It is well documented that the productivity of global agriculture must increase to feed a growing human population (Godfray et al., 2010). Declines in water availability and arable land suggest that production from current crop acreage must increase dramatically. One way to address crop productivity is to develop new cultivars that have greater yield potential, nutrient-use efficiency, and resistance to abiotic and biotic stresses. Understanding which collaborative partnerships that will best advance the collective goal of breeding programs to develop improved cultivars would be useful when time and resources come at a premium.

Consolidation of the global seed industry has resulted in far fewer private breeding programs over recent decades (Howard, 2009). Furthermore, the focus of many university breeding programs has transitioning from cultivar development toward emerging fields upstream such as genomics and bioinformatics, largely a consequence of funding shifts (Morris et al., 2006). It is imperative that remaining breeding programs collaborate to leverage resources including land, labor, capital, and infrastructure. There has been an extensive commitment to winter wheat (Triticum aestivum L.) breeding and cultivar development in the US public and private sectors. Many of these breeding programs have focused on the Southern US, where winter wheat is grown under diverse environmental conditions. Therefore, understanding the impact of selection location and environment on cultivar performance and adaptation is critical.

Yield Data from the Uniform Southern Soft Red Winter Wheat Nursery Emphasize Importance of Selection Location and Environment for Cultivar Development

Richard E. Boyles,* David S. Marshall, and Harold E. Bockelman

ABSTRACT

Yield and agronomic data from a regional soft red winter wheat (Triticum aestivum L.) nursery—consisting of 604 advanced breeding lines (ABLs) and 36 testing locations over a 21-yr period—were evaluated to understand recent genetic gains in wheat and determine the impact of selection location and environment on cultivar performance and adaptation. Relative mean yield improvement of ABLs with respect to historical cultivar AGS 2000 was 106 kg ha⁻¹ yr⁻¹ (1.58 bu acre⁻¹ yr⁻¹), equating to an annual genetic gain of 1.6%. Yield gains for wheat during this timespan were attributed to an increase in both yield potential and stability across environments. However, a strong tradeoff ($r = -0.36, p < 2.2 \times 10^{-16}$) was observed between yield potential and stability. Additionally, distance between selection and evaluation environments was significantly correlated with yield, with yield decreasing as distance between locations increased. Advanced breeding lines had a +221, +126, and −29.6 kg ha⁻¹ yr⁻¹ (+3.29, +1.88, and −0.44 bu acre⁻¹) yield difference over the location mean when the selection location was within, adjacent, and nonadjacent to the trial location zone, respectively. Advanced breeding lines in general performed poorly in production environments west of their selection site. Based on data analyzed, elevation and latitude are significant geographic parameters to consider when determining optimal selection location for a production environment. Meanwhile, change in growing degree days between selection and evaluation location had a stronger influence on yield than precipitation. Findings demonstrate the importance and benefits of breeder collaborations and multi-environment testing on crop improvement, which will be needed to maximize yield gains in the 21st century.
programs, including both public universities and private seed companies, do work together in various degrees. These collaborations are formed to pool different skill-sets, increase genetic diversity within individual gene pools, and expand evaluation trials to additional production environments—all of which would be challenging if attempted by individual programs. These syndicates also help to maximize the return on investment from available funding and get improved wheat cultivars to market at a faster rate—the former being important during a period when funding for plant cultivar development is constrained, and the latter being critical during a time of economic hardships for row crop farmers.

Direct climate variables (temperature and precipitation) or biotic stressors that thrive within specific climate regions generally obstruct the quest for broad adaptation of individual cultivars. Thus, multiple cultivars with different genetic backgrounds must be developed to maximize crop yield potential across production environments. The incorporation of new crop germplasm from outside sources into established breeding programs can increase genetic diversity and provide beneficial genes for target environments (Hoisington et al., 1999). The challenge is to determine which breeding programs offer the most appropriately adapted germplasm to incorporate for cultivar development (Calhoun et al., 1994). For instance, should breeders located within certain geographic or climatic regions more aptly share breeding lines than breeders across distinct environments? Even among geographic regions within the United States, there is an established wheat breeding program at nearly every land-grant university, aside from the multitude of private breeding locations. Currently, no empirical data are available to help expose and formalize strategic partnerships between breeding programs that would be most appropriate for wheat improvement. This information would further incentivize breeding programs to participate in material transfers for increased breeding efficiency.

