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Genetic mapping of resistance to *Fusarium* head blight in soft red winter wheat line NC13-20076

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Abstract

Fusarium head blight (FHB) infection causes yield loss, quality degradation, and the production of damaging mycotoxins in common wheat (*Triticum aestivum* L). Marker analysis suggests that NC13-20076 does not possess previously identified FHB resistance quantitative trait loci (QTL) screened for in eastern winter wheat germplasm. A doubled haploid population of 168 lines from the cross of GA06493-13LE6 and NC13-20076 was phenotyped in inoculated nurseries in six environments. Heading date, plant height, and visual ratings of *Fusarium* damage on heads were recorded in the field; percent *Fusarium* damaged kernels (FDK) and deoxynivalenol (DON) accumulation were recorded post-harvest. Interval and multiple QTL mapping were performed on each environment-by-trait combination. Plant height and heading date QTL were identified on chromosomes 4A, 5A, 6A, and 7B, and peak markers were used as covariates in mapping of disease response traits. Disease response QTL were identified on chromosomes 1A, 2A, 2B, 3A, 3B, 4A, 5A, 7A, and 7D. The largest percent variance (PV) QTL identified for FHB visual ratings (10.8%) and DON accumulation (10.1%) were found on chromosome 5A (*QFvr.nc-5A*, *QDon.nc-5A*). The largest PV (10.3%) QTL identified for FDK were found on 1A (*QFdk.nc-1A*). Disease response QTL for multi-environment scans of visual ratings, FDK, and DON accumulation accounted for 4.0%–10.8%, 4.1%–10.3%, and 4.9%–10.1% of the total variance, respectively. The present results indicate that NC13-20076 contains several FHB response QTL, which overlap with previously identified QTL and demonstrate the importance of NC13-20076 as a readily accessible source of FHB resistance.

Abbreviations: BLUE, best linear unbiased estimate; cM, centimorgan; DON, deoxynivalenol; FDK, *Fusarium* damaged kernels; FHB, *Fusarium* head blight; GBS, genotyping-by-sequencing; GS, genomic selection; KIN19, Cunningham Research Station, Kinston, NC in 2018–2019; KIN20, Cunningham Research Station, Kinston, NC in 2019–2020; LOD, Likelihood of odds; MAS, marker-assisted selection; Mbp, megabase pair; ppm, parts per million; QTL, quantitative trait loci; RAL19, Lake Wheeler Field Laboratory, Raleigh, NC in 2018–2019; RAL20, Lake Wheeler Field Laboratory, Raleigh, NC in 2019–2020; SUWWSN, Southern Uniform Winter Wheat Scab Nursery; USDA-ARS, United States Department of Agriculture—Agricultural Research Service; VR, *Fusarium* Head Blight Visual Ratings; VT, Virginia Polytechnic Institute and State University; WAR19, Eastern Virginia Agricultural Research Extension Center, Warsaw, Virginia in 2018–2019; WAR20, Eastern Virginia Agricultural Research Extension Center, Warsaw, Virginia in 2019–2020.

Plain Language Summary

Fusarium head blight, also referred to as head scab, is a major disease in wheat that threatens grower profitability, domestic food security, and public health. Scab reduces wheat yields and results in the production of dangerous mycotoxins, which are molecules produced by fungi that are toxic when consumed. Cultural controls can reduce the impact of scab, but they do not provide reliable year-to-year control of the disease. The most economically and environmentally efficient way to reduce the impact of scab is by breeding wheat, which is genetically resistant to the disease. In this publication, we created a designed wheat population to locate regions of the wheat genome that are associated with resistance to scab. We found, like many other publications of the same ilk, that the resistance in this population is due to many small effect genes working together. This information supports the use of the resistant parent from this experimental population (NC13-20076) in breeding programs.

1 | INTRODUCTION

Fusarium head blight (FHB) is one of the most economically detrimental diseases of wheat (*Triticum aestivum* L). In the United States, the predominant pathogen that causes FHB is *Fusarium graminearum* (Ward et al., 2008). Infection by pathogenic strains of *Fusarium* reduces yield, test weight, and grain quality and causes the accumulation of mycotoxins like deoxynivalenol (DON) (Burrows et al., 2008; Pestka, 2010). Thus, breeding wheat varieties with acceptable levels of resistance to FHB is paramount in programs that serve heavily affected areas.

Phenotyping FHB resistance traits in a small grains breeding program is a labor-cost-intensive process. Therefore, identification of molecular markers in tight linkage with quantitative trait loci (QTL) for use in marker-assisted selection (MAS) and inclusion as fixed effects for genomic selection (GS) models has been suggested as an alternative to traditional truncation selection through phenotyping alone (Arruda et al., 2016). Determining if a line may possess FHB resistance QTL can be done by classifying the allelic state of molecular markers that are in high linkage disequilibrium (LD) with the QTL, particularly in germplasm related to the original resistance QTL source for which haplotypes are assumed to be identical by descent (Arruda et al., 2016; Xu & Crouch, 2008).

