REVIEW ARTICLE

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Approaching 25 years of progress towards *Fusarium* head blight resistance in southern soft red winter wheat (*Triticum aestivum* L.)

Richard E. Boyles[1] | Carolina Ballén-Taborda[1] | Gina Brown-Guedira[2] |
Jose Costa[3] | Christina Cowger[2] | Noah DeWitt[4] | Carl A. Griffey[5] |
Stephen A. Harrison[4] | Amir Ibrahim[6] | Jerry Johnson[7] | Jeanette Lyerly[8] |
David S. Marshall[2] | R. Esten Mason[9] | Mohamed Mergoum[7] | J. Paul Murphy[8] |
Nicholas Santantonio[5] | Gautam Saripalli[3] | Russell Sutton[6] | Vijay Tiwari[3] |
David van Sanford[10] | Zachary J. Winn[9]

[1]Department of Plant and Environmental Sciences, Clemson University, Florence, South Carolina, USA

[2]Plant Science Research Unit, USDA-ARS SEA, Raleigh, North Carolina, USA

[3]Department of Plant Science and Landscape Architecture, University of Maryland, College Park, Maryland, USA

[4]School of Plant, Environmental and Soil Sciences, Louisiana State University, Baton Rouge, Los Angeles, USA

[5]Department of Crop and Soil Environmental Sciences, Virginia Polytechnic Institute and State University, Blacksburg, Virginia, USA

[6]AgriLife Research, Texas A&M University, College Station, Texas, USA

[7]Department of Crop and Soil Sciences, University of Georgia, Griffin, Georgia, USA

[8]Department of Crop and Soil Sciences, North Carolina State University, Raleigh, North Carolina, USA

[9]Soil and Crop Sciences Department, Colorado State University, Fort Collins, Colorado, USA

[10]Department of Plant and Soil Sciences, University of Kentucky, Lexington, Kentucky, USA

Correspondence
Richard E. Boyles, Department of Plant and Environmental Sciences, Clemson University, Florence, SC 29506, USA.
Email: rboyles@clemson.edu

Abstract

Tremendous progress has been made in variety development and host plant resistance to mitigate the impact of *Fusarium* head blight (FHB) since the disease manifested in the southeastern United States in the early 2000s. Much of this improvement was made possible through the establishment of and recurring support from the US Wheat & Barley Scab Initiative (USWBSI). Since its inception in 1997, the USWBSI has enabled land-grant institutions to make advances in reducing the annual threat of devastating FHB epidemics. A coordinated field phenotyping effort for annual germplasm screening has become a staple tool for selection in public and private soft red winter wheat (SRWW) breeding programmes. Dedicated efforts of many SRWW breeders to identify and utilize resistance genes from both native and exotic sources provided a strong foundation for improvement. In recent years, implementation of genomics-enabled breeding has further accelerated genetic gains in FHB resistance. This article reflects on the improvement of FHB resistance in southern SRWW and contextualizes the monumental progress made by collaborative, persistent, and good old-fashioned cultivar development.

KEYWORDS
breeding, Fusarium, genomics, prediction, resistance, wheat

1 | HISTORY OF *FUSARIUM* OUTBREAKS IN THE SOUTHEASTERN UNITED STATES AND THEIR IMPACTS ON REGIONAL WHEAT PRODUCTION

Descriptions of wheat production in 18th and 19th century America dealt primarily with cultivation methods, cultivar adaptation, the rusts (caused by *Puccinia triticina*, *Puccinia striiformis*, and *Puccinia graminis*), loose smut (caused by *Ustilago tritici*), and Hessian fly (*Mayetiola destructor Say*) (Ball, 1930; Gill, 1978). *Fusarium* head blight (FHB, caused by *Fusarium graminearum*) appeared absent or rare, although the crop was grown in close proximity to corn (*Zea mays*), and tillage methods likely left significant corn residue on the soil surface. A report from 1663 referred to wheat damaged by 'blast', but this could have referred to the impact of one or more biotic and abiotic stressors, not just scab (Flint, 1874). FHB was evidently frequent enough east of the Mississippi Valley in the 1930s to warrant inclusion in annual surveys (Dickson, 1942). Virginia and North Carolina recorded annual losses of 1360 to 2695 metric tons (50,000 to 99,000 bushels) from the disease, but these were relatively small compared to losses in Illinois, Indiana, and Ohio. While surveys did not extend into the entire southeastern US, annual losses of over 2177 metric tons (80,000 bushels) occurred in Texas.

During the 1990s, devastating outbreaks of FHB were observed in Minnesota and the Dakotas. Meanwhile, in the Southeast, FHB was sporadic and generally not considered a significant economic threat. In 1991, Arkansas, Kentucky, and other states in the region suffered enormous yield and quality losses due to FHB (McMullen et al., 1997). Arkansas was hard-hit again in 1996 along with Louisiana, possibly due to the amount of rice production in these two states. In southwestern Louisiana, the main rice-growing area of the state, producers were reluctant to grow wheat because of problems with FHB (S. Harrison, personal observation), which were likely attributable to the presence in rice fields of largely nivalenol-producing strains of *F. graminearum* and *F. asiaticum* (Gale et al., 2011). Elsewhere in the region, FHB was largely not on the wheat community's mind in the 1990s, although not completely absent; for example, naturally infected spikes were not difficult to locate in wheat fields across North Carolina in 1996 (Walker et al., 2001).

Then, in 2003, a major shift in disease presence and pressure occurred. A severe epidemic struck the Atlantic seaboard states from
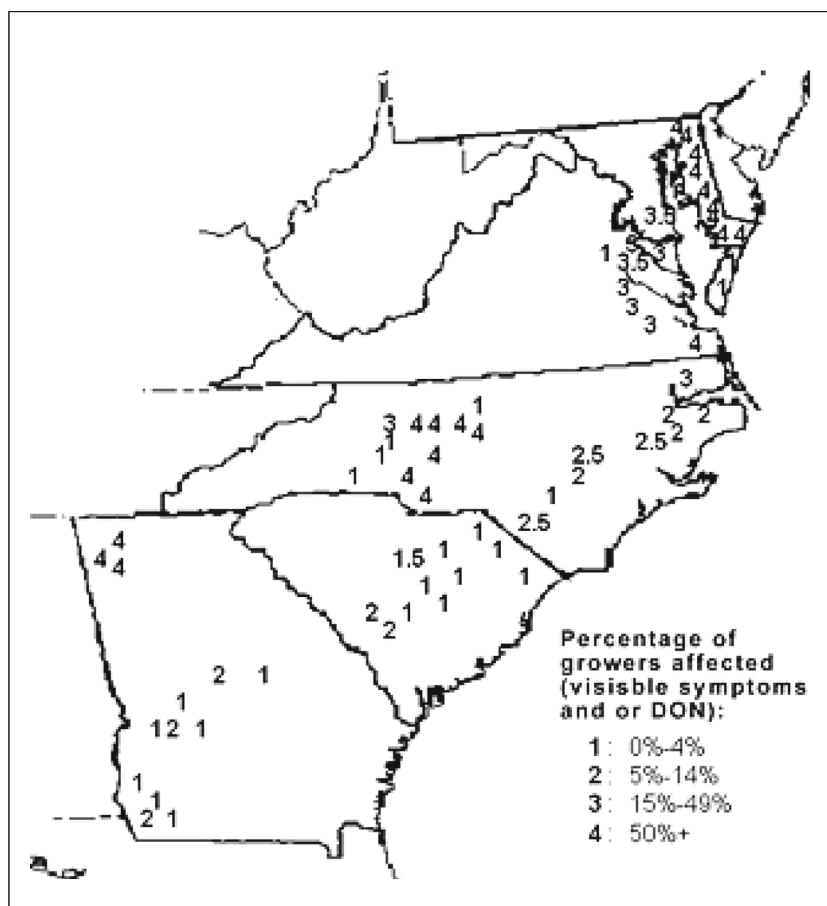
FIGURE 1 FHB distribution and estimated impact in the mid- and south-Atlantic United States in 2003. Reprinted by permission from Cowger and Sutton (2005), The Southeastern Fusarium head blight epidemic of 2003. Plant Health Progress, doi:10.1094/PHP-2005-1026-01-RS.

TABLE 1 FHB epidemic categories by state in the greater southeastern United States from 2003 to 2022. Epidemic severity was estimated by comparing contemporaneous accounts of damage to crops, geographic scale of effects, and degree of economic losses.

	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22
Delaware								A			S	M	L	L	L	A			A	L
Maryland	S							A	M	A	S	L	L	L	L	S	L	L	A	L
Virginia	S						S		A	A	S	M		L	L	M	M	M	A	L
Kentucky	S	S	A	L	L	A	S	L	S	A	L	S	A	A	A	L	M	L	M	M
Missouri									S			M	S	L	A	A	L	M	S	L
Tennessee							S				A	M			A	L	A	L	A	A
N. Carolina	S		L		M	S	S	A	A	A	M	M	M	M	L	L	A	L	A	A
S. Carolina	M								A	A									A	A
Georgia	M								A	A	A	S	S	S	L	A	S	L	A	A
Alabama									L		A	L		M					L	
Mississippi									L	A				L	A				A	A
Louisiana			L	A	A	A	A	A	A	A	A	M	S	S	S	A	L	L	L	L
Arkansas									L	A	A	M	S	L	L	A	L	A	L	L
Texas																			L	L

Note: S = severe, M = moderate, L = light, A = absent. Empty grey cells represent missing information.

Maryland to northern Georgia (Figure 1). Estimates put farmgate losses in 40 counties in Maryland, Virginia, and North Carolina at > $13.6 million, and those counties accounted for just 46%–72% of their respective states' wheat production, meaning that total 2003 FHB losses in those states were inevitably much higher (Cowger & Sutton, 2005). In that epidemic, grain purchasers suffered additional losses due to increased shipping, testing, and grain handling. The 2003 epidemic was also severe in Kentucky (Table 1).

The 2003 epidemic was early evidence that the damage done by FHB in the 1990s in the upper Great Plains and Midwest could occur elsewhere across the nation. The Southeast began learning about an unfamiliar and serious threat. From 2003 on, damaging FHB epidemics became an annual possibility: first in the northern states of the greater Southeast, which then diffused into southern states starting in 2014 (Table 1). For example, growers in the northeast corner of North Carolina reported deoxynivalenol (DON) levels of 3.6–15.2 ppm in loads of wheat they delivered to elevators in 2008 (C. Cowger, personal observation). In 2009, a large-scale FHB epidemic devastated producers in Virginia, North Carolina, Kentucky, and Tennessee, causing 40%–80% losses in susceptible wheat varieties. This same year, DON levels in Kentucky ranged from 2 to 20 ppm (D. Van Sanford, personal observation). Estimates for the 2009 epidemic in those four states totalled 19 million bushels lost (not counting abandoned acres), with a value of $102 million (C. Cowger, personal observation).

FHB struck in the southern tier of the Southeast region in 2014 (Table 1), robbing an estimated 5% of wheat yield in Georgia with a value of $4.3 million (A. Martinez, University of Georgia Extension, personal observation). Widespread severe FHB returned to Georgia in both 2015 and 2016, causing 5% and 8% yield loss in those 2 years, respectively, with a combined value of $4.85 million. Similarly, Louisiana experienced three consecutive years of severe FHB outbreaks starting in 2015. Yield and quality losses totalling 15%–25% of the Louisiana

wheat crop were attributed to FHB in the years 2015–2017. Missouri and Arkansas also suffered substantial losses due to FHB in 2014 and 2015. Largely in response to the severe epidemics they experienced in 2014–2017, growers by 2018 had slashed wheat area in Georgia, Arkansas, and Louisiana by 33%, 62%, and 91%, respectively.

To some extent, the timing of severe FHB-related losses in each state concurred with statewide planted corn area. The most outstanding example was Missouri, where corn area increased considerably in the 1990s, a trend not matched by other states in the region (Figure 2). Uncoincidentally, the University of Missouri was an early leader in developing FHB-resistant cultivars (further details below), although year-by-year information on FHB severity during that period in Missouri is unavailable. In the Deep South, the severe FHB epidemics that started in 2014 followed a 7-year period of increasing corn area in Georgia and an even greater increase in Louisiana. In other states, trends in corn area were not so clearly related to the frequency of severe FHB epidemics. For example, Kentucky, Tennessee, and North Carolina each saw a marginal decline in corn area between 1990 and 2006, although there were slight increases thereafter.

Together with generally increasing corn production, trends in tillage practices have likely played a role in making FHB a permanent fixture of southeastern US agriculture. During this period, more corn debris began to be left on the soil surface as growers embraced no-till and reduced-till planting of wheat. Nationwide, acres under reduced tillage increased 28% between 2012 and 2017 (USDA 2017 Census of Agriculture, https://www.nass.usda.gov/Publications/Highlights/2020/census-land-use-practices.pdf).