Genetic gain is dependent on genotype and genotype × environment interactions (Mulder and Bijma, 2005). Plant genomics research has revealed that quantitative traits (e.g., grain yield) have significant genotype × environment interactions underlying their genetic basis (Peterson et al., 1992; Mohammadi et al., 2007). Although most agronomic traits in wheat are highlyheritable, there is often an environmental component to each of significant effect. Analytical and statistical methods have been developed to quantify the effects of genotype × environment interactions (Nachit et al., 1992) and use this information to predict genotype performance across environments (Crossa et al., 2006; Burgueño et al., 2012). Optimizing the location and number of selection environments can increase selection intensity and thus help to maximize genetic gain from breeding populations. Calhoun et al. (1994) found that genotype evaluation under optimal (i.e., full irrigation) conditions can result in greater yield gains for water-limited environments. Previously, managed environments with degrees of abiotic stress have been implemented to try to increase the selection differential (and thus genetic gain) in wheat (Cooper et al., 1995). It has been shown that abiotic stresses such as temperature throughout the growing season significantly affect winter wheat grain yield (Yan and Hunt, 2001). In this finding, Yan and Hunt (2001) found that plant maturity and height were the two major traits underlying genotype × environment interactions where growing degree days (GDD) varied considerably across environments. For this reason, we not only use historical, multi-environment yield data to understand the importance of selection location and environment, but we also investigate the impact of heading date and plant height on wheat adaptation across both geographic and climatic zones.

This study was conducted to provide empirical evidence into how important selection location(s) and accompanying environmental conditions are to crop adaptation and ultimate agronomic performance of advanced breeding lines (ABLs). The questions that we intended to answer were: (i) does a significant relationship exist between wheat genotype performance and distance from location of selection? (ii) Do ABLs that were selected in an environment similar to the trial location tend to outperform ABLs that were selected in an environment with greater contrast? (iii) Based on genotype performance across locations, are there specific geographic and/or environmental parameters that are more important to consider for selection location(s)? To address these questions, a meta-analysis of US historical soft red winter wheat performance trials combined agronomic data from 36 different locations within 20 states from 1997 to 2017. An average of 36 ABLs were tested annually in ~20 locations for a total of 15,924 evaluations. Three or four check lines were included in each trial-year combination (Supplemental Fig. S1), including AGS 2000 as a historical check, to enable comparative analyses and estimate genetic gain.

MATERIALS AND METHODS

Plant Material

The Uniform Southern Soft Red Winter Wheat Nursery (USSRWWN) evaluates elite breeding lines from private and public breeding programs in major US soft red winter wheat growing regions. Although only elite lines are tested in this nursery, high genetic diversity exists among genotypes (Zhang et al., 2010), likely attributed to contributions from many different breeding programs. A mean of 36 breeding lines, ranging from 28 to 45, were evaluated annually along with two to four commercial checks for comparison. Including checks, 604 unique lines were entered into the USSRWWN from 1997 to 2017. Three double-haploid lines that were entered...
were classified as being immediately to the north, south, east, or west of each other. Nonadjacent zones were all the remaining combinations, including diagonal or separated directionally by one or more zones in between.

Relative Yield and Yield Stability
Similar to methods used by Graybosch and Peterson (2010), relative yield using the standard cultivar AGS 2000 was calculated each year to estimate genetic gain. Annual yield stability (% AGS 2000) was also measured using Wricke’s ecovalence values. Because 2000 was the first year that AGS 2000 was formally entered into the USSRWWN, relative yield results omitted 1997 to 1999 data.

Wricke’s ecovalence method (Wricke, 1962) was used to measure stability of ABLs across locations. This method was found previously to be advantageous in evaluating dynamic yield stability across genotypes (Piepho, 1994). Wricke’s ecovalence formula is defined as

\[ W^2_i = \sum (R_y - m_i - m_j + m)^2 \]

where \( R_y \) is the measured yield of genotype \( i \) in environment \( j \), \( m \) is the mean yield of genotype across environments, \( m_j \) is the mean yield of environment, and \( m_i \) is the grand yield mean. In this equation, highest attainable yield stability is \( W^2_i = 0 \).