Resistance to FHB has been identified in North American wheat germplasm, as well as germplasm from Asia, Europe, and South America. Resistance to FHB infection is highly polygenic with a complex genetic architecture; currently, over 50 different FHB resistance meta-QTL have been identified across the wheat genome with repeated occurrence on 3A, 5A, 7A, 1B, 3B, 4B, 5B, 6B, and 2D (H. Buerstmayr et al., 2009; Cai et al., 2019; Venske et al., 2019). Of the FHB resistance QTL identified, the *Fhb1* allele from the Chinese cultivar Sumai 3 has been utilized heavily by many wheat breeding programs due to its large effect (Boyles et al., 2024; Cowger, 2021; Cuthbert et al., 2006; Gaire et al., 2022; Zhu et al., 2019). Furthermore, the *Fhb1* locus has had wide deployment in North America, including the southeastern United States, due to the availability of tightly linked DNA markers that are predictive of the *Fhb1* haplotype (Su et al., 2019; Winn et al., 2022).

Several loci contributing to FHB resistance have been identified in soft red winter wheat from the southeastern United States. This includes the QTL *Qfhb.nc-2B* and *Qfhb.nc-4A* identified in the cultivars Bess and NC-Neuse, respectively (Petersen et al., 2016, 2017; Winn et al., 2022). Markers for the haplotype on chromosome 1B associated with *QFHB.vt-1B.1* and *QFHB.vt-1B.2*, identified in Jamestown, are often targets of MAS (Carpenter et al., 2020; Winn et al., 2022). In addition, novel effective resistance alleles on chromosomes 2A, 2D, and 3D were identified in the cultivar Truman (M. S. Islam et al., 2016).

Major physiological traits such as plant height and heading date are known to affect FHB reaction traits such as FHB visual ratings and DON (Klahr et al., 2007). One such example of this confounding effect can be seen in M. S. Islam et al. (2016), where the known photoperiodism locus *Ppd-D1* appears as resistance QTL on chromosome 2D for percent incidence and severity. This type of resistance is related to wheat plants escaping the window of infection via late or early flowering and larger distance from inoculum source (Schroeder & Christensen, 1963). These characteristics may be undesirable in cultivar development due to the rigid agronomic requirements for height and heading date that are commonplace in target growing regions. Moreover, negative effects on grain yield may be observed due to unoptimized heading date and height (Grogan et al., 2016; M. A. Islam et al., 2013).

The confounding effects of plant height and heading date are noted in other diseases of wheat, like *Septoria nodorum* blotch (*Parastagonospora nodorum*) (Francki et al., 2020; Rivera-Burgos et al., 2022). Prior literature has attempted to control for these confounding effects by including traits like plant height as fixed effects in mixed linear modeling (Francki et al., 2020). Rivera-Burgos et al. (2022) performed QTL mapping for *Septoria nodorum* blotch and included peak markers of identified plant height and heading date QTL as fixed effects in QTL mapping for disease response traits. Likewise, it is important to consider what effects plant height and heading date have on FHB infection due to their known association (Klahr et al., 2007), and to attempt to implement some type of control in analysis.

The United States Department of Agriculture-Agricultural Research Service (USDA-ARS) Eastern Small Grains Genotyping Laboratory annually evaluates eastern winter wheat germplasm with a panel of DNA markers to assay for the presence of loci associated with FHB resistance (Brown-Guedira, 2011; Winn et al., 2022). This panel includes markers flanking QTL identified in Bess, NC-Neuse, and Jamestown, as well as the *Fhb1* locus. Genotyped lines include entries in the annual Southern Uniform Winter Wheat Scab Nursery (SUWWSN), which consists of advanced lines from numerous public breeding programs evaluated for FHB reaction in inoculated nurseries grown at multiple locations. The SUWWSN is representative of the elite lines used for cultivar development in the southeastern United States (Murphy et al., 2019, 2020).

The soft red winter wheat cultivar Jamestown (PI 653731) (Griffey et al., 2010) is used annually as a resistant check in the SUWWSN (Winn et al., 2023). It is a frequent parent in cultivar development crosses in the southern United States, and it contributed one half of the parentage to a North Carolina breeding line NC13-20076 (PI 700335; Jamestown//GA951231-4E29/NCAG11). NC13-20076 exhibited exceptional resistance to FHB in the 2016 and 2017 SUWWSN (Murphy et al., 2016, 2017); moreover, the disease resistance observed in NC13-20076 was statistically similar to Jamestown, yet NC13-20076 was significantly taller and later maturing (Murphy et al., 2017).

Marker analysis indicated that NC13-20076 does not contain haplotypes associated with previously identified resistance QTL, including *Fhb1* or the 1B Jamestown haplotype associated with *QFHB.vt-1B.1* and *QFHB.vt-1B.2* (Murphy et al., 2016). Therefore, the objective of this research was to (1) evaluate reaction to FHB infection in a doubled-haploid population derived from a cross between NC13-20076 and GA06493-13LE6, (2) perform interval and multiple QTL mapping to identify what regions of the NC13-20076 haplotype are associated with FHB reaction, and (3) estimate the effects of these newly identified QTL.

Core Ideas

- Results indicate that NC13-20076 has several *Fusarium* head blight (FHB) response quantitative trait loci (QTL), which overlap with previously identified QTL.
- Using peak markers for plant height and heading date facilitates FHB QTL discovery.
- The FHB resistance observed in NC13-20076 is controlled by many small-effect reaction QTL.
- The FHB QTL identified in this study may be validated in separate populations and used in marker-assisted selection.
- NC13-20076 is a readily accessible source of native FHB QTL.