Throughout the region, multiple years of damaging epidemics were followed by the arrival of new resources and management approaches. Growers have increased adoption of variety resistance and FHB-targeted fungicides. This has led to a moderation in the severity of subsequent FHB epidemics, particularly observable

FIGURE 2 Planted corn area for the period 1990–2022 in (a) northern-tier states and (b) southern-tier states of the greater southeastern United States. Data from National Agricultural Statistics Service, USDA. [Color figure can be viewed at wileyonlinelibrary.com]
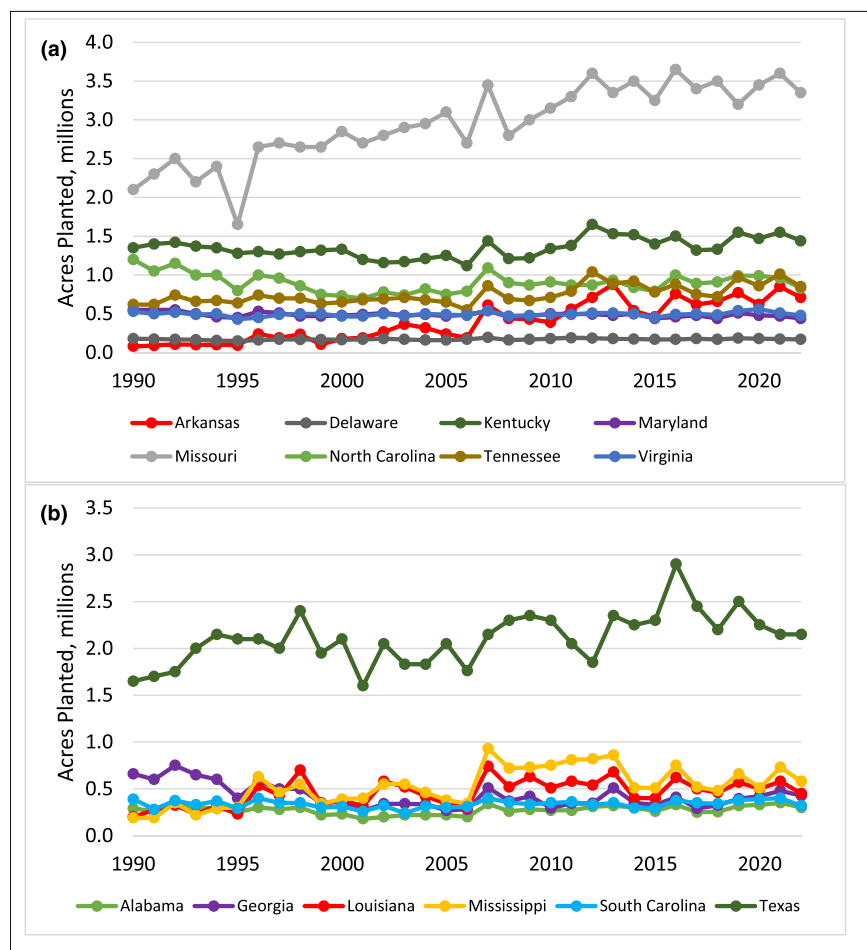
starting in 2017. Unconducive weather has likely also played a role, as La Nina has caused dry conditions in four of 6 years starting with 2016–2017 (https://ggweather.com/enso/oni.htm). With improved FHB management and rising wheat prices, wheat plantings have at least partially rebounded in states where they fell. Still, continued improvement of FHB resistance and commercialization of FHB- resistant cultivars will be imperative to retain soft red winter wheat (SRWW) in southeastern US cropping systems.

2 | EARLY SOURCES OF FHB RESISTANCE AND THEIR ADOPTION BY SOUTHERN SRWW BREEDING PROGRAMMES

Perhaps the first data on resistance to FHB in contemporary southern SRWW germplasm was from a Northrup-King yield trial under natural infection in Hopkinsville, KY, in 1990 (Collins et al., 1991). Although the data presented by Collins et al. (1991) represented a single location test with natural inoculation, there was a consistency in infections across heading dates, and the long-term susceptible check in the Southern Uniform Scab Nursery, 'Coker 9835' (PI 548846), was very susceptible in the test. In addition, 'Coker 9907' (PI 548847) was moderately resistant, and this variety served as a parent of 'NC-Neuse' (PI 633037; Murphy et al., 2004). Several moderate-effect FHB quantitative trait loci

(QTL) conferring partial resistance have been identified in the NC-Neuse haplotype, including *Qfhb.nc-1A*, *Qfhb.nc-4A*, and *Qfhb.nc-6A*. These QTL were validated in a separate population related to NC-Neuse (Petersen et al., 2016, 2017). Among these, *Qfhb.nc-1A* has consistently demonstrated a beneficial effect to reduce percent *Fusarium*-damaged kernels (FDK) and DON content in various SRWW backgrounds to signify partial FHB resistance, and presence of this QTL can be reliably predicted in early-generation material by implementing machine learning with genome-wide markers (Winn et al., 2022).

In total, nine of the 24 cultivars evaluated by Collins et al. (1991) were in the intermediate heading-date range and exhibited moderate resistance to FHB, with most of these originating from Coker's Pedigreed Seed Company, which had a large SRWW market share in the southern US at the time. In retrospect, there were probably more moderate-effect, partial-resistance QTL in the southern soft red germplasm than credited by breeders at the time, but a consensus prevailed that native resistance was sparse, and funding was limited to investigate this issue in depth. Only 5% of USWBSI funding was directed towards southern breeding programmes in 1999 (https://scabusa.org/db/documents.php). Due to the severity and regularity of FHB epidemics, accelerated improvement in resistance was desperately needed. As a result, moderate- to large-effect, partial-resistance QTL such as *Fhb1* (Waldron et al., 1999) were assigned higher priority, particularly as marker-assisted selection was being implemented on a large scale for the first time at the USDA-ARS

Eastern Regional Small Grains Genotyping laboratory (ERSGGL; Brown-Guedira et al., 2008; Van Sanford et al., 2001).

In Kentucky and the Mid-South, the first variety with *Fhb1* that was available to growers was Pioneer Brand 25R18 (WBGO195E2/2510//2510), released by Pioneer Hi-Bred in 1999 (Tamburic-Ilincic et al., 2006). WBGO195E2 was derived from Sumai 3, while '2510' was a late-maturing, high-yielding Pioneer wheat. After exceedingly severe FHB epidemics in the Mid-South in 1990 and 1991, concern over FHB ran high and grower adoption of this level of FHB resistance was unprecedented. Some breeders had concerns about linkage drag and yield penalty associated with *Fhb1* (Rollin Sears, personal communication, 2000), but initial evidence was anecdotal (refer to the 'Impact of Molecular Breeding …' section for empirical evidence of *Fhb1* linkage drag that was found just recently). In an elegant study using near-isogenic lines (NILs), Pumphrey et al. (2007) reported an average FHB reduction of 31% across 19 genetic backgrounds attributable to *Fhb1*. These authors, however, did not evaluate grain yield. Yield penalty aside, availability of reliable markers and the simplicity of dealing with a single gene led many breeders to begin incorporating *Fhb1* into their breeding programmes.

A critical effort that increased FHB resistance in SRWW was a collaboration among Dr. Jose Costa (University of Maryland), Dr. David Van Sanford (University of Kentucky), and USDA-ARS scientists to incorporate Chinese sources of resistance into adapted SRWW backgrounds. In 2003, three QTL were introgressed from spring wheat 'Ning 7840' using adapted high-yielding SRWW cultivars (Kang et al., 2011). Ning 7840 (PI 531188) was crossed with the SRWW 'McCormick' (Griffey et al., 2005), and then the F_1 was backcrossed to McCormick. Resulting BC_1F_1s were screened with several markers on chromosome 3B (*Fhb1*), 5A and 2DL. Moderately FHB resistant SRWW line 'KY06-11-3-10' was released from this stage by the University of Kentucky (Clark et al., 2014). Additional progenies possessing Ning 7840 resistant alleles at these QTL were crossed with 'SS 8641' to improve grain yield and quality (Johnson et al., 2007). Progeny lines from this pedigree that were homozygous for Ning 7840 resistance alleles at all three FHB QTL, plus alleles from SS 8641 indicative of the 1RS:1BL translocation from rye and the *Ae. ventricosum*-derived translocation on chromosome 2AS having resistance genes *Sr38/Lr37/Yr17*, were advanced to the F_5 generation in bulk, and several uniform head-rows with early-heading were selected and bulked for yield testing. Two lines (MDC07026-F2-19-13-1 and MDC07026-F2-19-13-4) that were high-yielding in consecutive regional nurseries have now been widely used by US Southern breeders.

It was during this same period that the cultivars 'Bess' (PI 642794) and 'Truman' (PI 634824) were released from the University of Missouri breeding programme (McKendry et al., 2005, 2007). These cultivars were adapted to the Mid- and Upper-South and possessed moderate native resistance. Truman was too late for growers who grew double-crop soybean immediately behind their wheat crop, and Bess did not shine in yield trials, but both were used heavily as parents in scab resistance breeding programmes. Their native resistance had not yet been resolved into QTL that could be tracked with markers, and thus they were less attractive than *Fhb1*. The QTL from

Bess were later validated by Petersen et al. (2017) as *Qfhb.nc-2B.1* and *Qfhb.nc-3B.2*, which are associated with reduced severity (*2B.1* and *3B.2*) and FDK (*2B.1*). Deployment of molecular markers for these QTL facilitated their incorporation into southern SRWW germplasm.

Shortly after the release of Bess, Virginia Tech released 'Jamestown' (PI 653731), an early-maturity, moderately FHB-resistant cultivar (Griffey et al., 2010). Originally, one large QTL region on chromosome 1B was identified in the Jamestown background; however, more recent research has uncovered two separate pericentromeric QTL (*Qfhb.vt-1B.1* and *Qfhb.vt-1B.2*) underlying resistance, which have been validated (Carpenter et al., 2020; Wright, 2014). An offspring of Jamestown, NC13-20076 (PI 700335) was identified as highly resistant, yet not positive for the Jamestown 1B haplotype (Murphy et al., 2017, 2016). A mapping study performed on a DH population found resistance QTL located on chromosomes 1A, 1D, 2B, 3B, 4B, and 5A; further, that research showed that of the QTL listed, *Qfhb.nc-1A*, *Qfhb.nc-1D*, *Qfhb.nc-3B*, and *Qfhb.nc-4B* significantly reduced FDK or DON accumulation (Winn, 2022).

3 | INCEPTION AND SIGNIFICANCE OF THE SOUTHERN UNIFORM WINTER WHEAT SCAB NURSERY (SUWWSN)

The USWBSI was formed in 1997 in response to severe FHB outbreaks across major productions regions of the United States in the 1990s. In October 1998, Congress approved $3.5M for the initiative in the 1999 Federal Fiscal Year (FY99) budget, which was immediately signed by the President; meanwhile, the inaugural National Fusarium Head Blight Forum was held in Minneapolis, MN in November 1998. Near this time, USWBSI executive and steering committees were assembled to allocate funds across the USDA Agricultural Research Service (ARS) and university programmes to combat the disease. In FY00, calls for proposals were solicited to ultimately fund $4.3M to 105 projects across 72 principal investigators and 24 institutions. Through this monumental effort of the USWBSI, the SUWWSN established a cooperative effort to evaluate breeding lines in the field with artificial inoculation and at a scale never before seen in the southern US. The SUWWSN was initiated in the 2000 growing season (Murphy et al., 2000). The nursery provided timely multi-state data on FHB resistance traits in advanced breeding lines, which were compared with the moderately resistant check cultivar 'Ernie' (PI 584525; McKendry et al., 1995) and the susceptible cultivar Coker 9835. The initial SUWWSN had 22 entries, including these two checks. Entries were submitted by Virginia Tech, NC State, Clemson, The University of Georgia, and Coker's Pedigreed Seed Company. Five locations returned data for FHB severity. The resistant check cultivar, Ernie, was not significantly better than Coker 9474 (PI 583357), 'Roane' (PI 612958; Griffey et al., 2001), or an NC-Neuse sib (NC96-13965).

The first use of molecular markers to determine the presence of *Fhb1* in nursery entries occurred in the 2001 SUWWSN (Murphy & Navarro, 2001). The subsequent role of the USDA-ARS ERSGGL in the development of scab-resistant germplasm cannot be

overemphasized; the facility now routinely provides wheat breeders information on more than 60 important QTL/genes, including nine directly related to FHB resistance (Lyerly et al., 2022; see 'Marker development and utilization for FHB resistance' for more details). The first inclusion of Chinese resistance sources was in the 2001 nursery in the form of entries from VA Tech possessing 'Yangmai 16' in their pedigrees (Murphy & Navarro, 2001). Yangmai 16 contains both QFhb.yaas-2DL and QFhb.yaas-3BL.