Determination of Advanced Breeding Line Performance across Selection and Trial Zones
For each trial zone, the mean yield of ABLs within each selection zone was classified as being optimal, favorable, or unfavorable. Each classification was determined using the formulas below:

- **Optimal**: Highest \( m_i - m_j \), where \( m_i \) is the mean yield of ABLs from selection zone \( i \) in trial zone \( j \), and \( m_j \) is the grain yield mean of trial zone \( j \).
- **Favorable**: \( m_i > m_j \)
- **Unfavorable**: \( m_i < m_j \)

Statistical Analysis
Geographic distance between selection and trial locations was calculated using a custom R script using the ‘Imap’ package (Wallace, 2012). The genotype plus genotype × environment (GGE) analysis was performed using the ‘gge’ package in R (Wright and Laflont, 2016), and the biplot was generated with the biplot function in the ‘stats’ package. The arguments origin=0 and scale=FALSE were used so that the biplot was centered and

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### Selection Locations
Selection location of breeding lines was derived by line designation and cooperator information. When applicable, plant variety protection certificates were individually mined to determine or confirm selection site. Contributors of remaining lines with unknown selection locations were contacted to provide selection site. Eight of the 601 lines were selected in multiple locations during development and were excluded from analyses.

### SE Only Dataset
This USSRWN is intended to serve as an evaluation of cultivar performance in the southeastern United States, primarily the following states: Alabama, Arkansas, Florida, Georgia, Louisiana, Mississippi, North Carolina, South Carolina, Tennessee, and Virginia. Because the original USSRWN dataset includes both genotypes selected and trial locations outside of the traditional southeastern United States, a “SE Only” data subset was selected for certain analyses. The SE Only data only included genotypes selected within Zones 08 to 15 and also discarded any trial data outside of this area. Thus, Trial Zones 01 to 07 were not part of the analyses for the SE Only subset. The SE Only subset included 480 lines (80%) and 9295 grain yield observations (60%) from the initial dataset.

### Trial Locations
The USSRWN over the past 21 yr has included over 80 different trial locations. Locations that were not represented five or more years during the 1997 to 2017 growing seasons were excluded from the analysis. After culling, 36 locations from 20 states remained for compilation (Fig. 1). We were able to record grain yield data from all 21 yr of the study at only 4 of the 36 locations: Belle Mina, AL, Griffin, GA, Plains, GA, and Warsaw, VA. Yield data for 10 or more years were collected at 22 of the 36 (61%) locations (Supplemental Table S1). Global positioning system (GPS) coordinates for each trial location were calculated based on zip code from the US Census Bureau 2013 Gazetteer files (www.census.gov/geo).

Zones were defined as being within (same zone), adjacent, or nonadjacent with respect to one another. Adjacent zones into more recent USSRWWN trials were excluded from the analysis because no early-generation field selections could have been made. As a result, 601 lines were used for studies when selection parameters were relevant in the analysis.

### Data Compilation
The USSRWN annual trial data are coordinated and maintained by the USDA-ARS (https://www.ars.usda.gov/pacific-west-area/aberdeen-id/small-grains-and-potato-germplasm-research/docs/uniform-nurseries/). Grain yield, heading date, plant height, and leaf rust ratings were analyzed for all ABLs but not in all locations. The mean number of locations with complete observations per year was 21 for grain yield (15,644 observations), 17 for heading date (12,510 observations), 17 for plant height (12,680 observations), and eight for leaf rust (5919 observations). Replicate means from each trial were used for all traits. Number of replications varied between two and three depending on trial location and year.

### Climate Data
All climate variable data were downloaded from the NOAA National Center for Environmental Information (www.ngdc.noaa.gov) in March 2018 and comprise 30-yr climate normals from 1981 to 2010. Variables included in the study were annual precipitation, GDD, average temperature, minimum temperature, maximum temperature, and frost date. A base temperature of 4.4°C was used to determine annual GDD. Annual frost date was defined as 50% probability date when minimum temperature reaches 0°C. Zip codes from both trial and selection location were inputted to find nearest weather station (Supplemental Table S1). Mean difference between field location and weather station was 0.089° lat. and 0.087° long.
axes were equally scaled, respectively, to avoid misinterpreta-
tion of the image (Malik and Piepho, 2018). Pearson pairwise
correlations between variables and corresponding \( p \) values were
generated with the 'cor' and 'cor.test' functions in R, respec-
tively. Outliers within each trial–year combination were defined
as 1.5 times outside the interquartile range. For grain yield, 326
(2%) and 174 (1.8%) observations were designated outliers from
the full and SE Only dataset, respectively, and were removed
from subsequent analyses. Of the 326 outliers, 261 (80%) were
low yields, which is likely a function of management (pesticide
or fertilizer application), mechanical (planting and harvesting),
or statistical errors rather than genetic factors.