2 | MATERIALS AND METHODS

2.1 | Plant materials

A doubled haploid population of 168 individuals was developed using the wheat by maize (*Zea maize* L) crossing system with F_1 seed from the cross between the FHB-resistant soft red winter wheat line NC13-20076 and the susceptible GA06493-13LE6. Both NC13-20076 and GA06493-13LE6 were genotyped for major loci known to affect height (*RhtB1* and *RhtD1*), photoperiod (*Ppd-A1*, *Ppd-B1*, and *Ppd-D1*), and vernalization requirements (*Vrn-A1, Vrn-B1*, and *Vrn-D1*). All loci, except *Vrn-A1*, were determined to be non-polymorphic (Supporting Information S1).

NC13-20076 (PI 700335; Jamestown//GA951231-4E29/NCAG11) was developed at North Carolina State University. Jamestown (PI 653731; Roane/Pioneer Brand 2691) is a cultivar developed by Virginia Polytechnic Institute and State University (VT) (Griffey et al., 2010). NCAG11 (PI 615588; Saluda*3/PI 427315) is an elite germplasm line, which was developed at North Carolina State University and possesses the *Pm37* powdery mildew resistance gene derived from *Triticum timopheevii* Zhuk. (Murphy et al., 2002; Perugini et al., 2008). GA06493-13LE6 (GA981394-16-2-1/AGS2035) was developed by the University of Georgia Small Grains Breeding and Genetics program.

2.2 | Experimental design

The population founders and doubled haploid lines were assessed in six environments (site-year combinations): Cunningham Research Station in Kinston, NC in 2018–2019 (KIN19) and 2019–2020 (KIN20); Lake Wheeler Field

Laboratory, Raleigh, NC in 2018–2019 (RAL19) and 2019–2020 (RAL20); and VT's Eastern Virginia Agricultural Research Extension Center, Warsaw, Virginia in 2018–2019 (WAR19) and 2019–2020 (WAR20). All lines were planted in mid to late October in single 1.2 m rows spaced 0.3 m apart in a randomized complete block design with two replicates in each environment.

For KIN19, KIN20, RAL19, and RAL20, *F. graminearum* inoculum was produced as follows. Corn kernels were measured into autoclavable bags at a rate of 1.5 kg per bag, and the bags were autoclaved on each of two successive days. Each bag was then inoculated with approximately 20 mL of a roughly equiproportional mixture of six *F. graminearum* isolates derived from wheat and barley (*Hordeum vulgare* L) spikes that had been collected in the previous year's FHB nursery. The inoculated corn was incubated for 14 days in the bags and then air-dried for 3 weeks. Corn inoculum was applied at a total rate of 1.5 kg per 80 lines in thirds: one third at Feekes 10.1, the second third at Feekes 10.3, and the final third at Feekes 10.52. All environments were mist-irrigated to increase the relative humidity during the window of infection to encourage an epidemic.

For WAR19 and WAR20, isolates collected from FHB-symptomatic wheat spikes by the VT Department of Plant Pathology, Physiology, and Weed Science were plated on full-strength potato dextrose agar media. Corn kernels were soaked overnight in autoclavable bags and then steam sterilized for 24 h and allowed to cool to 21°C before inoculation with FHB isolates. Mycelial *Fusarium* cultures were cut into 1 cm^2 pieces and incubated with corn kernels at room temperature for 21 days. After incubation, corn inoculum was dried from 4 to 7 days in a greenhouse. A single application of corn inoculum was applied at 4 kg per 80 lines at Feekes stage 10, and mist irrigation was applied to increase relative humidity and promote an epidemic.

2.3 | Phenotyping

Heading date was recorded as the day of the year from January 1 at RAL19, RAL20, KIN20, and WAR20 when approximately 50% of the heads had emerged from the boot in a plot. Plant height was measured in centimeters from the plant base at the center of the plot to the tip of the spike, excluding awns, at KIN20 and RAL20. A visual rating for FHB ranging from 0 to 9 was taken at RAL19, RAL20, KIN19, KIN20, and WAR20, where 0 indicated 0% of the spikelets in a plot showed symptoms and 9 indicated that 100% of spikelets in a plot showed symptoms.

At physiological maturity, plots were hand harvested, dried, and threshed using an Almaco stationary electrical thresher (Almaco) with the fan disabled. Grains were manually cleaned using hand sieves and low-speed table fans to ensure retention of *Fusarium* damaged kernels (FDK). Percent FDK was visually scored for all environments by referencing standards that ranged from 0% to 100% scabby seed in 5% increments. Kernels were considered damaged if they had a shriveled, white-to-gray-to-pink appearance.

A subsample of 60–100 g of seed was taken from the bulked seed of each plot, and DON concentration was measured using gas chromatography-mass spectrometry at the University of Minnesota DON Testing Lab for KIN19, KIN20, RAL19, RAL20, and WAR19. The subsamples taken from WAR20 were measured for DON via gas chromatography-mass spectrometry at VT. Concentrations of DON were reported in parts per million (ppm).