The first doubled haploid (DH) produced within the Southern CP (short for the Variety Development and Host Resistance Southern Winter Wheat Coordinated Project that is funded by the USWBSI) was entered by VA Tech in the 2002 SUWWSN. VA01W476 (also designated VA01-476) was developed by Jianli Chen and Carl Griffey from an F$_1$ using the corn pollination method. The pedigree of VA01W476 is CJ W14 (PI641164) X Roane. CJ W14 is a Chinese spring wheat containing Fhb1 and a resistance QTL on chromosome 5AS (Jiang et al., 2006). Roane is a SRWW with partial resistance to FHB (Griffey et al., 2001). VA01W476 was a very important parent in the initial development of FHB-resistant germplasm in the Southern region.

The 2003 SUWWSN saw the first inclusion of a series of lines from Gene Milus at the University of Arkansas with FHB resistance from 'Catbird', a spring wheat from CIMMYT containing a resistance QTL on 7D (Cativelli et al., 2013). These Arkansas lines were used as parents across the region over the next few years. The number of entries in the 2005 SUWWSN increased to 48, among them entries from Romania, and data were returned from up to nine field locations including Hungary and Romania in addition to the standard US locations (Murphy & Navarro, 2005). Pedigrees of entries indicated that sources of FHB resistance came from the US soft red, Chinese, Mexican and European gene pools. Four of the 36 entries contained Fhb1 and three contained Qfhs.ifa-5A from Ning 7840 in the 2006 nursery (Murphy et al., 2006). In the late 2000s, Bess and Jamestown (see above section for cultivar details) were added as moderately resistant checks in the SUWWSN because both cultivars were being used extensively in crossing programmes (Murphy & Navarro, 2008).

In 2011, the SUWWSN reached 60 entries for the first time, submitted by eight public and two private programmes (Murphy & Navarro, 2011). Pedigrees of entries included resistant lines from Brazil (i.e., 'Frontana' [PI 500147]) and China as well as native-resistance cultivars including: Ernie, Truman, 'Freedom' (PI 562382; Gooding et al., 1997), Jamestown, McCormick, NC-Neuse, and from Brazil, plus familiar Chinese sources. Diverse, native sources of resistance were showing up at a great frequency in advanced-generation lines from numerous programmes, sometimes in combination with non-native sources.

The 2012 SUWWSN saw the entry of a series of lines from Jose Costa at the University of Maryland (Murphy & Navarro, 2012). These entries had pedigree combinations involving Ning 7840, McCormick, and Southern States 8641 (GA 96229-3A41; 'SS 8641'), contained Fhb1, and had competitive yields. These lines served as popular parents over several years in the region. The 2012 nursery also saw the introduction of a series of doubled haploid lines developed at NC State. These frequently contained Fhb1 and/or other exotic sources of resistance combined with native sources and were designed to speed up the integration of Fhb1 into more competitive-yielding backgrounds. The 2014 nursery contained lines from NC State such as NC11-22289 with the 'Coker 9511' native resistance (Murphy & Petersen, 2014). It exhibited some of the best levels of scab resistance in the nursery and contained no previously named resistance QTL. It was widely used as a parent in the region over the next few years.

The 2016 SUWWSN saw eight programmes contributing lines including two new private companies in the region, KWS and Limagrain Cereal Seeds (Murphy et al., 2016). In addition, the nursery database was increased annually to provide an update on the presence and impact (i.e., efficacy) of established FHB resistance QTL in nursery entries. This facilitated marker-assisted selection by pinpointing the QTL that had the greatest impact on resistance in SRWW germplasm.

The 2017 SUWWSN report contained the first genomic predictions of FHB resistance for entered lines, and genomic estimated breeding values (GEBVs) were tested for accuracy against observed multienvironmental means (Murphy et al., 2017). The training population was created using curated historical data from the 2011–2016 uniform FHB nurseries. Accuracy estimates provided an annual evaluation of this FHB resistance training population being utilized in the region. Correlations between predicted measures and multi-environmental means ranged from .44 for DON to .59 for severity, demonstrating the potential usefulness of applying genomic prediction for FHB resistance improvement. The 2017 nursery also provided the first output from PopVar (Mohammadi et al., 2015) to enhance efficiencies in parental selection among nursery entries. PopVar uses genome-wide marker data on potential parent lines to determine optimal cross combinations that maximize the number of resistant progeny by predicting both population mean and genetic variance for each biparental cross. In the 2017 PopVar output, the top 25% of proposed crosses for severity included entries from nine different programmes, suggesting that a diversity of resistance genes remained across SRWW breeding programmes.

The SUWWSN has played a central role in the development of FHB-resistant germplasm in the region. As a testament, average levels of FHB resistance among entries have increased significantly over time and entries contain a diversity of resistance factors each year. For example, only 11% of entries in the initial 2000 SUWWSN were statistically similar to the resistant check Ernie in FHB severity (Murphy et al., 2000). In contrast, 77% of entries in the 2022 nursery were statistically similar to Ernie for FHB rating (Lyerly et al., 2022). Further, the average narrow-sense genomic heritability across locations that reported both FDK and DON from the years 2010–2019 in the SUWWSN was .73 DON and .78 for FDK (Winn et al., 2023). Thus, the SUWWSN was and remains a critical tool for generating high-quality data and for tracing the development of FHB-resistant germplasm over numerous programmes in the region. Currently, the USWBSI funds 12 projects (eight southeastern US soft red winter wheat breeding programmes) through the Variety Development and Host Resistance Southern Soft Winter Wheat Coordinated Project.

Phenotypic data as well as marker information from these annual nurseries can be found within published SUWWSN reports available at https://scabusa.org/research_vdhr-sww.

4 | OBJECTIVE EVALUATION OF FHB RESISTANCE TRAITS THROUGH IMAGING AND PHENOMICS

With the advent of high-throughput phenotyping derived from image analysis, there has been a great interest in reducing bias in visual ratings and increasing productivity through the assistance of trained machine-learning algorithms. It is well understood that there is significant person-to-person variation in rating disease incidence and severity (Bock et al., 2020); thus, there is a shared desire among FHB researchers to automate and improve rating consistency. Visual ratings of FHB severity and incidence are often taken in the field during grain-fill to obtain an estimate of a line's resistance to FHB. This trait, however, can be quite daunting to phenotype due to the interplay between disease progression, maturation of the wheat plant, and how easily resistance may be confounded with lateness and height of lines (Klahr et al., 2007). Several studies have attempted to automate FHB visual ratings (Gu et al., 2020; Huang et al., 2019; Jirsa & Polišenská, 2014; Zhang et al., 2019); however, their throughput and sampling parameters may not be amenable to practical implementation in a breeding programme. Methods to detect visual FHB symptoms via multispectral and hyperspectral unoccupied aerial vehicle (UAV) technology have also been suggested (Francesconi et al., 2021; Liu et al., 2020) because they are easily collected and non-destructive. As such, the throughput of UAV phenotyping of FHB field ratings may allow/warrant its adoption in breeding programmes, further research is needed to compare accuracy with manual field ratings and downstream FHB phenotyping methods explained hereafter.

A trait highly correlated with DON is a visual rating of percent FDK—the percentage of a subsample that visually appears damaged by FHB infection. The generally accepted method for assaying percent FDK involves visual comparison of FHB infected kernels to a range of standards that have been counted and measured for the ratio of damaged kernels to healthy kernels (Jirsa & Polišenská, 2014). While having standards available for reference reduces bias, it does not eliminate it. Thus, there have been many studies involving automation of percent FDK data collection.

Preliminary studies of FDK automation focused on processing simple red-blue-green (RGB) spectral images of scabby kernels through software and assessing the correlation of the number of scabby kernels with indices derived from image processing (Jirsa & Polišenská, 2014; Maloney et al., 2014). Maloney et al. (2014) demonstrated that spectral reflectance of RBG analysed through an ImageJ algorithm had a moderately high correlation with manually counted scabby seeds out of a sample. Furthermore, Maloney et al. (2014) indicated that the digital image analysis they implemented was many times faster than manual counting (53 images analysed per hour vs. 18 samples manually counted per hour). This further stimulated

interest in automation of FDK data collection. More recent methods have employed the use of multispectral and hyperspectral cameras, in conjunction with machine learning, to estimate FDK from images (Ackerman et al., 2022; Delwiche et al., 2019). Ackerman et al. (2022) showed that images analysed using the Vibe QM3 (Vibe Imaging Analytics, Capitola, CA) produced ratings with the highest broad-sense heritability in comparison to manually counting seeds and using standards to estimate FDK. Furthermore, Ackerman et al. (2022) found that FDK scored using the Vibe QM3 platform had a stronger correlation with DON content than either visual scoring or manually counting FDK. Breeding programmes have even leveraged optical sorting instrumentation to recognize and subsequently eliminate FDK in bulk-selected grain and therefore successfully decreased the percentage of FHB-susceptible genotypes in the subsequent generation (Carmack et al., 2019).

While visual FHB resistance scoring on spikes in the field or harvested kernels remains a tool in wheat breeding programmes, the ultimate objective of breeders is to reduce DON content. Deoxynivalenol concentration in contaminated grain samples remains the gold standard of quantifying FHB resistance in wheat. Through funding by the USWBSI, DON testing laboratories using gas chromatography–mass spectrometry to quantify mycotoxin levels were established or made available in strategic wheat regions to breeding programmes (Khatibi et al., 2012; Mirocha et al., 1998). As a result, multiyear and multilocation DON data collected from misted, inoculated nurseries have enabled a robust training population for genomic prediction (Larkin et al., 2020; Verges et al., 2020). This coordinated phenotyping effort paved the way for accelerating progress on FHB resistance through molecular breeding strategies. It still serves as a major asset by screening new sources of FHB resistance, confirming estimated resistance (or susceptibility) from genomic predictions, and selecting early-generation lines from segregating populations. Deoxynivalenol content is not limited by its accuracy but rather by its cost and time constraints. Because of high cost and low throughput, measuring DON content is common only at the end of the breeding process (i.e., advanced or elite lines).

Typically, the common way to predict DON content in early lines is using genomic estimated breeding values (GEBVs) generated by genomic prediction models (Gaire et al., 2022; Rutkoski et al., 2012). Gaire et al. (2022) demonstrated that inclusion of FDK as a covariate in multivariate genomic prediction models significantly increased ability to predict DON, which may indicate that the use of high-throughput image analysis techniques to generate FDK proxy traits can aid in prediction of DON as well. While genomic prediction remains the standard for DON prediction, it does not often incorporate or rely on spectral covariates, and, from this review, it appears that minimal work has been done on estimating DON content from visual analysis of grain samples prior to milling.

While directly estimating DON from high-throughput visual analysis of kernels prior to milling has eluded study thus far, a newer field of phenomic prediction has slowly come to prominence. Phenomic prediction is the use of spectral information derived from plants to capture relationships among individuals and produce an estimated

breeding value from a training population and spectral information on a candidate panel (Rincent et al., 2018; Robert et al., 2022). This method has been shown so far to produce comparable results to genomic selection for grain yield and heading date in wheat, several wood quality traits in poplar (*Populus grandidentata*), and grain yield in corn (Lane et al., 2020; Rincent et al., 2018). Perhaps a useful future direction for prediction of DON from image analysis could be through phenomic prediction of DON.

5 | IMPACT OF MOLECULAR BREEDING TO ACCELERATE IMPROVEMENT OF FHB RESISTANCE

The potential of genomics-assisted improvement of FHB resistance was a driving force for the establishment of USDA-ARS efforts in small grains genotyping. It was the identification of the *Fhb1* locus of relatively large effect, and the hope to identify more such loci, that ignited the push for federal resources for marker-assisted breeding in support of public cultivar development efforts (Van Sanford et al., 2001). In addition to conferring resistance to a (1) difficult to breed for, (2) environmentally sensitive, and (3) economically damaging disease, alleles of flanking simple sequence repeat (SSR) markers from an unadapted source were rare in North American germplasm (Liu & Anderson, 2003), contributing to the successful marker-assisted introgression of *Fhb1* as noted below. By late 2004, the ERSGGL was being established in the Plant Science Research Unit in Raleigh, NC with a focus on FHB resistance.