RESULTS
Yield Potential vs. Yield Stability

A significant tradeoff \( (r = -0.36, \ p \ \text{value} < 2.2 \times 10^{-16}) \) was
observed between maximum grain yield and yield stability. The
tradeoff was even stronger \( (r = -0.45) \) for new breeding
lines that were entered into the nursery after excluding
standard check entries. In this evaluation, maximum grain
yield represents yield potential of an ABL given that (i) it
is similar to the CIMMYT mega-environment testing
scheme (Braun et al., 1996), (ii) optimal management prac-
tices by location are typically implemented to evaluate the
USSRWWN, and (iii) the high number of environments
represented in the study include multiple high wheat yield
growing locations. Thus, a strong negative relationship was
indeed demonstrated between yield potential and yield
stability across environment (Fig. 2).

Because nearly all entries in the USSRWWN repre-
sent newly developed genotypes introduced by regional
breeders, yield statistics of ABLs over the 21-yr period were
evaluated to understand potential changes in yield potential
and stability over time. Pairwise correlations using
data means of 588 genotypes (excluding checks) from 36
locations revealed a positive mean grain yield trend over
time \( (r = 0.25, \ p \ \text{value} < 2.2 \times 10^{-10}) \). The mean relative
yield—the percentage yield of an ABL compared with the
historical check AGS 2000—of experimental lines also
increased significantly (Fig. 3a). Comparing relative yield
statistics of breeding lines from all locations from 2000
to 2017 (18 yr) further suggested improvement in relative
yield potential and yield stability over time (Fig. 3a).
When observing the yield trend within each of these trial
locations separately, a significant increase in relative yield
was demonstrated by ABLs in Plains, GA, whereas minor
gains were observed in Belle Mina, AL, and Warsaw, VA

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Fig. 1. Selection sites for the 604 advanced breeding lines entered into the 1997 to 2017 Uniform Southern Soft Red Winter Wheat Nursery and trial locations for agronomic evaluation. Refer to Supplemental Table S1 for geographic and climatic information on individual locations.

Fig. 2. A tradeoff between yield stability and maximum grain yield was found among 604 wheat advanced breeding lines (ABLs) during a 21-yr period. The ABL with the highest maximum yield, mean yield, and yield stability is labeled in green, blue, and red, respectively. The ABL ‘D04’5526’ labeled in orange represents the only ABL in top 15 maximum-yielding lines with a yield stability in the top 50th percentile.
zones (Table 1, Supplemental Table S3). Several of these ABLs are licensed as cultigens to private companies and widely used for commercial wheat production such as ‘SS 8641’ and ‘Hilliard’. The greatest annual mean yield of the 604 wheat ABLs during the 21-yr timespan was in 2014 and belonged to ABL ‘GA035640-12E6’ (licensed as L11544; Johnson et al., 2017). Not unrelated, 2014 was the most favorable production year over the period. ‘GA035640-12E6’ was the highest ranked ABL when taking into account maximum grain yield, mean grain yield, and yield stability (Supplemental Table S4). The most stable ABL entered into the USSRWWN (Fig. 3b). Relative to AGS 2000, wheat ABLs (within the SE Only dataset) entered into the USSRWWN during this time period exhibited an average grain yield improvement of 106 kg ha⁻¹ yr⁻¹ (1.58 bu acre⁻¹ yr⁻¹). This yield trend equates to a 1.6% annual genetic gain for soft red winter wheat in the southeastern United States.

Statistics of Top Performing Advanced Breeding Lines

The 10 ABLs exhibiting the highest average grain yield difference above location means were developed by multiple breeders and selected across several geographic

Table 1. A list of the top 10 advanced breeding lines for highest mean yield difference above the trial zone mean when averaged over all 13 trial zones.