2.4 | Phenotypic analysis

Data were analyzed using R statistical software version 4.4.1 (R Core Team, 2024). Data were quality checked for incorrect data input and violations of assumptions of linearity using QQ plots from the base R package "stats." Non-normality for FHB visual ratings, percent FDK, and DON was observed due to their zero-inflated nature. A series of mixed linear models and generalized linear models were employed via the function "asreml" in the package "asreml" in R statistical software (Butler et al., 2009). A normal Gaussian distribution was used for heading date and plant height, and a Poisson distribution was used for FHB visual ratings, FDK, and DON to account for non-normality. For single environment analysis, if semi-parametric generalized mixed linear models for FHB reaction traits failed to converge, a normal distribution was utilized instead. For single environment analysis, the following model was utilized:

$$y_{ij} = \mu + G_i + r_j + \varepsilon_{ij}$$

where y is the response, μ is the mean, G is the genotype effect and is treated as fixed, r is the replication effect and is treated as random, and ε is the residual error where $\varepsilon \sim (0, \sigma^2_\varepsilon)$. Best linear unbiased estimates (BLUEs) of the genotype effect were calculated from each single environment model. The following multi-environment model was used to calculate BLUEs across years:

$$y_{ijk} = \mu + G_i + e_j + ge_{ij} + er_{jk} + \varepsilon_{ijk}$$

where y is the response, μ is the mean, G is the fixed genotype effect when estimating BLUEs and the random genotype effect when estimating variance, e is the random environment effect, ge is the random genotype-by-environment effect, er is the random environment-by-replication effect, and ε is the residual error where $\varepsilon \sim (0, \sigma^2_\varepsilon)$. Trait correlations were calculated using BLUEs derived from multi-environment

models and visualized using the R package "psych" (Revelle, 2024). To assess significance of genotype-by-environment interactions, the following mixed model was implemented:

$$y_{ijk} = \mu + G_i + E_j + GE_{ij} + er_{jk} + \varepsilon_{ijk}$$

where y is the response, μ is the mean, G is the fixed genotype effect when estimating, E is the fixed environment effect, GE is the fixed genotype-by-environment effect, er is the random environment-by-replication effect, and ε is the residual error where $\varepsilon \sim (0, \sigma^2_\varepsilon)$.

Variance component estimates were drawn from fully random multi-environment models, and heritability's of all traits on a per-plot and entry-mean basis were estimated as described by Holland et al. (2003). Per-plot, narrow-sense heritability was calculated using the following equation:

$$h^2_{pp} = \frac{\sigma^2_G}{\sigma^2_G + \sigma^2_{GE} + \sigma^2_\varepsilon}$$

where σ^2_G is the genotypic variance, σ^2_{GE} is the genotype-by-environment variance, and σ^2_ε is the error variance. Entry-mean heritability was estimated using the following formula:

$$h^2_{em} = \frac{\sigma^2_G}{\sigma^2_G + \frac{\sigma^2_{GE}}{e} + \frac{\sigma^2_\varepsilon}{er}}$$

where σ^2_G is the genotypic variance, σ^2_{GE} is the genotype-by-environment variance, σ^2_ε is the error variance, e is the harmonic mean of the number of environments for which the response of the individuals was observed, and r is the harmonic mean of the number of replicates for which the response was recorded.

2.5 | Genotyping

Genomic DNA was isolated from tissue samples taken from all lines of the doubled haploid population and population parents at the seedling stage using sbeadex plant maxi kits (LGC Genomics). Genotyping-by-sequencing (GBS) was performed as described in Poland et al. (2012), and 96-plex libraries were sequenced on an Illumina HiSeq 2500. Reads were aligned to the Chinese Spring RefSeqv1.0 assembly (Consortium [IWGSC] et al., 2018) via Tassel5GBSv2 pipeline version 5.2.35 (Glaubitz et al., 2014) using the Burrows-Wheeler aligner version 0.7.12 to call SNPs (Li & Durbin, 2009). The raw data produced were filtered by removing SNPs at a minor-allele frequency of <5%, SNPs that had a heterozygous call frequency of >10%, SNPs with >20% missing data, and SNPs with a read-depth >100.

2.6 | Linkage map construction and QTL analysis

Molecular markers were ordered in linkage groups using the algorithm by Wu et al. (2008) in the package "ASMap" in R (Taylor & Butler, 2017). The following parameters were used in the "mstmap" function: population type was set to doubled haploid, and the missing marker data threshold was 30%. The function "pullcross" was used to remove markers that did not fit a chi-square analysis for 1:1 ratio at a p-value of 0.0001 and to select only one marker in regions of co-located markers.

Interval mapping was conducted using the R package "qtl" (Broman & Sen, 2009; Broman et al., 2003; Jansen, 1993). Genotype probabilities were calculated with an error probability of $p = 0.0001$ using a step of two centimorgans (cMs), a fixed step width, and the Kosambi function. Genotypes were simulated with 128 draws and an error probability of $p = 0.0001$. Using the genotype probabilities and simulated genotypes, the following options were used for the function "scanone" to perform interval mapping: The model was set to normal, Haley–Knott regression was the method of likelihood of odds (LOD) calculation, and LOD thresholds were set using 1000 permutations at $\alpha = 0.05$.