Initial *Fhb1* introgressions consisted of a relatively large region from unadapted sources (e.g., Sumai 3). Fine mapping efforts, resulting in development of closely linked SNP markers (Cuthbert et al., 2006; Liu et al., 2006) and cloning of *Fhb1* candidate genes (Liu et al., 2008; Su et al., 2019), have provided more accurate markers amenable to high-throughput genotyping using Kompetitive Allele Specific PCR (KASP) approach. Since 2008, the ERSGGL has developed publicly available marker reports for FHB and additional traits on advanced nurseries and the SUWWSN, which can be found at https://www.ars.usda.gov/southeast-area/raleigh-nc/plant-science-research/docs/small-grains-genotyping-laboratory/regional-nursery-marker-reports/cooperative-uniform-winter-wheat-scab-nurseries/. Marker-assisted selection of stable FHB resistance QTL served and continues to serve as an important complementary tool to phenotypic selection in inoculated nurseries. Year-over-year MAS provided a reliable approach to consistently increase the frequency of resistance alleles, especially in seasons when environments were not conducive to high disease pressure.

Poorly adapted potential sources of *Fhb1*, including Sumai 3 and lines developed from Sumai 3 by breeding programmes in regions outside the southeastern US, prompted a marker enrichment topcross programme spearheaded by Dr. Carl Griffey at Virginia Tech. F_1 plants derived from a (relatively) adapted *Fhb1* donor and an adapted southern SRWW line were top-crossed to an additional adapted parent, resulting in genetically heterogeneous F_1 progeny segregating for

Fhb1. Tissue was collected from 3-way F_1 seedlings, sent to the ERSGGL for marker analysis, and individual plants were selected based on *Fhb1* and other QTL marker calls. Selected seedlings were vernalized and transported for DH population development. This project facilitated the introgression of *Fhb1* into material adapted to the southeastern US, resulting in both *Fhb1*-containing parental lines and direct cultivar releases (e.g., 15VDH-FHB-MAS33-13, 15VDH-FHB-MAS38-01, and GA15VDH-FHB-MAS23-18LE43F [AGS 4043]). This effort continues, with the goals of further increasing the frequency of *Fhb1* in breeding populations (Figure 3) and potentially introducing additional exotic FHB QTL (e.g., *Fhb7*).

Advances in wheat genomics beyond use of microsatellite or SSR markers were necessary for the identification and deployment of QTL for resistance in regionally adapted germplasm. As the new highly parallel multiplex genotyping platforms including Diversity Array Technologies (DArT; Akbari et al., 2006), Illumina Infinity platforms allowing for genotyping of 9000 and 90,000 SNP variants (Wang et al., 2014) as well as two-enzyme complexity reduction genotyping-by-sequencing approaches became available (Poland et al., 2012), they have been used for construction of linkage maps for QTL analysis (Buerstmayr et al., 2009) and GWAS (Arruda et al., 2016; Ghimire et al., 2022). Contextual sequences have been used to develop KASP assays flanking these QTL for use in MAS and germplasm evaluation, and marker haplotypes have been used to predict the presence of QTL. Since the first reports on presence of *Fhb1* in nursery entries in 2001, numerous marker assays have been developed and deployed to track resistance alleles in early-generation and elite lines (Winn et al., 2022). Since 2016, GBS technology has been used to identify thousands of DNA variants in the southern FHB nurseries, including previous year's entries for which phenotypic information was available in unbalanced multiyear, multilocation datasets. This resource has been instrumental for developing training populations for the application of genomic selection for FHB resistance, as noted below. Recently, marker calls for presence of resistance loci, large
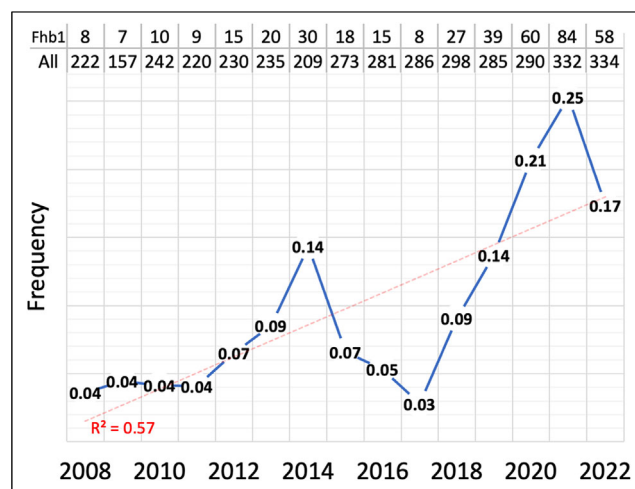
FIGURE 3 Frequency of Fhb1 in southern SRWW cooperative nurseries. [Color figure can be viewed at wileyonlinelibrary.com]

genome-wide marker datasets and phenotypic data have been used in combination with machine learning approaches to predict QTL presence in thousands of early-generation lines (Winn et al., 2022) and to validate marker effects. Specifically, this approach was used to provide QTL estimates for scab in the more than 3000 lines that were genotyped-by-sequencing in 2021, primarily for genomic prediction. Forward-validation accuracies for estimating QTL presence were as high as .85 for *Qfhb.nc-1A*, .98 for *Qfhb.vt-1B*, .89 for *Qfhb.nc-4A*, and .97 for *Fhb1* (Winn et al., 2022). Incorporating this machine learning approach to predict QTL affects both time and cost, since estimates of the presence of QTL can be obtained earlier in the breeding pipeline and methods capitalize on investments already committed to genotyping. This approach has been expanded to include QTL estimates for additional FHB QTL and other disease and insect resistance traits.

Historical data for FHB partial-resistance QTL were used to assess potential yield drag for several moderate effect QTL across three major southern SRWW production environments (Ballén-Taborda et al., 2022). The three resistance QTL selected were *Qfhb.nc-1A*, *Qfhb.vt-1B*, and *Fhb1* based on their utilization/efficacy and mix of native (1A and 1B) and exotic (*Fhb1*) sources. The frequencies of *Qfhb.nc-1A*, *Qfhb.vt-1B*, and *Fhb1* in the SRWW breeding pool were 23.8%, 34.3%, and 7.3%, respectively. While lines with either native QTL (*Qfhb.nc-1A* or *Qfhb.vt-1B*) yielded on par with FHB-susceptible lines, *Fhb1* lines demonstrated lower grain yield than non-*Fhb1* lines; however, the yield difference was only significant in the Gulf region (AR, LA, and eastern TX). This finding suggests some linkage drag likely persists, albeit to a much smaller extent than once present, with the *Fhb1* introgression from Sumai 3. This effort to assess QTL-by-environment interaction will be expanded to much larger SRWW populations using the machine-learning QTL prediction method recently developed by Winn et al. (2022).

6 | PURGING OF FHB SUSCEPTIBILITY (S) GENES AND REMOVING LINKAGE DRAG FROM AGRONOMICALLY FAVOURABLE QTL

Since economic losses due to FHB are expected to increase (Luck et al., 2011), it is important to explore alternative approaches to further enhance resistance (Rawat et al., 2016; Kazan & Gardiner, 2018; H. Wang et al., 2020). The concept of S genes, or S factors, was defined in 2002 (van Schie, 2014; Vogel et al., 2002). Susceptibility genes in plants facilitate successful pathogen infection, and their manipulation can make plants resistant to pathogens and offer a transformative alternative to developing resistant cultivars (Eckardt, 2002; van Schie, 2014; Vogel et al., 2002). An excellent example of an S gene is the Barley *mlo* gene. It is a loss-of-function mutation providing broad-spectrum resistance against powdery mildew. It is a classic example of a susceptibility factor used for over 35 years in many plant species (Acevedo-Garcia et al., 2017; Büschges et al., 1997; Garcia-Ruiz et al., 2021).

The first documented evidence of S genes in wheat came from Ma et al. (2006), as this study showed that ditelosomic lines lacking in specific chromosome arms suggested enhanced resistance to *F. graminearum* infection. Usually, S genes work as dominant genes in wild-type plants, and their deletion/loss-of-function mutations can lead to recessive resistance (Pavan et al., 2010). Garvin et al. (2015) further showed that deletion of 19% of the chromosome 3DL arm increases FHB resistance (Garvin et al., 2015). A more recent study by Hales et al. (2020) reported that deletion of a 32-Mb region on chromosome 4D significantly increased FHB resistance while (Chhabra, Singh, et al., 2021) later identified a major and conserved S factor or gene on wheat chromosome 7A localized in a 40-Mb region. These studies indicate that engineering S genes using a precise and efficient gene-editing approach has great potential to enhance FHB resistance in wheat (Garcia-Ruiz et al., 2021; Zaidi et al., 2018). However, there are some challenges involved while imparting resistance through loss of function mutations/deletions in S-genes and these challenges or pitfalls are mostly reflected in terms of reduced yield and/or plant growth (Langner et al., 2018). In the case of barley *mlo* alleles, spontaneous callose deposition (papillae) and spontaneous cell death was observed in mesophyll cells in the absence of pathogens. Some susceptibility against other pathogens like blast fungus *M. oryzae* was also observed in the barley plants carrying *mlo* alleles (Kumar et al., 2001). Such pitfalls could be circumvented by precise genome editing strategies as demonstrated in rice where multiple S-genes were edited to engineer broad-spectrum resistance (Tao et al., 2021; for more details, see review by Zaidi et al., 2018).

With this stated, knowledge remains limited about S genes in wheat and their potential to increase FHB resistance (Chhabra, Tiwari, et al., 2021; Fabre et al., 2020; Hales et al., 2020). However, wheat TILLING populations and their forward genetic screening suggest an exciting route to perform genome-wide discovery of novel S genes (Chhabra, Singh, et al., 2021). In the study by Chhabra, Tiwari, et al. (2021), the authors screened a highly susceptible winter wheat EMS-induced TILLING population of cultivar 'Jagger', and repetitive phenotypic validations of mutant phenotypes allowed them to identify 12 different phenotypic mutants. The identification of these phenotype-associated base-pair changes through MutMap (Abe et al., 2012) or MutMap+ (Fekih et al., 2013) approaches could identify QTL or candidate genes that can be introduced into adapted SRWW germplasm.

An ancillary avenue for improving predictions for FHB relies on a better understanding of the underlying mechanisms of resistance. Resistance QTL that act through secondary traits may only be useful in certain environments or genetic background. An example of this are QTL that improve FHB resistance through altering anther extrusion, which have proven effective in southern SRWW. Similarly, earlier-heading lines tend to display increased susceptibility to FHB, and mapping studies often find overlap between mapped QTL for heading date and FHB resistance (Gervais et al., 2003; He et al., 2016; Schmolke et al., 2005); however, when individual plots are inoculated at anthesis, this association disappears (Buerstmayr et al., 2000), suggesting that this relationship results from timing of exposure of heads to inoculum and the environmental conditions experienced by plants relative to anthesis. Modelling approaches that adjust for heading date

as a covariate or in a multi-trait model when mapping FHB QTL or predicting line resistance may improve power and reduce unintended effects on heading when selecting on FHB. By considering heading date, QTL that affect FHB resistance and not heading can be identified and estimates of a given line's FHB merit independent of maturity can be made (Moreno-Amores et al., 2020).

Plant height is another important secondary trait that is perceived to confound FHB resistance. A decrease in mature plant height may bring wheat heads closer to the soil surface and increase exposure of plants to rain-splashed pathogens. Recent work however has suggested a link between plant height reduction and increased FHB susceptibility primarily as a result of using green revolution genes *Rht-B1* and *Rht-D1*, and not as a general relationship between the two phenotypes (Akohoue et al., 2022; Srinivasachary et al., 2008; Voss et al., 2008). Both homeologous copies of *Rht1* encode DELLA proteins that, beyond their role in directly regulating the gibberellic acid response, additionally interact with signalling pathways implicated in plant response to biotic stress (Navarro et al., 2008). Other research has implicated closely linked S factors on the group 4 chromosomes in the apparent effect of the *Rht1* genes on FHB (He et al., 2016; Thambugala et al., 2020). If the association between plant height and FHB susceptibility is largely driven by the specific interactions of the *Rht1* genes, other common plant height genes such as *Rht8* on 2D, *Rht24* on 6A (Herter et al., 2018; Miedaner et al., 2022), and *Rht25* on 6A may be used to breed plants of short stature that have better baseline FHB resistance, potentially from reduced linkage.

7 | IMPLEMENTATION OF GENOMIC SELECTION FOR FHB RESISTANCE

Because host resistance to FHB is genetically complex and quantitative, genomic prediction provides an avenue to make genetic gains in the absence of known causal genes or resistance pathways. Genomic selection allows for the calculation of predictions about the performance of breeding material, before it is evaluated in the field, using high-throughput genotyping, marker data, and statistical modelling (Meuwissen et al., 2001). Genomic selection is a valuable tool for breeders to gain insight into the value of individuals with limited information, and to assist with decisions about advancement, product development, and potential parents to include in crossing programmes. It has become widely used for improvement of FHB resistance in wheat (Arruda et al., 2015; Ballén-Taborda et al., 2022; Gaire et al., 2022; Larkin et al., 2020; Verges et al., 2020). Severity, FDK, and DON are desirable targets for prediction due to the labour and cost associated with phenotyping these traits.