<table>
<thead>
<tr>
<th>Advanced breeding line</th>
<th>Cultivar name</th>
<th>Developer (institution‡)</th>
<th>Trial year</th>
<th>Selection zone</th>
<th>Relative grain yield % AGS 2000 kg ha⁻¹ (bu acre⁻¹)</th>
<th>Trait difference over trial zone mean (R̄j − mj)†</th>
<th>Grain yield</th>
<th>Heading date</th>
<th>Plant height</th>
</tr>
</thead>
<tbody>
<tr>
<td>96229-3A41</td>
<td>SS 8641</td>
<td>Johnson (UGA)</td>
<td>2005</td>
<td>12</td>
<td>128.1 (13.59)</td>
<td>913.9 (13.59)</td>
<td>0.29</td>
<td>0.83</td>
<td></td>
</tr>
<tr>
<td>VA12W-68</td>
<td></td>
<td>Griffey (VA Tech)</td>
<td>2016</td>
<td>09</td>
<td>157.9 (12.43)</td>
<td>835.9 (12.43)</td>
<td>0</td>
<td>1.09</td>
<td></td>
</tr>
<tr>
<td>VA11W-108</td>
<td></td>
<td>Griffey (VA Tech)</td>
<td>2016</td>
<td>09</td>
<td>114.1 (11.38)</td>
<td>765.3 (11.38)</td>
<td>2.62</td>
<td>3.42</td>
<td></td>
</tr>
<tr>
<td>VA09MAS1-12-8-4</td>
<td></td>
<td>Griffey (VA Tech)</td>
<td>2017</td>
<td>09</td>
<td>154.5 (10.28)</td>
<td>756.6 (10.28)</td>
<td>−0.03</td>
<td>1.57</td>
<td></td>
</tr>
<tr>
<td>VA97W-206</td>
<td></td>
<td>Griffey (VA Tech)</td>
<td>2000</td>
<td>09</td>
<td>96.6 (10.28)</td>
<td>718.2 (10.28)</td>
<td>−0.54</td>
<td>−0.52</td>
<td></td>
</tr>
<tr>
<td>LA95181BUB40-1</td>
<td></td>
<td>Harrison (LSU)</td>
<td>2005</td>
<td>14</td>
<td>123.2 (10.59)</td>
<td>712.2 (10.59)</td>
<td>−2.25</td>
<td>4.9</td>
<td></td>
</tr>
<tr>
<td>VA04W-90</td>
<td>SW0490-29104</td>
<td>Griffey (VA Tech)</td>
<td>2009</td>
<td>09</td>
<td>115.0 (10.28)</td>
<td>691.3 (10.28)</td>
<td>−0.54</td>
<td>−0.52</td>
<td></td>
</tr>
<tr>
<td>GA035640-12E6</td>
<td>L11544</td>
<td>Johnson (UGA)</td>
<td>2014</td>
<td>12</td>
<td>118.1 (10.26)</td>
<td>690 (10.26)</td>
<td>−0.45</td>
<td>−1.78</td>
<td></td>
</tr>
<tr>
<td>GA991209-6E33</td>
<td></td>
<td>Johnson (UGA)</td>
<td>2008</td>
<td>12</td>
<td>109.4 (9.95)</td>
<td>669.1 (9.95)</td>
<td>−3.89</td>
<td>1.54</td>
<td></td>
</tr>
<tr>
<td>MD09W272-8-4-13-3-15</td>
<td></td>
<td>Wight (UMD)</td>
<td>2016</td>
<td>07</td>
<td>152.3 (9.87)</td>
<td>663.8 (9.87)</td>
<td>−1.32</td>
<td>−5.4</td>
<td></td>
</tr>
</tbody>
</table>

† R̄j, observation R measured for genotype i in environment j; mj, phenotypic mean of all observations in environment j.
‡ UGA, University of Georgia; VA Tech, Virginia Tech; LSU, Louisiana State University; UMD, University of Maryland.
in this period was ‘VA 94-54-479’ (Fig. 2), which was evaluated in the 1997 nursery. Finally, experimental line ‘TX94D1320’ in the 2000 Aberdeen, ID environment exhibited the greatest yield potential by having the highest recorded grain yield at 9886 kg ha\(^{-1}\) (147 bu acre\(^{-1}\)). Given the tradeoff between yield potential and stability, it was unsurprising to find that ‘TX94D1320’ was in the top 10% of most unstable ABLs (567 out of 604). Although most ABLs with high yield potential were ranked near the bottom for yield stability, ‘D04*5526’ was the only ABL of the top 15 maximum yielding lines to have a yield stability rank in the 50th percentile (226 of 604).

### Impact of Selection Location on Grain Yield within Trial Zones

Selection and trial locations were grouped into geographic zones by latitude and longitude. Individual zones comprised 10° lat. and 2.5° long. To determine the importance of selection location on ABL performance, grain yields from all ABLs selected within each geographic zone were averaged. Advanced breeding line means within trial zones (where ABLs were evaluated) for selection zones (where ABLs were developed) exhibited a clear relationship between geographic position and crop performance. Trial Zones 04 and 05 as well as Selection Zones 01 and 02 were not included in the analysis as a result of poor sample size. Additionally, when specifically observing ABL yield changes across four popular trial locations, ABLs that were selected at selection sites near each trial location generally displayed a mean yield advantage over ABLs from more distant sites (Supplemental Fig. S2).