Multiple QTL mapping was conducted using the function "addqtl" via the following steps. Previously identified QTL from interval mapping scans were placed into an object via the "makeqtl" function and used as covariates in an additional scan for QTL via the Haley–Knott regression method. New QTL identified in each round of multiple QTL mapping were checked for significance via the function "fitqtl"; any QTL that had a p-value ≤ 0.05 were dropped from the QTL object. Several rounds of multiple QTL mapping were performed until no new significant peaks were detected. A final round of marker regression was performed to check model significance and single marker significance, and any markers that had a p-value ≤ 0.05 were dropped from the QTL object. Only additive effects were estimated among QTL (e.g., no epistatic, or QTL-by-QTL interactions). Percent variance explained and marker effect were drawn from final "fitqtl" model drop-one analysis results.

Peak positions of significant QTL identified by interval mapping and multiple QTL mapping were refined using the iterative LOD optimization algorithm in the "refineqtl" function. Support intervals of QTL were drawn using the function "lodint" with the parameter "drop" set to 1.5 LOD, indicating that all QTL intervals were defined by all surrounding markers that were 1.5 LOD less than the peak marker.

To meet the assumptions required for a QTL analysis, FHB reaction traits (visual ratings, FDK, and DON) were subjected to semi-parametric analysis (generalized linear mixed model) as stated in the prior section. This led to a rescaling of the FHB reaction trait BLUEs, and thus the estimated effects derived

from "fitqtl" are stated in the scale of those BLUEs (e.g., visual ratings were 0–9 as observations, and after adjustment they were bound between 0 and approximately 2 as BLUEs).

To provide estimates, which are interpretable to the reader, multiple marker regression on unadjusted observations across all environments was conducted for QTL identified in multi-environment models. The multiple linear regression model utilized in this estimation is as follows:

$$y_i = \beta_0 + \beta_1 x_{i,1} + \cdots + \beta_{p-1} x_{i,p-1} + \varepsilon_i$$

where y_i is the ith unadjusted observations of the trait (e.g., visual ratings) across all environments, p is the total number of peak markers assessed in the model, β_0 is the intercept, β_1 is the peak marker associated with the first QTL identified in the multi-environment QTL scan, β_{p-1} is the peak marker of the final QTL identified in the multi-environment QTL scan, and ε is the residual error, which is independent and identically distributed. Non-additive effects (e.g., epistatic, or QTL-by-QTL interactions) were not estimated. Marker effects are stated in relation to inheriting the resistant form (NC13-20076) of the locus.

To control for this confounding of plant height and heading date with visual scores, FDK, and DON, all heading date and plant height QTL peak markers identified in the multi-environment analyses were fit as fixed effects in interval and multiple QTL mapping scans for FHB reaction traits. To do this, an initial round of interval and multiple QTL mapping was performed for heading date and plant height. Those QTL identified from initial scans for heading date and plant height were then delimited using the same 1.5 LOD support intervals method as previously described. The peak markers of multi-environment heading date and plant height QTL were then placed in a matrix and fit as fixed effects in interval and multiple QTL mapping scans of FHB visual rating, FDK, and DON.

3 | RESULTS

3.1 | Phenotypic evaluation and linkage map construction

When plot-level observations were examined via histograms and quantile-quantile plots within and across environments, no obvious outliers were evident. Therefore, all collected data were utilized for the data analyses. For all trait-by-environment combinations, the genotypic effect was significant ($p < 0.05$). After subjecting FHB reaction traits (FHB visual ratings, FDK, and DON) to semi-parametric generalized mixed linear model analysis, BLUEs were rescaled to new distributions (Figure 1; Table 1). The multi-environment BLUEs of visual ratings were bound between 0.31 and .92 with a mean of 1.58 and were 0.46 for NC13-20076 and 1.92

TABLE 1 Table of summary statistics for multi-environment best linear unbiased estimates of all traits.

Trait	Summary statistics				Parental BLUEs[a]		Per-plot heritability		Entry-mean heritability	
	Minimum	Mean	Maximum	SD	NC13-20076	GA06493-13LE6	h^2_{pp} [b]	SE	h^2_{em} [c]	SE
Deoxynivalenol content	0.40	1.88	3.53	0.50	0.40	3.53	0.10	0.01	0.83	0.02
Fusarium damaged kernels	1.97	3.23	4.35	0.43	1.97	4.35	0.02	0.00	0.60	0.03
Heading date	92.2	99.4	104.1	2.0	96.8	101.3	0.52	0.03	0.93	0.01
Plant height	74.4	91.7	105.0	5.7	91.8	92.9	0.62	0.04	0.89	0.02
Visual ratings	0.31	1.16	1.92	0.33	0.47	1.92	0.18	0.02	0.87	0.02

Note: Visual ratings, *Fusarium* damaged kernels, and deoxynivalenol (DON) content are stated in the scale determined by semi-parametric analysis. Heading date starts in days from the first of January. Plant height is stated in centimeters. Resistant (NC13-20076) and susceptible (GA06493-13LE6) parental means are to the right of summary statistics. Per-plot and entry-mean heritability and their resultant standard errors are given in the final four columns.

