rust
¶ erect flag leaf angle
# 500 kernel weight
†† Spike length
‡‡ Harvest index

Table 5. Mean yields for treated and untreated yield plots of 50 wheat cultivars grown at Warsaw in 2010 and 2011 and Holland in 2011 with percentage yield difference.

Cultivar	Year of Release	Warsaw 2010 treated	Warsaw 2010 untreated	Warsaw 2010 % change	Warsaw 2011 Treated	Warsaw 2011 untreated	Warsaw 2011 % change	Holland 2011 treated	Holland 2011 untreated	Holland 2011 % change
		kg/ha			kg/ha			kg/ha		
Red May	1919	3490	1729	**-50**	4161	1907	**-54**	4267	3783	**-11**
Seneca	1950	3783	3038	**-20**	5015	3671	**-27**	4437	4560	**3**
Wakeland	1959	4258	3593	**-16**	5743	4150	**-28**	5023	5089	**1**
Redcoat	1960	4172	3286	**-21**	4870	3983	**-18**	4899	4170	**-15**
Blueboy	1966	4231	3207	**-24**	6270	3820	**-39**	5802	5055	**-13**
Arthur	1968	4601	4038	**-12**	6648	5584	**-16**	5179	4999	**-3**
Coker 68-15	1971	4822	3823	**-21**	6946	4881	**-30**	5840	5847	**0**
Potomac	1975	4814	3242	**-33**	6902	4222	**-39**	5930	5279	**-11**
Coker 747	1976	4434	3947	**-11**	6389	5687	**-11**	5269	5469	**4**
Wheeler	1980	4681	3669	**-22**	6988	5668	**-19**	5388	5373	**0**
Coker 916	1980	4806	4007	**-17**	7339	6057	**-17**	6118	5502	**-10**
Tyler	1980	4913	3496	**-29**	7429	4410	**-41**	6046	5469	**-10**
Massey	1981	5336	3551	**-33**	6807	4562	**-33**	5438	5328	**-2**
Coker 983	1983	4898	3767	**-23**	7070	5328	**-25**	5736	5725	**0**
Saluda	1983	5123	3657	**-29**	7620	5104	**-33**	5969	6194	**4**
Pioneer 2555	1986	4970	4880	**-2**	7945	6203	**-22**	6039	6128	**1**
Pioneer 2548	1988	4782	4023	**-16**	7314	5070	**-31**	6317	5779	**-9**
Madison	1990	5033	4985	**-1**	6992	6496	**-7**	5750	5794	**1**
Coker 9835	1990	5080	4619	**-9**	7269	6880	**-5**	6595	6299	**-4**
Coker 9803	1990	5112	4740	**-7**	7824	6639	**-15**	6274	6374	**2**
Wakefield	1990	5491	4711	**-14**	8004	6164	**-23**	6167	5990	**-3**
FFR 555W	1991	5281	4297	**-19**	8043	5661	**-30**	5908	6242	**6**
Pioneer 2684	1992	5238	5020	**-4**	7842	6089	**-22**	5774	6110	**6**
Coker 9134	1992	5263	5112	**-3**	7771	6200	**-20**	6478	6313	**-3**
Pioneer 2643	1993	4976	5057	**2**	7539	6792	**-10**	5496	6096	**11**
Jackson	1993	5237	4448	**-15**	7305	5427	**-26**	6304	6459	**2**
Pioneer 2580	1993	5512	4688	**-15**	7734	5574	**-28**	6160	5429	**-12**
Florida 302	1994	4893	4713	**-4**	7544	5339	**-29**	5961	5942	**0**
Coker 9663	1997	5285	4304	**-19**	7483	6664	**-11**	6196	6298	**2**
Roane	1999	5022	4662	**-7**	7370	6247	**-15**	5635	6144	**9**
Pioneer 26R24	1999	5833	5479	**-6**	8365	7132	**-15**	7051	6868	**-3**
USG 3209	1999	5455	4230	**-22**	8144	5769	**-29**	6427	6271	**-2**
SS 520	2000	5885	5462	**-7**	8657	7363	**-15**	6192	6210	**0**
AGS 2000	2000	5457	5152	**-6**	7960	7104	**-11**	6702	5962	**-11**
Sisson	2000	6248	4410	**-29**	8347	5601	**-33**	6352	6410	**1**
SS 560	2001	5652	5008	**-11**	8167	6403	**-22**	6709	5736	**-15**
Tribute	2002	5340	4839	**-9**	7631	6571	**-14**	6192	6470	**4**
Pioneer 26R15	2003	5885	4979	**-15**	8178	7116	**-13**	5904	6502	**10**
Pioneer 25R47	2003	6006	4847	**-19**	7890	6876	**-13**	6809	6275	**-8**
Branson	2004	5454	5188	**-5**	7996	6614	**-17**	6352	5864	**-8**
Coker 9436	2004	5062	4522	**-11**	7270	5680	**-22**	6149	5567	**-9**
Dominion	2005	5302	4580	**-14**	8067	6645	**-18**	5948	6410	**8**
MPV 57	2005	5645	4849	**-14**	8130	7019	**-14**	5820	6016	**3**
Panola	2005	5282	4803	**-9**	7954	5849	**-26**	5714	5922	**4**
Pioneer 26R31	2005	5751	4807	**-16**	7865	6017	**-23**	6204	6574	**6**
USG 3555	2007	5295	5382	**2**	8394	6142	**-27**	5842	5981	**2**
Shirley	2008	5611	5807	**3**	7319	7249	**-1**	6340	6754	**7**
SS 5205	2008	5438	5124	**-6**	7967	7414	**-7**	6984	6722	**-4**
Oakes	2009	5500	4958	**-10**	7835	6873	**-12**	6448	6481	**1**
Merl	2009	5566	4910	**-12**	8178	7192	**-12**	6075	5945	**-2**
Mean		5144	4433	-14	7410	5862	-21	5972	5884	-1
CV (%)		12.6	17.7		13.1	20.7		11.3	11.5	
Tukey HSD (α=0.05)		972.7	1089.9		1192.3	1576.5		1374.3	943.8	

Table 6. Significant traits with coefficients from linear regression models for yield of 50 untreated cultivars of wheat grown at Warsaw in 2010 and 2011 and Holland in 2011, including coefficient of determination (r^2) for the model in each environment.