As expected, ABLs tended to yield more grain when evaluated in a trial zone that was within or adjacent to their selection zone. In all trial zones represented, the matching selection zone had a positive grain yield difference over grand mean, but only two out of the 13 possible pairwise events did the optimal selection zone match the trial zone (Zones 06 and 11). Advanced breeding lines evaluated in the same geographic zone where they were selected had a mean yield of 221 kg ha\(^{-1}\) (3.3 bu acre\(^{-1}\)) over the location (i.e., trial zone); meanwhile, all additional ABLs had a mean yield that was 20.2 kg ha\(^{-1}\) (0.3 bu acre\(^{-1}\)) below the location mean. Yield data where the ABL selection zone was nonadjacent to the trial zone displayed the lowest difference from the trial zone mean (Table 2). Adjacent selection zones had a +128 kg ha\(^{-1}\) (+1.9 bu acre\(^{-1}\)) grain yield difference with respect to the trial zone mean yield. In terms of ABLs that were developed in selection zones and evaluated in adjacent trial zones, direction of adjacency had a significant impact. Advanced breeding lines selected in geographic zones that were both north and west of trial zones were higher yielding on average. Intriguingly, ABLs in general were not well adapted to locations west of their selection site. Similar relationships were identified in the “SE Only” data subset (Table 2).

The optimal selection zone for each trial zone was defined as having the greatest mean yield differential with respect to the grand mean of the trial zone (Fig. 4). For each trial zone, ABLs originating from the optimal selection zone had a mean grain yield of 296 kg ha\(^{-1}\) (4.4 bu acre\(^{-1}\)) above the grand mean of the trial zone, with a range from 679 kg ha\(^{-1}\) (10.1 bu acre\(^{-1}\), Trial Zone 03) to 101 kg ha\(^{-1}\) (1.5 bu acre\(^{-1}\), Trial Zone 02). Geographic Zones 06 and 09 were the optimal selection zones for four and three of the 13 trial zones, respectively. Further, Zone 09 was a favorable selection zone (i.e., positive mean grain yield difference compared with trial zone mean) for 11 of the 13 soft red winter wheat trial zones represented. Consistent with the overall data trend, the two trial zones where Selection Zone 09 was not favorable were positioned to the southwest of Zone 09 (Fig. 5b). Selection zones with poorest mean yield across trial zones were Selection Zones 04, 03, and 13. Each of the three selection zones had a positive mean grain yield difference for two or fewer trial zones. Zones 14 and 15 were also relatively unproductive locations for ABL selection as they had the two lowest average yields—4317 and 4196 kg ha\(^{-1}\) (64.2 and 62.4 bu acre\(^{-1}\)), respectively—from the combined 13 trial zones under evaluation.

### Data Trends with Geographic and Environmental Parameters

Pairwise correlation of physical distance between selection site and trial location was significantly correlated with grain yield. Grain yield declined as distance increased between selection and trial locations (Table 3). This same

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**Table 2. Selection zone location with respect to trial zone and its association with grain yield.**

<table>
<thead>
<tr>
<th>Selection location</th>
<th>All trial zones</th>
<th>SE Only (Trial Zones 08–15)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(n)</td>
<td>Grain yield difference over trial zone mean</td>
</tr>
<tr>
<td></td>
<td></td>
<td>kg ha(^{-1}) (bu acre(^{-1}))</td>
</tr>
<tr>
<td>Within</td>
<td>1524</td>
<td>221 (3.29)</td>
</tr>
<tr>
<td>Nonadjacent</td>
<td>9642</td>
<td>−29.6 (−0.44)</td>
</tr>
<tr>
<td>Adjacent</td>
<td>4202</td>
<td>126 (1.88)</td>
</tr>
<tr>
<td>Adjacent north</td>
<td>1192</td>
<td>234 (3.48)</td>
</tr>
<tr>
<td>Adjacent south</td>
<td>1051</td>
<td>84.1 (1.25)</td>
</tr>
<tr>
<td>Adjacent east</td>
<td>780</td>
<td>−55.8 (−0.83)</td>
</tr>
<tr>
<td>Adjacent west</td>
<td>1179</td>
<td>200 (2.98)</td>
</tr>
</tbody>
</table>
trend was found in the SE Only subset, which included only observations from, and genotypes that were selected in, Zones 08 to 15 (Supplemental Table S5). The GGE biplot analysis using multiyear trial location data shows that trial locations positioned near one another tended to cluster together (Fig. 6). However, there were multiple exceptions where adjacent locations failed to cluster together, as well as where geographically distant locations clustered tightly together. Also, environment clusters were found to expand across longitude and latitude. That being said, Pearson correlation results demonstrate that both latitudinal and longitudinal deviations between selection and trial location had a significant impact on genotype productivity. When removing positive elevation change (defined as trial location elevation exceeding selection site elevation) from pairwise correlation analysis, plant height increased as elevation change decreased. Otherwise stated, ABLs tended to be shorter when trial location elevation became increasingly lower than the elevation of where the ABL was originally selected. No relationship existed between plant height and elevation change when trial location elevation exceeded selection site elevation. Greater deviation in temperature metrics (GDD and average, maximum, and minimum temperatures) between trial and selection location resulted in ABLs having later heading date, shorter plant height, and lower grain yield (Table 3, Supplemental Table S5). Although precipitation changes between selection and trial location significantly affected plant height, no significant correlation was observed with grain yield.