Abbreviations: SD, standard deviation; SE, standard error.

[a]Best linear unbiased estimates of parental values.

[b]Per-plot heritability.

[c]Entry mean heritability.

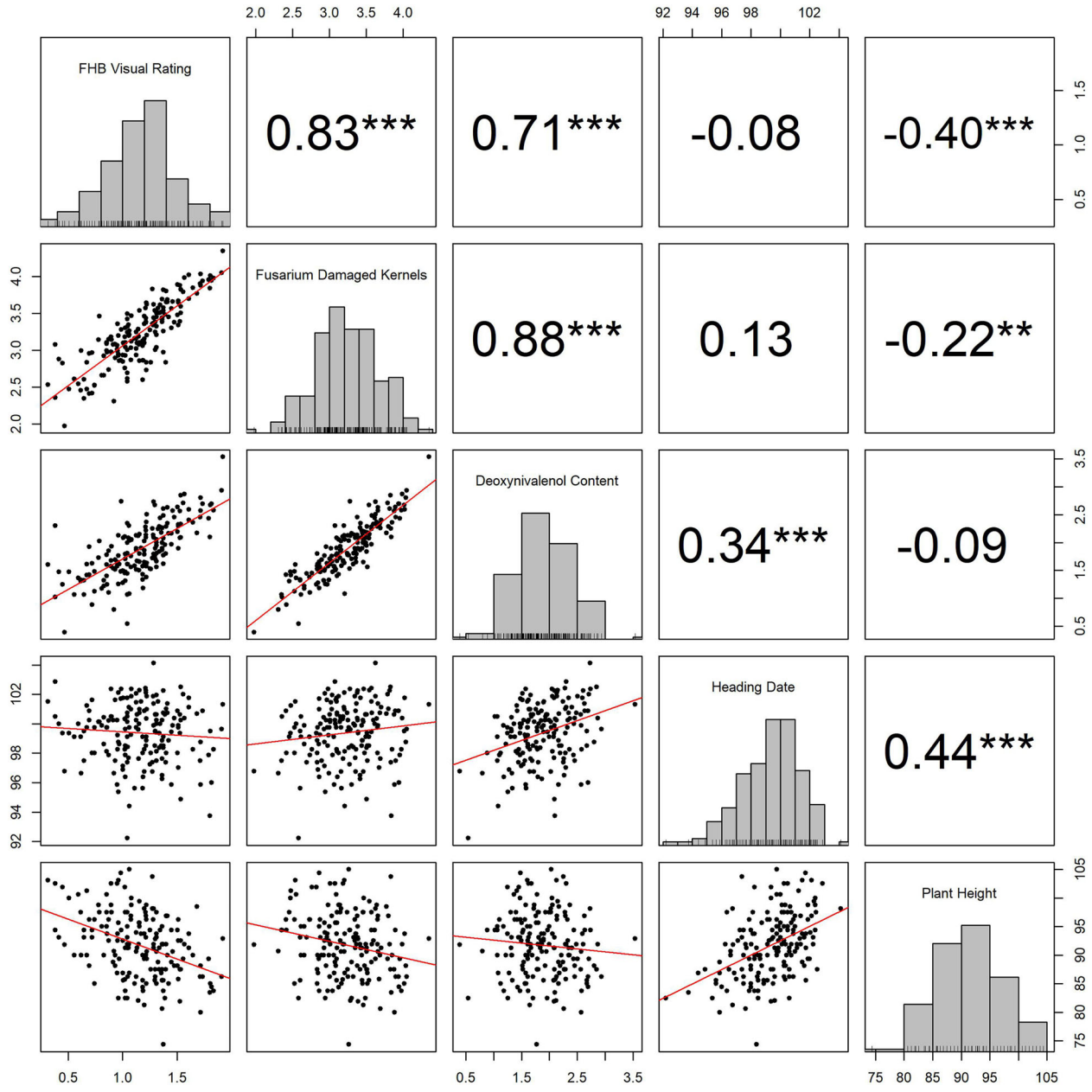

FIGURE 1 A pairs plot of multi-environment best linear unbiased predictions for visual ratings of *Fusarium* head blight (FHB) damage, *Fusarium* damaged kernels, deoxynivalenol (DON) content, heading date, and plant height. The diagonal of the pairs plot shows the histogram of each trait denoted by the text in the box. The lower left triangle shows a scatter plot of the corresponding traits, fitted with a linear regression to show a linear relationship among traits. The top right triangle displays Pearson's correlation coefficient followed by a significance indicator. Significance is denoted as $*p(t) < 0.05$, $**p(t) < 0.01$, and $***p(t) < 0.001$.

for GA06493-13LE6. Multi-environment BLUEs of FDK were bound between 1.97 and 4.35 with a mean of 3.23 and were 1.97 for NC13-20076 and 4.35 for GA06493-13LE6. Multi-environment BLUEs of DON were bound between 0.39 and 3.53 with a mean of 1.88 and were 0.39 for NC13-20076 was and 3.53 for GA06493-13LE6. Significant correlations were observed between multi-environment BLUEs for all pairs of traits, except in the case of heading date versus FHB visual ratings and FDK and DON versus plant height (Figure 1).