In 2017, SUWWSN collaborators began a joint project in conjunction with the ERSGGL to explore the impact of incorporating genomic selection into wheat breeding programmes. Historical SUWWSN data collected from 2011 to 2016 was curated to create an initial training population. Historical data sets are a rich resource for genomic selection, as they are frequently comprised of quality data for traits of interest over a range of environments (Boyles et al., 2019), and

studies have demonstrated their utility in genomics-assisted breeding (Dawson et al., 2013; Rutkoski et al., 2015; Sarinelli et al., 2019; Storlie & Charmet, 2013; Verges et al., 2020). Research has examined various strategies for optimizing training populations based on genetic relationships, population size and structure, marker density and significance, heritability, and environment similarity (Berro et al., 2019; Lozada et al., 2019; Norman et al., 2018; Verges et al., 2021). In the SUWWSN, environments were selected for inclusion based on biplot analysis and performance of the resistant and susceptible check varieties in a given location and year. Data quality is critical for success, and curation to remove poor-quality data where heritability is low or check varieties are poorly distinguished can have a positive impact on prediction accuracy (Winn et al., 2023).

As described above, the SUWWSN training population has been updated with data each year since inception, and genomic predictions have been provided to breeders for multiple traits including severity, FDK, and DON. In the first year, around 2900 lines were submitted for GS from university breeding programmes in the Southeastern University Small Grains Breeding Cooperative (SunGrains; Harrison et al., 2017). By 2022, over 20,000 SunGrains lines and nearly 3000 advanced nursery lines had been analysed via the genomic selection pipeline. Predicted values are correlated each year with observed multi-environmental means for each trait to generate a measure of accuracy and evaluate the performance of the training population over time. Accuracy for DON has remained stable; however, increases have been observed in accuracy for FDK ($+0.08$) and severity ($+0.13$) from 2017 to 2022 (https://scabusa.org/research-reportspublications). Exploring methods to increase the accuracy of predictions is a continuous, iterative process. Including significant markers as fixed effects in prediction models and selecting markers based on GWAS analysis has achieved some success in improving prediction accuracy (Larkin et al., 2020; Lozada et al., 2019; Verges et al., 2020; Verges et al., 2021). Cluster analysis to select environments for training population construction has also been shown to improve prediction accuracy for FDK and DON (Winn et al., 2023) and provide additional support concerning decisions about including the highest-quality data.

8 | FURTHER LEVERAGING GENOMIC SELECTION TO ACCELERATE CULTIVAR DEVELOPMENT

Collectively, SunGrains and collaborating programmes have generated a data set and workflow for implementing genomic selection in real-world breeding programmes. Past efforts initially focused on assignment of genetic value to later-stage individuals for their use as parents for germplasm sharing and final advancement. Today, breeders are increasingly using predictions as a selection tool to advance early-stage material (e.g., first-year observation lines) into multistate yield trials. As sufficient information is collected in related germplasm and prediction accuracies are validated, we expect programmes to leverage GEBVs to best select and recycle preliminary lines as parents, which can increase genetic gain through a reduction in cycle time.

To enhance the utility of predictions in earlier generations, studies should now assess the feasibility of genotyping greater numbers of plants, reducing generation time, and accelerating the average rate of genetic gain. While many studies have shown the benefits of reducing generation time in simulations (Bernardo, 2020; Sabadin et al., 2022), evaluation of real-world efficacy will rely on understanding the costs of restructuring breeding programmes to handle increased labour, the efficacy of within-family predictions using models trained on historic data, and increased genotyping costs associated with greater sampling. As lines are selected earlier in the breeding programme pipeline, a greater emphasis will be placed on within-family than among-family selection. The relative efficacy of a given genomic selection model on predicting within-family relies on the genetic architecture of the considered trait and the population structure and diversity of the training population (Werner et al., 2020). Genomic selection models for yield trained on historic SunGrains trials have improved prediction accuracy relative to pedigree best linear unbiased prediction (BLUP), models but have little to no predictive power within crosses (Sarinelli et al., 2019; Unpublished data). 'Test-and-shelf' genomic selection approaches, where custom training populations consisting of subsets of one or multiple related families are used to predict the entirety of a genotyped but unobserved family, may be considered as one approach for selecting the best individuals out of high-value families. Use of large numbers of full or half-sibs as a training population for prediction of the same families maximizes within-family genomic prediction accuracy (Lehermeier et al., 2014; Würschum et al., 2017). This approach can be complemented with the use of DHs to rapidly generate a training population for a larger population of single-seed descent. The greatest improvements in yearly genetic gain may come from using genomic predictions to recycle families back into the crossing block at an earlier generation, with minimal within-family selection, effectively partitioning programmes into population improvement and cultivar development components (Merrick et al., 2022). Understanding the ability of current FHB training population approaches to make accurate selections at early generations, and if necessary, altering training population structure or developing alternative models, will be necessary to make the next jump forward and reduce overall cycle time.

9 | CONCLUSION

Exceptional progress in development and release of cultivars with improved resistance has been made over the past 25 years in the southeastern United States. This is underscored by the increasing number of lines entered in the SUWWSN that annually demonstrate FHB resistance that is equal to or greater than resistant checks (77% in 2022), as well as the recent dearth in regional FHB outbreaks. It was early identification and adoption of native FHB resistance QTL that drew a roadmap to achieving moderate resistance levels and avoiding catastrophic FHB losses. This identification of FHB-resistant sources, particularly native sources, was greatly facilitated by

dedicated field screening led by established regional breeding programmes, which would not have been feasible without committed year-over-year support from the US Wheat & Barley Scab Initiative. Other key efforts such as introgression of exotic, major-effect FHB QTL (i.e., *Fhb1*) are now paying off as recent SRWW releases possess elevated FHB resistance while retaining exceptional agronomic performance. At the same time, it is important to acknowledge that effective fungicides, which were nonexistent in the 1990s, can now play a supportive role in management of FHB. And, while the SRWW community appears in a good place to thwart FHB epidemics in the near-term, breeders are not getting complacent. Multifaceted approaches—using inoculated nurseries, marker-assisted selection, and genomic prediction—are now entrenched within the southern breeding community to continue combining favourable alleles from exotic FHB sources for improved resistance while eliminating deleterious mutations causing yield drag. Meanwhile, new efforts such as leveraging mutant populations to purge FHB susceptibility genes are underway to further advance resistance levels. On a related note, as genomic selection models begin to utilize environmental data to predict plant performance as a function of target environment(s) conditions, outcomes from this approach may improve our ability to deploy FHB-resistant cultivars to more specific production regions. After all, FHB resistance improvement must work within the greater confines of desirable agronomics and superior productivity. Thus, breeding programmes that are dedicated to making simultaneous genetic gains across this array of traits are essential to supporting the long-term production of safe, quality wheat.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data referenced in this review are openly available at https://scabusa.org/research_vdhr-sww, specifically Uniform Southern Soft Winter Wheat Scab Nursery reports.

ORCID

Richard E. Boyles https://orcid.org/0000-0003-1366-7659

REFERENCES

Abe, A., Kosugi, S., Yoshida, K., Natsume, S., Takagi, H., Kanzaki, H., Matsumura, H., Yoshida, K., Mitsuoka, C., Tamiru, M., Innan, H., Cano, L., Kamoun, S., & Terauchi, R. (2012). Genome sequencing reveals agronomically important loci in rice using MutMap. *Nature Biotechnology*, 30(2), 174–178. https://doi.org/10.1038/nbt.2095

Acevedo-Garcia, J., Spencer, D., Thieron, H., Reinstädler, A., Hammond-Kosack, K., Phillips, A. L., & Panstruga, R. (2017). Mlo-based powdery mildew resistance in hexaploid bread wheat generated by a non-transgenic TILLING approach. *Plant Biotechnology Journal*, 15(3), 367–378. https://doi.org/10.1111/pbi.12631

Ackerman, A. J., Holmes, R., Gaskins, E., Jordan, K. E., Hicks, D. S., Fitzgerald, J., Griffey, C. A., Mason, R. E., Harrison, S. A., Murphy, J. P., Cowger, C., & Boyles, R. E. (2022). Evaluation of methods for measuring Fusarium-damaged kernels of wheat. *Agronomy*, 12(2), 532. https://doi.org/10.3390/agronomy12020532

Akbari, M., Wenzl, P., Caig, V., Carling, J., Xia, L., Yang, S., Uszynski, G., Mohler, V., Lehmensiek, A., Kuchel, H., Hayden, M. J., Howes, N., Sharp, P., Vaughan, P., Rathmell, B., Huttner, E., & Kilian, A. (2006). Diversity arrays technology (DArT) for high-throughput profiling of the hexaploid wheat genome. *Theoretical and Applied Genetics*, 113(8), 1409–1420. https://doi.org/10.1007/s00122-006-0365-4

Akohoue, F., Koch, S., Plieske, J., & Miedaner, T. (2022). Separation of the effects of two reduced height (Rht) genes and genomic background to select for less Fusarium head blight of short-Strawed winter wheat (*Triticum aestivum* L.) varieties. *Theoretical and Applied Genetics*, 135(12), 4303–4326. https://doi.org/10.1007/s00122-022-04219-4

Arruda, M. P., Brown, P., Brown-Guedira, G., Krill, A. M., Thurber, C., Merrill, K. R., Foresman, B. J., & Kolb, F. L. (2016). Genome-wide association mapping of Fusarium head blight resistance in wheat using genotyping-by-sequencing. *The Plant Genome*, 9(1), plantgenome2015.04.0028. https://doi.org/10.3835/plantgenome2015.04.0028

Arruda, M. P., Brown, P. J., Lipka, A. E., Krill, A. M., Thurber, C., & Kolb, F. L. (2015). Genomic selection for predicting Fusarium head blight resistance in a wheat breeding program. *The Plant Genome*, 8(3), eplantgenome2015.01.0003. https://doi.org/10.3835/plantgenome2015.01.0003

Ball, C. R. (1930). The history of American wheat improvement. *Agricultural History*, 4, 48–71.

Ballén-Taborda, C., Lyerly, J., Smith, J., Howell, K., Brown-Guedira, G., Babar, M. A., Harrison, S. A., Mason, R. E., Mergoum, M., Murphy, J. P., Sutton, R., Griffey, C. A., & Boyles, R. E. (2022). Utilizing genomics and historical data to optimize gene pools for new breeding programs: A case study in winter wheat. *Frontiers in Genetics*, 13, 964684. https://doi.org/10.3389/fgene.2022.964684

Bernardo, R. (2020). Reinventing quantitative genetics for plant breeding: Something old, something new, something borrowed. *Something BLUE. Heredity*, 125(6), 375–385. https://doi.org/10.1038/s41437-020-0312-1

Berro, I., Lado, B., Nalin, R. S., Quincke, M., & Gutiérrez, L. (2019). Training population optimization for genomic selection. *The Plant Genome*, 12(3), 1–14. https://doi.org/10.3835/plantgenome2019.04.0028

Bock, C. H., Barbedo, J. G. A., Del Ponte, E. M., Bohnenkamp, D., & Mahlein, A. K. (2020). From visual estimates to fully automated sensor-based measurements of plant disease severity: Status and challenges for improving accuracy. *Phytopathology Research*, 2(1), 9. https://doi.org/10.1186/s42483-020-00049-8

Boyles, R. E., Marshall, D. S., & Bockelman, H. E. (2019). Yield data from the uniform southern soft red winter wheat nursery emphasize importance of selection location and environment for cultivar development. *Crop Science*, 59(5), 1887–1898. https://doi.org/10.2135/cropsci2018.11.0685

Brown-Guedira, G., Griffey, C., Kolb, F., McKendry, A., Murphy, J. P., & Van Sanford, D. (2008). Breeding FHB-resistant soft winter wheat: Progress and prospects. *Cereal Research Communications*, 36, 31–35. https://doi.org/10.1556/CRC.36.2008.Suppl.B.5

Buerstmayr, H., Ban, T., & Anderson, J. A. (2009). QTL mapping and marker-assisted selection for Fusarium head blight resistance in wheat: A review. *Plant Breeding*, 128(1), 1–26. https://doi.org/10.1111/j.1439-0523.2008.01550.x

Buerstmayr, H., Steiner, B., Lemmens, M., & Ruckenbauer, P. (2000). Resistance to Fusarium head blight in winter wheat: Heritability and trait associations. *Crop Science*, 40(4), 1012–1018. https://doi.org/10.2135/cropsci2000.4041012x