**DISCUSSION**

Developing plant cultivars with broader adaptation that have stable agronomic performance across locations and environments is often desired (Thomason and Phillips, 2006). This simplifies seed production by limiting the number of cultivars needed to fit multiple geographic regions without sacrificing yield potential and productivity. Although high yield potential under optimal conditions is important, yield stability of a cultivar under unfavorable environmental conditions (i.e., drought and abnormal temperatures) can minimize crop loss and prevent
against complete crop failure. In this study of historical yield data for over 600 ABLs from the USSRWWN, a tradeoff between yield potential and yield stability was found. This was concluded from evaluating the relationship of maximum yield of each ABL with its calculated Wricke’s ecovalence value, which is a trusted method for measuring dynamic stability (Piepho, 1994). This identified tradeoff was consistent with wheat yield trends over a similar timespan for Argentina, Australia, Italy, and the United Kingdom (Calderini and Slafer, 1999). However, Fig. 5. Mean performance of advanced breeding lines with respect to the trial zone mean from individual Selection Zones (a) 03, (b) 09, (c) 10, and (d) 14. Selection zones are outlined in red. Each geographic zone represents a 2.5° lat. by 5° long. area.

Table 3. Relationship of relative cultivar performance by location for agronomic traits with geographic and climatic differences between trial (i.e., location of evaluation) and selection site (i.e., location of development).

<table>
<thead>
<tr>
<th>Trait</th>
<th>Grain yield</th>
<th>Heading date</th>
<th>Plant height</th>
<th>Leaf rust</th>
</tr>
</thead>
<tbody>
<tr>
<td>Δ (trial – selection)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Distance</td>
<td>−0.147</td>
<td>0.031</td>
<td>−0.038</td>
<td>NS‡</td>
</tr>
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</tr>
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<td>NS</td>
</tr>
<tr>
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</tr>
<tr>
<td>Growing degree days§</td>
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<td>−0.076</td>
<td>0.101</td>
</tr>
<tr>
<td>Abs</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Δ (trial – selection)</td>
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<td></td>
<td></td>
<td></td>
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<tr>
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<tr>
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<td>0.039</td>
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<td>0.044</td>
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<td>Mean df (SD)</td>
<td>15,388 (68)</td>
<td>12,308 (58)</td>
<td>12,447 (68)</td>
<td>5819 (2.5)</td>
</tr>
</tbody>
</table>

† $R_{ij}$, observation $R$ measured for genotype $i$ in environment $j$; $m_j$, phenotypic mean of all observations in environment $j$.
‡ NS, not significant at the 0.001 probability level.
§ Calculated using a base temperature of 40°C.
Fig. 6. Multiyear clustering of trial locations in the Uniform Southern Soft Red Winter Wheat Nursery is observed using a (a) genotype plus genotype × environment (GGE) biplot analysis and (b) regional map schematic of correlated environments. Solid yellow lines encircle highly correlated trial locations, whereas dashed yellow lines depict moderately related sites with larger location clusters. The CL, PL, and OV locations that are surrounded by the solid orange clustered tightly together in the biplot analysis although geographically distant. Refer to Supplemental Table S1 for specific details on individual locations.
whereas grain yields reported by Calderini and Slafer (1999) became increasingly unstable as genetic gains improved yield potential, the opposite trend was found in the USSRWWN. This finding of improved stability was more consistent with a separate study by Calderini and Slafer (1998), which found no decrease or even a slight rise in stability of yield for wheat production among 21 countries (including the United States) during the 20th century. This latter finding could be a confounding result of more appropriate cropping systems and management practices to mitigate adverse environmental impacts on wheat production. No management factors were taken into account by Calderini and Slafer (1998, 1999), as was the case in this study because of the difficulty in collecting this information and then quantifying its impact. Another plausible cause for this increase in yield stability is the focus of regional wheat breeders on improving host plant resistance to major pests (Cambron et al., 2010; Hao et al., 2011; Liu et al., 2013; Petersen et al., 2015).