Variable	Warsaw 2010	Warsaw 2011	Holland 2011
Intercept	14315	7291.75	-1934.39
Powdery mildew†	-123.22**	-156.40**	-
Leaf rust‡	-11.97**	-17.68**	-
Spikelets/ Spike	67.74**	99.10**	516.85*
Erect flag leaf angle	126.12**	-	203.45**
Harvest index	-	79.18**	84.71**
Flowering date	-96.4**	-86.84**	-
Spikes/m^2	0.94**	-	0.88*
Spike length	-	-15.70*	-11.27*
NDVI§	699.53*	3484.04**	-
Peduncle length	4.32*	-	-2.37*
Seeds/ Spike	-	-	-228.98*
Green leaf retention¶	-	11.00**	-
500 kernel weight	48.87**	-	-
Seeds/ Spikelet	-	-	3515.88*
Ash	-	2072.89**	-
Test weight	-	-	35.88*
Floret fertility	1867.12*	-	-
Crude fiber	-	-391.82*	-
Starch	-	-	-93.37*
Protein	-124.40**	-	-
Fat	-578.86**	-	-
r^2	**0.84**	**0.88**	**0.75**

† Powdery mildew rating, significant ratings taken on 20 April 2010 and 11 May 2011 at Warsaw
‡ Leaf rust rating, significant ratings taken on 10 May 2010 and 11 May 2011 at Warsaw
§ Normalized Difference Vegetative Index
¶ Significant rating taken on 30 May 2011 at Warsaw

Table 7. Pearson correlation coefficients (α=0.05) of yield and final mean disease severity (MDS) ratings for powdery mildew (PM) and leaf rust (LR) with select agronomic, yield component and spike characteristic traits of 50 wheat cultivars grown in disease controlled (treated) and untreated yield plots at Warsaw in 2010 and 2011 and Holland in 2011.

	Treatment	Warsaw 2010			Warsaw 2011			Holland 2011	
		MDS LR†	MDS PM‡	Yield	MDS LR	MDS PM	Yield	MDS PM	Yield
MDS PM	Untreated	0.19	1	-	0.15	1	-	1	-
	Treated	-	-	-	-	-	-	-	-
Yield	Untreated	-0.47**	-0.45**	1	-0.58**	-0.48**	1	-0.46**	1
	Treated	-	-	-	-	-	-	-	-
GS 25 Tillers	Untreated	0.03	0.11	-0.12	0.07	0.34**	-0.15	0.13	-0.10
	Treated	-	-	0.06	-	-	0.17	-	0.04
Biomass	Untreated	-0.27**	-0.15	0.43**	-0.38**	-0.14	0.40**	-0.02	0.22**
	Treated	-	-	0.38**	-	-	0.29**	-	-0.05
Harvest Index	Untreated	-0.36**	-0.41**	0.75**	-0.44**	-0.51**	0.85**	-0.54**	0.79**
	Treated	-	-	0.53**	-	-	0.75**	-	0.64**
Test Weight	Untreated	-0.35**	0.14	0.18	-0.37**	0.13	0.31**	0.02	0.14
	Treated	-	-	0.11	-	-	0.31**	-	0.04
500 Kernel Weight	Untreated	-0.40**	-0.07	0.41**	-0.16	-0.17*	0.14	0.07	-0.02
	Treated	-	-	0.10	-	-	0.19*	-	0.01
Seeds/Spike	Untreated	-0.01	-0.33**	0.46**	-0.01	-0.24**	0.38**	-0.26**	0.34**
	Treated	-	-	0.42**	-	-	0.19*	-	0.43**
Spikes/m^2	Untreated	-0.27**	-0.06	0.29**	-0.28**	-0.21*	0.50**	-0.21**	0.51**
	Treated	-	-	0.35**	-	-	0.47**	-	0.26**
Spikelets/Spike	Untreated	0.13	-0.09	0.01	0.18*	0.05	-0.06	0.00	-0.02
	Treated	-	-	0.10	-	-	-0.06	-	0.01
Seeds/Spikelet	Untreated	-0.11	-0.31**	0.51**	-0.16	-0.33**	0.53**	-0.34**	0.45**
	Treated	-	-	0.34**	-	-	0.27**	-	0.53**
Floret Fertility	Untreated	-0.16	-0.25*	0.53**	-0.22**	-0.15	0.47**	-0.27**	0.38**
	Treated	-	-	0.17	-	-	0.30**	-	0.45**
Spike Length	Untreated	0.34**	0.12	-0.37	0.33**	0.08	-0.38**	0.21*	-0.32**
	Treated	-	-	-0.33**	-	-	-0.33**	-	-0.20*

† Mean Final Disease Severity Rating, leaf rust
‡ Mean Final Disease Severity Rating, powdery mildew

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