Büschges, R., Hollricher, K., Panstruga, R., Simons, G., Wolter, M., Frijters, A., van Daelen, R., van der Lee, T., Diergaarde, P., Groenendijk, J., Töpsch, S., Vos, P., Salamini, F., & Schulze-Lefert, P. (1997). The barley Mlo gene: A novel control element of plant pathogen resistance. *Cell*, 88(5), 695–705. https://doi.org/10.1016/S0092-8674(00)81912-1

Carmack, W. J., Clark, A. J., Dong, Y., & Van Sanford, D. A. (2019). Mass selection for reduced deoxynivalenol concentration using an optical sorter in SRW wheat. *Agronomy*, 9(12), 816. https://doi.org/10.3390/agronomy9120816

Carpenter, N. R., Wright, E., Malla, S., Singh, L., Van Sanford, D., Clark, A., Harrison, S.,, Murphy, J. P., Costa, J., Chao, S., Brown-Guedira, G. L., McMaster, N., Schmale, III, D. G., Griffey, C. A., & Rawat, N. (2020). Identification and validation of Fusarium head blight resistance QTL in the U.S. soft red winter wheat cultivar 'Jamestown'. *Crop Science*, 60, 2919–2930. https://doi.org/10.1002/csc2.20307

Cativelli, M., Lewis, S., & Appendino, M. L. (2013). A Fusarium head blight resistance quantitative trait locus on chromosome 7D of the spring wheat cultivar catbird. *Crop Science*, 53(4), 1464–1471. https://doi.org/10.2135/cropsci2012.07.0435

Chhabra, B., Singh, L., Wallace, S., Schoen, A., Dong, Y., Tiwari, V., & Rawat, N. (2021). Screening of an ethyl methane sulfonate mutagenized population of a wheat cultivar susceptible to Fusarium head blight identifies resistant variants. *Plant Disease*, 105(11), 3669–3676. https://doi.org/10.1094/PDIS-03-21-0670-RE

Chhabra, B., Tiwari, V., Gill, B. S., Dong, Y., & Rawat, N. (2021). Discovery of a susceptibility factor for Fusarium head blight on chromosome 7A of wheat. *Theoretical and Applied Genetics*, 134(7), 2273–2289. https://doi.org/10.1007/s00122-021-03825-y

Clark, A. J., Costa, J. M., Griffey, C. A., Brown-Guedira, G. L., Dong, Y., Souza, E. J., Murphy, J. P., & Van Sanford, D. (2014). Registration of scab-resistant KY06C-11-3-10 soft red winter wheat germplasm. *Journal of Plant Registrations*, 8(2), 211–216. https://doi.org/10.3198/jpr2013.07.0039crg

Collins F, Hancock J, Allen C. 1991. Northrup King Company, *Annual Wheat Newsletter*. 37. https://wheat.pw.usda.gov/ggpages/awn/37/

Cowger, C., & Sutton, A. L. (2005). The southeastern U.S. Fusarium head blight epidemic of 2003. *Plant Health Progress*, 6(1), 4. https://doi.org/10.1094/PHP-2005-1026-01-RS

Cuthbert, P. A., Somers, D. J., Thomas, J., Cloutier, S., & Brulé-Babel, A. (2006). Fine mapping Fhb1, a major gene controlling Fusarium head blight resistance in bread wheat (*Triticum aestivum* L.). *Theoretical and

Applied Genetics, 112(8), 1465–1472. https://doi.org/10.1007/s00122-006-0249-7

Dawson, J. C., Endelman, J. B., Heslot, N., Crossa, J., Poland, J., Dreisigacker, S., Manès, Y., Sorrells, M. E., & Jannink, J. L. (2013). The use of unbalanced historical data for genomic selection in an international wheat breeding program. Field Crops Research, 154, 12–22. https://doi.org/10.1016/j.fcr.2013.07.020

Delwiche, S. R., Torres Rodriguez, I., Rausch, S. R., & Graybosch, R. A. (2019). Estimating percentages of Fusarium-damaged kernels in hard wheat by near-infrared hyperspectral imaging. Journal of Cereal Science, 87, 18–24. https://doi.org/10.1016/j.jcs.2019.02.008

Dickson, J. G. (1942). Scab of wheat and barley and its control. USDA Farmers' Bull. No. 1599 (revised):1–22.

Eckardt, N. A. (2002). Plant disease susceptibility genes? The Plant Cell, 14(9), 1983–1986. https://doi.org/10.1105/tpc.140910

Fabre, F., Rocher, F., Alouane, T., Langin, T., & Bonhomme, L. (2020). Searching for FHB resistances in bread wheat: Susceptibility at the crossroad. Frontiers in Plant Science, 11(June), 731. https://doi.org/10.3389/fpls.2020.00731

Fekih, R., Takagi, H., Tamiru, M., Abe, A., Natsume, S., Yaegashi, H., Sharma, S., Sharma, S., Kanzaki, H., Matsumura, H., Saitoh, H., Mitsuoka, C., Utsushi, H., Uemura, A., Kanzaki, E., Kosugi, S., Yoshida, K., Cano, L., Kamoun, S., & Terauchi, R. (2013). MutMap+: Genetic mapping and mutant identification without crossing in rice. PLoS ONE, 8(7), e68529. https://doi.org/10.1371/journal.pone.0068529

Flint, C. L. (1874). A hundred years of progress. Report of the Commissioner of Agriculture for 1872 (pp. 274–304). Government Printing Office.

Francesconi, S., Harfouche, A., Maesano, M., & Balestra, G. M. (2021). UAV-based thermal, RGB imaging and gene expression analysis allowed detection of Fusarium head blight and gave new insights into the physiological responses to the disease in durum wheat. Frontiers in Plant Science, 12, 628575. https://doi.org/10.3389/fpls.2021.628575

Gaire, R., de Arruda, M. P., Mohammadi, M., Brown-Guedira, G., Kolb, F. L., & Rutkoski, J. (2022). Multi-trait genomic selection can increase selection accuracy for deoxynivalenol accumulation resulting from Fusarium head blight in wheat. The Plant Genome, 15(1), e20188. https://doi.org/10.1002/tpg2.20188

Gale, L. R., Harrison, S. A., Ward, T. J., O'Donnell, K., Milus, E. A., Gale, S. W., & Kistler, H. C. (2011). Nivalenol-type populations of Fusarium graminearum and F. asiaticum are prevalent on wheat in southern Louisiana. Phytopathology, 101(1), 124–134. https://doi.org/10.1094/PHYTO-03-10-0067

Garcia-Ruiz, H., Szurek, B., & Van den Ackerveken, G. (2021). Stop helping pathogens: Engineering plant susceptibility genes for durable resistance. Current Opinion in Biotechnology, 70, 187–195. https://doi.org/10.1016/j.copbio.2021.05.005

Garvin, D. F., Porter, H., Blankenheim, Z. J., Chao, S., & Dill-Macky, R. (2015). A spontaneous segmental deletion from chromosome arm 3DL enhances Fusarium head blight resistance in wheat. Genome, 58(11), 479–488. https://doi.org/10.1139/gen-2015-0088

Gervais, L., Dedryver, F., Morlais, J. Y., Bodusseau, V., Negre, S., Bilous, M., Groos, C., & Trottet, M. (2003). Mapping of quantitative trait loci for field resistance to Fusarium head blight in an European winter wheat. Theoretical and Applied Genetics, 106(6), 961–970. https://doi.org/10.1007/s00122-002-1160-5

Ghimire, B., Mergoum, M., Martinez-Espinoza, A. D., Sapkota, S., Pradhan, S., Babar, M. A., Bai, G., Dong, Y., & Buck, J. W. (2022). Genetics of Fusarium head blight resistance in soft red winter wheat using a genome-wide association study. The Plant Genome, 15(3), e20222. https://doi.org/10.1002/tpg2.20222

Gill, H. B. Jr. (1978). Wheat culture in colonial Virginia. Agricultural History, 52, 380–393.

Gooding, R. W., Lafever, H. N., Campbell, K. G., & Herald, L. D. (1997). Registration of 'freedom' wheat. Crop Science, 37(3), 1007–1007. https://doi.org/10.2135/cropsci1997.0011183X003700030057x

Griffey, C. A., Rohrer, W. L., Pridgen, T. H., Brooks, W. S., Chen, J., Wilson, J. A., Nabati, D., Brann, D. E., Rucker, E. G., Behl, H. D., Vaughn, M. E., Sisson, W. L., Randall, T. R., Corbin, R. A., Kenner, J. C., Dunaway, D. W., Pitman, R. M., Bockelman, H. E., Gaines, C., & Whitcher, L. (2005). Registration of 'McCormick' wheat. Crop Science, 45(1), 417–419. https://doi.org/10.2135/cropsci2005.0417

Griffey, C. A., Starling, T. M., Price, A. M., Sisson, W. L., Das, M. K., Pridgen, T. H., Vaughn, M. E., Rohrer, W. L., & Brann, D. E. (2001). Registration of 'Roane' wheat. Crop Science, 41(4), 1359–1360. https://doi.org/10.2135/cropsci2001.4141359x

Griffey, C. A., Thomason, W. E., Pitman, R. M., Beahm, B. R., Paling, J. J., Chen, J., Fanelli, J. K., Kenner, J. C., Dunaway, D. W., Brooks, W. S., Vaughn, M. E., Hokanson, E. G., Behl, H. D., Corbin, R. A., Hall, M. D., Liu, S., Custis, J. T., Waldenmaier, C. M., Starner, D. E., ... Cambron, S. E. (2010). Registration of 'Jamestown' wheat. Journal of Plant Registrations, 4(1), 28–33. https://doi.org/10.3198/jpr2009.05.0257crc

Gu, C., Wang, D., Zhang, H., Zhang, J., Zhang, D., & Liang, D. (2020). Fusion of deep convolution and shallow features to recognize the severity of wheat Fusarium head blight. Frontiers in Plant Science, 11, 599886. https://doi.org/10.3389/fpls.2020.599886

Hales, B., Steed, A., Giovannelli, V., Burt, C., Lemmens, M., Molnár-Láng, M., & Nicholson, P. (2020). Type II Fusarium head blight susceptibility conferred by a region on wheat chromosome 4D. Journal of Experimental Botany, 71(16), 4703–4714. https://doi.org/10.1093/jxb/eraa226

Harrison, S. A., Babar, M. A., Barnett, R. D., Blount, A. R., Johnson, J. W., Mergoum, M., Mason, R. E., Murphy, J. P., Simoneaux, B., & Ibrahim, A. M. H. (2017). 'LA05006', a dual-purpose oat for Louisiana and other southeastern regions of the USA. Journal of Plant Registrations, 11(2), 89–94. https://doi.org/10.3198/jpr2016.08.0040crc

He, X., Lillemo, M., Shi, J., Wu, J., Bjørnstad, A., Belova, T., Dreisigacker, S., Duveiller, E., & Singh, P. (2016). QTL characterization of Fusarium head blight resistance in CIMMYT bread wheat line Soru#1. PLoS ONE, 11(6), e0158052. https://doi.org/10.1371/journal.pone.0158052

He, X., Singh, P. K., Dreisigacker, S., Singh, S., Lillemo, M., & Duveiller, E. (2016). Dwarfing genes Rht-B1b and Rht-D1b are associated with both type I FHB susceptibility and low anther extrusion in two bread wheat populations. PLoS ONE, 11(9), e0162499. https://doi.org/10.1371/journal.pone.0162499

Herter, C. P., Ebmeyer, E., Kollers, S., Korzun, V., Leiser, W. L., Würschum, T., & Miedaner, T. (2018). Rht24 reduces height in the winter wheat population 'Solitär × Bussard' without adverse effects on Fusarium head blight infection. Theoretical and Applied Genetics, 131(6), 1263–1272. https://doi.org/10.1007/s00122-018-3076-8

Huang, L., Wu, Z., Huang, W., Ma, H., & Zhao, J. (2019). Identification of Fusarium head blight in winter wheat ears based on Fisher's linear discriminant analysis and a support vector machine. Applied Sciences, 9(18), 3894. https://doi.org/10.3390/app9183894

Jiang, G. L., Huang, D., Shen, Q., Yang, Z., Lu, W., Shi, J., Zhu, H., Chen, Z., & Ward, R. (2006). Registration of wheat germplasms CJ W14 and CJ 9306 highly resistant to Fusarium head blight. Crop Science, 46(5), 2326–2328. https://doi.org/10.2135/cropsci2005.10.0394

Jirsa, O., & Polišenská, I. (2014). Identification of Fusarium damaged wheat kernels using image analysis. Acta Universitatis Agriculturae et Silviculturae Mendelianae Brunensis, 59(5), 125–130. https://doi.org/10.11118/actaun201159050125

Johnson, J. W., Buck, J. W., Buntin, G. D., & Chen, Z. (2007). University of Georgia Experiment Station and the USDA–ARS. Griffin. Annual Wheat Newsletter., 53, 104–105.