Significant positive correlations were observed among disease response traits ($r: 0.71 \leq r \leq 0.88$). A significant positive correlation was observed between DON and heading date ($r = 0.34$). Furthermore, significant correlations were observed for plant height versus FHB visual ratings ($r = -0.40$) and FDK ($r = -0.22$). This indicates that plant height and heading date may affect disease ratings by contributing to avoidance (Schroeder & Christensen, 1963). The wide range of heights and heading dates in this population may have had an effect on disease interaction, and these

correlations are expected and consistent with previous literature (Klahr et al., 2007). Per-plot heritability's across environments ranged from exceptionally low for FDK ($h^2_{pp} = 0.02$) to moderately high for plant height ($h^2_{pp} = 0.62$; Table 1). Entry-mean heritability's ranged from moderately high for FDK ($h^2_{em} = 0.60$) to exceptionally high for heading date ($h^2_{em} = 0.93$), indicating that all traits were moderately to highly heritable over environments.

Multi-environmental analysis with fixed effects for genotype, environment, and genotype-by-environment interaction indicated significant genotype ($p < 0.05$), environment ($p < 0.05$), and genotype-by-environment ($p < 0.05$) interactions for all observed traits (Supporting Information S2). Correlation of plant height among the two locations assessed was high ($R = 0.74$) and significant ($p < 0.05$). Correlations among environments for heading date were significant ($p < 0.05$) and ranged from 0.65 to 0.73. Correlations of visual ratings among environments were significant ($p < 0.05$) and ranged from 0.30 to 0.75. Correlations of FDK among environments were significant ($p < 0.05$) and ranged from 0.39 to 0.56. Correlations of DON content were significant ($p < 0.05$) and ranged from 0.44 to 0.64. Due to significant correlations among environments, yet significant genotype by environment interactions, a mixed approach of single-environment and multi-environment analysis was adopted for QTL mapping.

After filtering SNPs and constructing a linkage map, a final map of 1984 polymorphic SNPs across 21 linkage groups was made, and all linkage groups were designated by the chromosome of marker origin based on alignment to the Chinese Spring v1.0 reference genome (Supporting Information S3). The number of markers per linkage group ranged from seven markers on chromosome 3D up to 216 markers on 3B. Marker density was notably lower on the D sub-genome, particularly for chromosomes 3D and 4D that are not well represented in the linkage map. This is likely due to low polymorphism between the establishing lines of the population. Low coverage on the D genome is also consistent with many other studies of wheat populations (Brenchley et al., 2012).

3.2 | Identification plant height and heading date QTL

For QTL scans of multi-environment BLUEs, significant heading date QTL were identified on chromosomes 4A, 5A, 6D, and 7B (Figure 2). The QTL, which accounted for the highest percentage (18.1%) of variance for heading date, were identified on chromosome 5A (*QHd.nc-5A.1*) from 574.7 to 595.5 megabase pairs (Mbp) and detected in three of four environments where heading date was recorded (Table 2). Scan plots and tables for plant height and heading date QTL scans are provided for each environment-by-trait combination and the multi-environment BLUEs (Supporting Information S4). A visualization of all QTL 1.5-LOD support intervals identified across all environment-by-trait combinations and the multi-environment scans is also provided (Supporting Information S5).

The known location of the vernalization locus *Vrn-A1* resides within the *QHd.nc-5A.1* support interval. A SNP marker located in exon 4 of the *Vrn-A1* locus associated with copy number variation and differences in heading date (Díaz et al., 2012) was polymorphic between the parents of the population (Supporting Information S1). Previous marker assays have indicated that NC13-20076 possesses the short vernalization allele associated with two copies of the winter allele of the *Vrn-A1* locus, which is associated with earlier heading (Supporting Information S1). For its part, GA06493-13LE6 possesses the vernalization allele associated with three copies of the winter allele of *Vrn-A1* and a later heading date (Brown-Guedira, 2016; Díaz et al., 2012). This suggests that high percent variance QTL (18.1%) are associated with differences at the *Vrn-A1* locus. An additional locus on 5A for heading date was detected distal to *Vrn-A1* (Table 2; Figure 3).

The QTL located on the short arm of chromosome 7B (11.4–53.7 Mbp) were detected in all four environments where heading date was recorded and accounted for a relatively small amount of the total variance (9.2%). The 7B QTL, *QHd.nc-7B*, encompass a region that may contain or be in linkage with the gene *Vrn-B3*, which is located at 9.7 Mbp in the Chinese spring v1.0 reference genome (Consortium (IWGSC) et al., 2018; Yan et al., 2006). Finally, two QTL were identified on 4A and 6D, respectively. *QHd.nc-4A* and *QHd.nc-6D* were only detected in one and two environments, respectively, and explained less variation than QTL on 5A or 7B (Table 2).

Significant plant height QTL were identified on chromosomes 4A and 6A (Figure 3). The plant height QTL (*QPht.nc-6A*) that accounted for the largest percent variance (22.2%) and had the largest effect (+2.7 cm) were detected in both environments and are located on chromosome 6A between 52 and 100 cM (52.0–636 Mbp) (Table 2). Within this peak lies the known location of the height reduction loci *Rht24* and *Rht25* (Mo et al., 2018; Tian et al., 2017, 2022; Zhang et al., 2023), which may be related to the QTL observed in this population. The physical location of plant height QTL on chromosome 4A (603.1–636.1 Mbp) overlapped with the observed QTL for heading date.