It should be noted that although an increase in genetic gain of 1.6% (106 kg ha\(^{-1}\) yr\(^{-1}\)) was observed over the 21-yr period using historical check AGS 2000 as the common denominator, this relative increase may be inflated by the downward productivity of AGS 2000 over years (Supplemental Fig. S3). Decreased yield of AGS 2000 is likely a result of increased pest and disease susceptibility. Nevertheless, the percentage of ABLs outperforming AGS 2000 from year to year increased significantly over time. The genetic gain of 1.6% calculated from the USSRWWN is comparable with a global breeding program (Crespo-Herrera et al., 2017, 2018) but markedly higher than findings in other US winter wheat nurseries (Cox et al., 1988; Graybosch and Peterson, 2010; Green et al., 2012).

Data from long-term winter wheat evaluation nurseries demonstrate the importance of selection location and environment in cultivar development. The concern with marker-assisted and double-haploid breeding is that these methods eliminate or reduce early generations of field selection for agronomic traits, therefore stripping plant breeders of the opportunity to select most adapted lines within segregating populations. This selection process is arguably of increasing importance to US autogamous, nonhybrid crops such as wheat and peanut (Arachis hypogaea L.). Further, this study provides empirical evidence for developing public and public–private collaborations across specific geographic zones to share breeding lines for cultivar development and testing. Specific for soft red winter wheat in the southeastern United States, favorable selection zones existed to develop wheat ABLs for production (i.e., trial) zones. In several cases, the optimal selection zone and trial zone were different, but often they were adjacently located.

One critical component this study was not able to address was the impact that individual breeders or breeding programs have on the selection process. Because ABLs that were selected in target environments were often developed and evaluated by individual breeders in that same location, there was no way to separate this relationship in the meta-analysis. All plant breeders and breeding programs are not interchangeable, and it is likely that several established and successful US wheat breeding programs would be successful irrespective of headquarters. Also, the selection process for each line was subject to change. Although the majority of lines were advanced in early generations by modifications of the bulk breeding method, some lines were advanced one or multiples generations in the greenhouse or via marker-assisted selection. Several double-haploid lines that were entered into more recent USSRWWN trials were intentionally removed because no early-generation selections could be made. Further, the study could not factor in the degree of genetic diversity and quality of germplasm within each selection location, which could both impede dissecting causal relationships between selection environment and ABL performance. Genetic diversity of elite lines within the USSRWWN was previously reported to be relatively high (Zhang et al., 2010).

Finally, development of advanced high-throughput phenotyping platforms will enable more genotype evaluations per generation; however, the number of early generations available for selection will remain static. This shifts emphasis on selection environment(s) throughout the breeding cycle. Cooper et al. (1997) created artificial selection environments with gradient levels of abiotic stress (H\(_2\)O and N) to find that stress selection nurseries do not correlate with trial locations, even those with similar stress levels. Therefore, maintaining—or potentially increasing—the number of natural selection environments distributed across geographic and climatic regions would enhance the breeding efficiency of winter wheat. Increasing selection environments used by individual breeding programs will require a significant investment in resources. It seems more feasible and appropriate to form regional collaborations between breeding programs to leverage existing infrastructure and enable germplasm sharing. Some established small grains breeding programs have formed such a collaboration called the Southeastern University Grains (SunGrains) cooperative, which has been successful in accelerating cultivar development (Harrison et al., 2017; Johnson et al., 2017, Mason et al., 2018).

**CONCLUSIONS**

Multi-environment testing of new ABLs will continue to be an essential component to optimize genotypes for an environment and maximize cultivar adaptation for commercial production. Insights gained from this study demonstrate the value of annual multi-environment trials such as the USSRWWN, which serve as valuable
resources for breeders to determine not only regional ABL performance but also level of adaptation. The added value includes empirical data that are helpful to determine the number and distribution of selection sites across potential target production environments needed to increase or maximize breeding efficiency. Because selection environment does matter, strategic collaborations between breeding programs to share infrastructure and germplasm will help to advance crop yields to keep pace with an increasing global population. Advanced breeding lines entered into more recent USSRWWN trials, on average, exhibited increased yield potential and stability to provide optimism for wheat producers and the breeding programs that work to support them.

Supplemental Material
Supplemental material is available online for this article.

Conflict of Interest
The authors declare that there is no conflict of interest.

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References