Kang, J., Clark, A., Van Sanford, D., Griffey, C., Brown-Guedira, G., Dong, Y., Murphy, J. P., & Costa, J. (2011). Exotic scab resistance quantitative trait loci effects on soft red winter wheat. Crop Science, 51(3), 924–933. https://doi.org/10.2135/cropsci2010.06.0313

Kazan, K., & Gardiner, D. M. (2018). Transcriptomics of cereal–*Fusarium graminearum* interactions: What we have learned so far. *Molecular Plant Pathology*, 19(3), 764–778. https://doi.org/10.1111/mpp.12561

Khatibi, P. A., Berger, G., Liu, S., Brooks, W. S., Griffey, C. A., & Schmale, D. G. (2012). Resistance to Fusarium head blight and Deoxynivalenol accumulation in Virginia barley. *Plant Disease*, 96(2), 279–284. https://doi.org/10.1094/PDIS-07-11-0551

Klahr, A., Zimmermann, G., Wenzel, G., & Mohler, V. (2007). Effects of environment, disease Progress, plant height and heading date on the detection of QTLs for resistance to Fusarium head blight in an European winter wheat cross. *Euphytica*, 154, 17–28. https://doi.org/10.1007/s10681-006-9264-7

Kumar, J., Huckelhoven, R., Beckhove, U., Nagarajan, S., & Kogel, K.-H. (2001). A compromised *Mlo* pathway affects the response of barley to the necrotrophic fungus Bipolaris sorokiniana (teleomorph: *Cochliobolus sativus*) and its toxins. *Phytopathology*, 91, 127–133. https://doi.org/10.1094/PHYTO.2001.91.2.127

Lane, H. M., Murray, S. C., Montesinos-López, O. A., Montesinos-López, A., Crossa, J., Rooney, D. K., Barrero-Farfan, I. D., De La Fuente, G. N., & Morgan, C. L. S. (2020). Phenomic selection and prediction of maize grain yield from near-infrared reflectance spectroscopy of kernels. *The Plant Phenome Journal*, 3(1), e20002. https://doi.org/10.1002/ppj2.20002

Langner, T., Kamoun, S., & Belhaj, K. (2018). CRISPR crops: Plant genome editing toward disease resistance. *Annual Review of Phytopathology*, 56, 479–512. https://doi.org/10.1146/annurev-phyto-080417-050158

Larkin, D. L., Holder, A. L., Mason, R. E., Moon, D. E., Brown-Guedira, G., Price, P. P., Harrison, S. A., & Dong, Y. (2020). Genome-wide analysis and prediction of Fusarium head blight resistance in soft red winter wheat. *Crop Science*, 60(6), 2882–2900. https://doi.org/10.1002/csc2.20273

Lehermeier, C., Krämer, N., Bauer, E., Bauland, C., Camisan, C., Campo, L., Flament, P., Melchinger, A. E., Menz, M., Meyer, N., Moreau, L., Moreno-González, J., Ouzunova, M., Pausch, H., Ranc, N., Schipprack, W., Schönleben, M., Walter, H., Charcosset, A., & Schön, C. C. (2014). Usefulness of multiparental populations of maize (*Zea mays* L.) for genome-based prediction. *Genetics*, 198(1), 3–16. https://doi.org/10.1534/genetics.114.161943

Liu, L., Dong, Y., Huang, W., Xiaoping, D., & Ma, H. (2020). Monitoring wheat Fusarium head blight using unmanned aerial vehicle hyperspectral imagery. *Remote Sensing*, 12(22), 3811. https://doi.org/10.3390/rs12223811

Liu, S., & Anderson, J. A. (2003). Marker assisted evaluation of Fusarium head blight resistant wheat germplasm. *Crop Science*, 43(3), 760–766. https://doi.org/10.2135/cropsci2003.7600

Liu, S., Pumphrey, M., Gill, B., Trick, H., Zhang, J., Dolezel, J., Chalhoub, B., & Anderson, J. (2008). Toward positional cloning OfFhb1, a major QTL for Fusarium head blight resistance in wheat. *Cereal Research Communications*, 36(Supplement 6), 195–201. https://doi.org/10.1556/CRC.36.2008.Suppl.B.15

Liu, S., Zhang, X., Pumphrey, M. O., Stack, R. W., Gill, B. S., & Anderson, J. A. (2006). Complex microcolinearity among wheat, rice, and barley revealed by fine mapping of the genomic region harboring a major QTL for resistance to Fusarium head blight in wheat. *Functional & Integrative Genomics*, 6(2), 83–89. https://doi.org/10.1007/s10142-005-0007-y

Lozada, D. N., Esten Mason, R., Sarinelli, J. M., & Brown-Guedira, G. (2019). Accuracy of genomic selection for grain yield and agronomic traits in soft red winter wheat. *BMC Genetics*, 20(1), 82. https://doi.org/10.1186/s12863-019-0785-1

Luck, J., Spackman, M., Freeman, A., Tre̦bicki, P., Griffiths, W., Finlay, K., & Chakraborty, S. (2011). Climate change and diseases of food crops. *Plant Pathology*, 60(1), 113–121. https://doi.org/10.1111/j.1365-3059.2010.02414.x

Lyerly JH, Murphy JP, Winn Z, Page J, Brown-Guedira G. 2022. Southern Uniform Winter Wheat Scab Nursery. 2022 Nursery Report. https://scabusa.org/pdfs_dbupload/suwwsn22_report.pdf

Ma, H.-X., Bai, G.-H., Gill, B. S., & Patrick Hart, L. (2006). Deletion of a chromosome arm altered wheat resistance to Fusarium head blight and Deoxynivalenol accumulation in Chinese spring. *Plant Disease*, 90(12), 1545–1549. https://doi.org/10.1094/PD-90-1545

Maloney, P. V., Petersen, S., Navarro, R. A., Marshall, D., McKendry, A. L., Costa, J. M., & Paul Murphy, J. (2014). Digital image analysis method for estimation of Fusarium-damaged kernels in wheat. *Crop Science*, 54, 2077–2083. https://doi.org/10.2135/cropsci2013.07.0432

McKendry, A. L., Berg, J. E., Tague, D. N., & Kephart, K. D. (1995). Registration of 'Ernie' wheat. *Crop Science*, 35, 1513. https://doi.org/10.2135/cropsci1995.0011183x003500050061x

McKendry, A. L., Tague, D. N., Wright, R. L., & Tremain, J. A. (2007). Registration of 'Bess' wheat. *Journal of Plant Registrations*, 1(1), 21–23. https://doi.org/10.3198/jpr2006.06.0405crc

McKendry, A. L., Tague, D. N., Wright, R. L., Tremain, J. A., & Conley, S. P. (2005). Registration of 'Truman' wheat. *Crop Science*, 45, cropsci2005.0421. https://doi.org/10.2135/cropsci2005.0421

McMullen, M., Jones, R., & Gallenberg, D. (1997). Scab of wheat and barley: A re-emerging disease of devastating impact. *Plant Disease*, 81(12), 1340–1348. https://doi.org/10.1094/PDIS.1997.81.12.1340

Merrick, L. F., Herr, A. W., Sandhu, K. S., Lozada, D. N., & Carter, A. H. (2022). Utilizing genomic selection for wheat population development and improvement. *Agronomy*, 12(2), 522. https://doi.org/10.3390/agronomy12020522

Meuwissen, T. H., Hayes, B. J., & Goddard, M. E. (2001). Prediction of total genetic value using genome-wide dense marker maps. *Genetics*, 157(4), 1819–1829. https://doi.org/10.1093/genetics/157.4.1819

Miedaner, T., Lenhardt, M., Grehl, J., Gruner, P., & Koch, S. (2022). Dwarfing gene Rht24 does not affect Fusarium head blight resistance in a large European winter wheat diversity panel. *Euphytica*, 218(6), 73. https://doi.org/10.1007/s10681-022-03028-6

Mirocha, C. J., Kolaczkowski, E., Xie, W., Hui, Y., & Jelen, H. (1998). Analysis of deoxynivalenol and its derivatives (batch and single kernel) using gas chromatography/mass spectrometry. *Journal of Agricultural and Food Chemistry*, 46(4), 1414–1418. https://doi.org/10.1021/jf970857o

Mohammadi, M., Tiede, T., & Smith, K. P. (2015). PopVar: A genome-wide procedure for predicting genetic variance and correlated response in biparental breeding populations. *Crop Science*, 55(5), 2068–2077. https://doi.org/10.2135/cropsci2015.01.0030

Moreno-Amores, J., Michel, S., Thomas Miedaner, C., Longin, F. H., & Buerstmayr, H. (2020). Genomic predictions for Fusarium head blight resistance in a diverse durum wheat panel: An effective incorporation of plant height and heading date as covariates. *Euphytica*, 216(2), 22. https://doi.org/10.1007/s10681-019-2551-x

Murphy, J. P., Lyerly, J. H., Acharya, R., Sarinelli, J. M., Tyagi, P., Page, J., & Brown-Guedira, G. (2017). Southern Uniform Winter Wheat Scab Nursery: 2017 Nursery Report. https://scabusa.org/pdfs_dbupload/suwwsn17_report.pdf

Murphy, J. P., Lyerly, J. H., Sarinelli, J. M., Tyagi, P., & Brown-Guedira, G. (2016). Southern Uniform Winter Wheat Scab Nursery: 2016 Nursery Report. https://scabusa.org/pdfs_dbupload/suwwsn16_report.pdf

Murphy, J. P., & Navarro, R. (2001). Uniform Southern Soft Red Winter Wheat Fusarium Head Blight Nursery. 2001 Nursery Report. https://scabusa.org/pdfs_dbupload/srwwn01_report.pdf

Murphy, J. P., & Navarro, R. (2005). Uniform Southern Soft Red Winter Wheat Fusarium Head Blight Nursery: 2005 Nursery Report. https://scabusa.org/pdfs_dbupload/swwn05_report.pdf

Murphy, J. P., & Navarro, R. (2008). Uniform Southern Soft Red Winter Wheat Fusarium Head Blight Nursery: 2008 Nursery Report. https://scabusa.org/pdfs_dbupload/srwwn08_report.pdf

Murphy, J. P., & Navarro, R. (2011). Uniform Southern Soft Red Winter Wheat Fusarium Head Blight Nursery. 2011 Nursery Report. https://scabusa.org/pdfs_dbupload/suwwsn11_report.pdf

Murphy, J. P., & Navarro, R. (2012). Uniform Southern Soft Red Winter Wheat Fusarium Head Blight Nursery. 2012 Nursery Report. https://scabusa.org/pdfs_dbupload/suwwsn12_report.pdf

Murphy, J. P., Navarro, R., & Lyerly, J. (2006). Uniform Southern Soft Red Winter Wheat Fusarium Head Blight Nursery: 2006 Nursery Report. https://scabusa.org/pdfs_dbupload/srwwn06_report.pdf

Murphy, J. P., Navarro, R. A., Leath, S., Bowman, D. T., Weisz, P. R., Ambrose, L. G., Pate, M. H., & Fountain, M. O. (2004). Registration of 'NC-Neuse' wheat. *Crop Science*, 44, 1479–1480. https://doi.org/10.2135/cropsci2004.1479

Murphy, J. P., Navarro, R., & Srnic, G. (2000). Uniform Southern Soft Red Winter Wheat Fusarium Head Blight Nursery: 2000 Nursery Report. https://scabusa.org/pdfs_dbupload/srwwn00_report.pdf

Murphy, J. P., & Petersen, S. (2014). Uniform Southern Soft Red Winter Wheat Fusarium Head Blight Nursery: 2014 Nursery Report. https://scabusa.org/pdfs_dbupload/suwwsn14_report.pdf

Navarro, L., Bari, R., Achard, P., Lisón, P., Nemri, A., Harberd, N. P., & Jones, J. D. G. (2008). DELLAs control plant immune responses by modulating the balance of Jasmonic acid and salicylic acid signaling. *Current Biology: CB*, 18(9), 650–655. https://doi.org/10.1016/j.cub.2008.03.060

Norman, A., Taylor, J., Edwards, J., & Kuchel, H. (2018). Optimising genomic selection in wheat: Effect of marker density, population size and population structure on prediction accuracy. *G3*, 8(9), 2889–2899.

Pavan, S., Jacobsen, E., Visser, R. G. F., & Bai, Y. (2010). Loss of susceptibility as a novel breeding strategy for durable and broad-spectrum resistance. *Molecular Breeding: New Strategies in Plant Improvement*, 25(1), 1–12. https://doi.org/10.1007/s11032-009-9323-6

Petersen, S., Lyerly, J. H., Maloney, P. V., Brown-Guedira, G., Cowger, C., Costa, J. M., Dong, Y., & Murphy, J. P. (2016). Mapping of Fusarium head blight resistance quantitative trait loci in winter wheat cultivar NC-Neuse. *Crop Science*, 56(4), 1473–1483. https://doi.org/10.2135/cropsci2015.05.0312

Petersen, S., Lyerly, J. H., McKendry, A. L., Sariful Islam, M., Brown-Guedira, G., Cowger, C., Dong, Y., & Murphy, J. P. (2017). Validation of Fusarium head blight resistance QTL in US winter wheat. *Crop Science*, 57(1), 1–12. https://doi.org/10.2135/cropsci2015.07.0415

Poland, J. A., Brown, P. J., Sorrells, M. E., & Jannink, J.-L. (2012). Development of high-density genetic maps for barley and wheat using a novel two-enzyme genotyping-by-sequencing approach. *PLoS ONE*, 7(2), e32253. https://doi.org/10.1371/journal.pone.0032253

Pumphrey, M. O., Bernardo, R., & Anderson, J. A. (2007). Validating the Fhb1 QTL for Fusarium head blight resistance in near-isogenic wheat lines developed from breeding populations. *Crop Science*, 47(1), 200–206. https://doi.org/10.2135/cropsci2006.03.0206

Rawat, N., Pumphrey, M. O., Liu, S., Zhang, X., Tiwari, V. K., Ando, K., Trick, H. N., Bockus, W. W., Akhunov, E., Anderson, J. A., & Gill, B. S. (2016). Wheat Fhb1 encodes a chimeric lectin with agglutinin domains and a pore-forming toxin-like domain conferring resistance to Fusarium head blight. *Nature Genetics*, 48(12), 1576–1580. https://doi.org/10.1038/ng.3706

Rincent, R., Charpentier, J.-P., Faivre-Rampant, P., Paux, E., Le Gouis, J., Bastien, C., & Segura, V. (2018). Phenomic selection is a low-cost and high-throughput method based on indirect predictions: Proof of concept on wheat and poplar. *G3*, 8(12), 3961–3972. https://doi.org/10.1534/g3.118.200760

Robert, P., Brault, C., Rincent, R., & Segura, V. (2022). Phenomic selection: A new and efficient alternative to genomic selectiongenomic selection (GS). In N. Ahmadi & J. Bartholomé (Eds.), *Genomic prediction of complex traits: Methods and protocols* (pp. 397–420). Springer US.

Rutkoski, J., Singh, R. P., Huerta-Espino, J., Bhavani, S., Poland, J., Jannink, J. L., & Sorrells, M. E. (2015). Efficient use of historical data for genomic selection: A case study of stem rust resistance in wheat. *The Plant Genome*, 8(1), eplantgenome2014.09.0046. https://doi.org/10.3835/plantgenome2014.09.0046

Rutkoski, J., Benson, J., Jia, Y., Brown-Guedira, G., Jannink, J.-L., & Sorrells, M. (2012). Evaluation of genomic prediction methods for Fusarium head blight resistance in wheat. *The Plant Genome*, 5(2), 51–61. https://doi.org/10.3835/plantgenome2012.02.0001

Sabadin, F., DoVale, J. C., Platten, J. D., & Fritsche-Neto, R. (2022). Optimizing self-pollinated crop breeding employing genomic selection: From schemes to updating training sets. *Frontiers in Plant Science*, 13, 935885. https://doi.org/10.3389/fpls.2022.935885

Sanford, V., David, J. A., Campbell, K., Costa, J., Cregan, P., Griffey, C., Hayes, P., & Ward, R. (2001). Discovery and deployment of molecular markers linked to Fusarium head blight resistance: An integrated system for wheat and barley. *Crop Science*, 41(3), 638–644. https://doi.org/10.2135/cropsci2001.413638x

Sarinelli, J., Martin, J. P., Murphy, P. T., Holland, J. B., Johnson, J. W., Mergoum, M., Mason, R. E., Babar, A., Harrison, S., Sutton, R., Griffey, C. A., & Brown-Guedira, G. (2019). Training population selection and use of fixed effects to optimize genomic predictions in a historical USA winter wheat panel. *Theoretical and Applied Genetics*, 132(4), 1247–1261. https://doi.org/10.1007/s00122-019-03276-6

Schmolke, M., Zimmermann, G., Buerstmayr, H., Schweizer, G., Miedaner, T., Korzun, V., Ebmeyer, E., & Hartl, L. (2005). Molecular mapping of Fusarium head blight resistance in the winter wheat population dream/lynx. *Theoretical and Applied Genetics*, 111(4), 747–756. https://doi.org/10.1007/s00122-005-2060-2

Srinivasachary, N., Gosman, A., Steed, J., Simmonds, M., Leverington-Waite, Y., Wang, J. S., & Nicholson, P. (2008). Susceptibility to Fusarium head blight is associated with the Rht-D1b semi-dwarfing allele in wheat. *Theoretical and Applied Genetics*, 116(8), 1145–1153. https://doi.org/10.1007/s00122-008-0742-2

Storlie, E., & Charmet, G. (2013). Genomic selection accuracy using historical data generated in a wheat breeding program. *The Plant Genome*, 6(1), plantgenome2013.01.0001. https://doi.org/10.3835/plantgenome2013.01.0001

Su, Z., Bernardo, A., Tian, B., Chen, H., Wang, S., Ma, H., Cai, S., Liu, D., Zhang, D., Li, T., Trick, H., St. Amand, P., Yu, J., Zhang, Z., & Bai, G. (2019). A deletion mutation in TaHRC confers Fhb1 resistance to Fusarium head blight in wheat. *Nature Genetics*, 51(7), 1099–1105. https://doi.org/10.1038/s41588-019-0425-8

Tamburic-Ilincic, L., Schaafsma, A. W., Falk, D., Laskar, B., Fedak, G., & Somers, D. (2006). Registration of winter wheat germplasm line RCATL33 with Fusarium head blight resistance and reduced deoxynivalenol accumulation. *Crop Science*, 46(3), 1399–1400. https://doi.org/10.2135/cropsci2005.06-0113

Tao, H., Shi, X., He, F., Wang, D., Xiao, N., Fang, H., Wang, R., Zhang, F., Wang, M., Li, A., Liu, X., Wang, G. L., & Ning, Y. (2021). Engineering broad spectrum disease resistant rice by editing multiple susceptibility genes. *Journal of Integrative Plant Biology*, 63(9), 1639–1648.

Thambugala, D., Brûlé-Babel, A. L., Blackwell, B. A., Fedak, G., Foster, A. J., MacEachern, D., Gilbert, J., Henriquez, M. A., Martin, R. A., McCallum, B. D., Spaner, D., Iqbal, M., Pozniak, C. J., N'Diaye, A., & McCartney, C. A. (2020). Genetic analyses of native Fusarium head blight resistance in two spring wheat populations identifies QTL near the B1, Ppd-D1, Rht-1, Vrn-1, Fhb1, Fhb2, and Fhb5 loci. *Theoretical and Applied Genetics*, 133(10), 2775–2796. https://doi.org/10.1007/s00122-020-03631-y

van Schie, C. C. N., & Takken, F. L. W. (2014). Susceptibility genes 101: How to be a good host. *Annual Review of Phytopathology*, 52(June), 551–581. https://doi.org/10.1146/annurev-phyto-102313-045854

Verges, V. L., Brown-Guedira, G. L., & Van Sanford, D. A. (2021). Genome-wide association studies combined with genomic selection as a tool to increase Fusarium head blight resistance in wheat. *Crop Breeding, Genetics and Genomics*, 3(4), e210007. https://cbgg.hapres.com/UpLoad/PdfFile/CBGG_1419.pdf

Verges, V. L., Lyerly, J., Dong, Y., & Van Sanford, D. A. (2020). Training population design with the use of regional Fusarium head blight nurseries to predict independent breeding lines for FHB traits. *Frontiers in Plant Science*, 11(July), 1083. https://doi.org/10.3389/fpls.2020.01083

Vogel, J. P., Raab, T. K., Schiff, C., & Somerville, S. C. (2002). *PMR6*, a pectate lyase-like gene required for powdery mildew susceptibility in Arabidopsis. *The Plant Cell*, 14(9), 2095–2106. https://doi.org/10.1105/tpc.003509

Voss, H.-H., Holzapfel, J., Hartl, L., Korzun, V., Rabenstein, F., Ebmeyer, E., Coester, H., Kempf, H., & Miedaner, T. (2008). Effect of the *Rht-D1* dwarfing locus on Fusarium head blight rating in three segregating populations of winter wheat. *Plant Breeding*, 127(4), 333–339. https://doi.org/10.1111/j.1439-0523.2008.01518.x

Waldron, B. L., Moreno-Sevilla, B., Anderson, J. A., Stack, R. W., & Frohberg, R. C. (1999). RFLP mapping of QTL for Fusarium head blight resistance in wheat. *Crop Science*, 39(3), 805–811. https://doi.org/10.2135/cropsci1999.0011183X003900030032x

Walker, S. L., Leath, S., Hagler, W. M., & Paul Murphy, J. (2001). Variation among isolates of *Fusarium graminearum* associated with Fusarium head blight in North Carolina. *Plant Disease*, 85(4), 404–410. https://doi.org/10.1094/PDIS.2001.85.4.404

Wang, H., Sun, S., Ge, W., Zhao, L., Hou, B., Wang, K., Lyu, Z., Chen, L., Xu, S., Guo, J., Li, M., Su, P., Li, X., Wang, G., Bo, C., Fang, X., Zhuang, W., Cheng, X., Wu, J., & Kong, L. (2020). Horizontal gene transfer of Fhb7 from fungus underlies Fusarium head blight resistance in wheat. *Science*, 368(6493), eaba5435. https://doi.org/10.1126/science.aba5435

Wang, S., Wong, D., Forrest, K., Allen, A., Chao, S., Huang, B. E., Maccaferri, M., Salvi, S., Milner, S. G., Cattivelli, L., Mastrangelo, A. M., Whan, A., Stephen, S., Barker, G., Wieseke, R., Plieske, J., International Wheat Genome Sequencing Consortium, Lillemo, M., Mather, D., & Akhunov, E. (2014). Characterization of polyploid wheat genomic diversity using a high-density 90,000 single nucleotide polymorphism array. *Plant Biotechnology Journal*, 12(6), 787–796. https://doi.org/10.1111/pbi.12183

Werner, C. R., Chris Gaynor, R., Gorjanc, G., Hickey, J. M., Kox, T., Abbadi, A., Leckband, G., Snowdon, R. J., & Stahl, A. (2020). How population structure impacts genomic selection accuracy in cross-validation: Implications for practical breeding. *Frontiers in Plant Science*, 11, 592977. https://doi.org/10.3389/fpls.2020.592977

Winn, Z. J., Lyerly, J., Brown-Guedira, G. J., Murphy, J. P., & Mason, E. (2023). Utilization of a publicly available diversity panel in genomic prediction of Fusarium head blight resistance traits in wheat. BioRxiv. https://doi.org/10.1101/2023.02.15.528729

Winn, Z. J., Lyerly, J., Ward, B., Brown-Guedira, G., Boyles, R. E., Mergoum, M., Johnson, J., Harrison, S., Babar, A., Mason, R. E., Sutton, R., & Murphy, J. P. (2022). Profiling of Fusarium head blight resistance QTL haplotypes through molecular markers, genotyping-by-sequencing, and machine learning. *Theoretical and Applied Genetics*, 135(9), 3177–3194. https://doi.org/10.1007/s00122-022-04178-w

Winn, Z. J. (2022). Investigation of Fusarium Head Blight and Hessian Fly Resistance QTL and QTL Profiling via Machine Learning in Soft Red Winter Wheat.

Wright, E. E. (2014). *Identification of native FHB resistance QTL in the SRW wheat cultivar Jamestown*. Virginia Tech. https://vtechworks.lib.vt.edu/handle/10919/64327

Würschum, T., Maurer, H. P., Weissmann, S., Hahn, V., & Leiser, W. L. (2017). Accuracy of within- and among-family genomic prediction in triticale. *Plant Breeding*, 136(2), 230–236. https://doi.org/10.1111/pbr.12465

Zaidi, S. S., Mukhtar, M. S., & Mansoor, S. (2018). Genome editing: Targeting susceptibility genes for plant disease resistance. *Trends in Biotechnology*, 36(9), 898–906. https://doi.org/10.1016/j.tibtech.2018.04.005

Zhang, N., Pan, Y., Feng, H., Zhao, X., Yang, X., Ding, C., & Yang, G. (2019). Development of Fusarium head blight classification index using hyperspectral microscopy images of winter wheat spikelets. *Biosystems Engineering*, 186, 83–99. https://doi.org/10.1016/j.biosystemseng.2019.06.008