There was a wide range of phenotypic values observed for heading date and plant height in the current population (Figure 1). Moreover, significant correlations were observed for plant height and heading with FHB reaction traits (Figure 1). Additionally, our initial QTL scan identified plant height and heading date QTL on chromosomes 4A, 5A, and 6A that were co-located with FHB reaction QTL (Supporting Information S4, Supporting Information S5). Therefore,

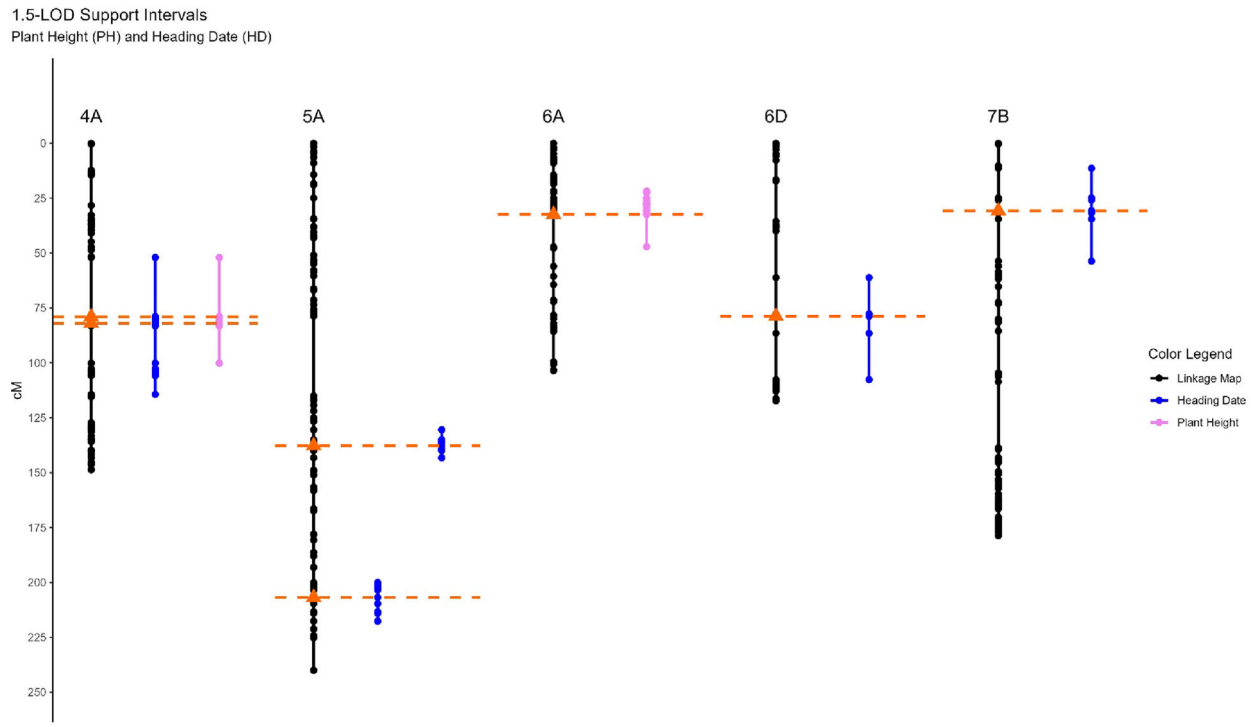

FIGURE 2 A visualization of linkage groups (chromosomes) with 1.5 likelihood of odds (LOD) quantitative trait loci (QTL) support intervals for multi-environment scans of heading date and plant height. The *y*-axis displays the length of chromosomes in recombination-based centimorgan (cM) distance. Chromosomes are visualized as lines (demonstrating the length between markers) and dots (demonstrating the position of each marker). Each chromosome is denoted by the label at the top of each line graph. Each bar to the right of each chromosome denotes the length and general location of a 1.5-LOD support interval, and the color of the bar, as denoted by the figure legend on the right, indicates the trait to which the 1.5-LOD support interval belongs. Peak markers labeled with orange, enlarged triangles and dashed lines were used as covariates for scans of *Fusarium* head blight reaction traits.

TABLE 2 Table of plant height and heading date quantitative trait loci (QTL) information.

			Left flanking position		Peak position		Right flanking position				
QTL[a]	N[b]	Chr[c]	cM[d]	Mbp[e]	cM	Mbp	cM	Mbp	LOD	PV[f]	Effect[g]
QHd.nc-4A	1	4A	52.0	603.1	82.0	618.4	114.4	695.7	5.5	6.4	−0.5
QHd.nc-5A.1	3	5A	130.5	574.7	138.0	584.8	143.2	595.4	13.8	18.1	−0.8
QHd.nc-5A.2	3	5A	200.1	673.7	208.0	684.9	217.7	690.2	9.4	11.6	−0.7
QHd.nc-6D	2	6D	61.2	38.8	82.0	422.1	107.6	455.5	1.7	1.9	−0.3
QHd.nc-7B	4	7B	11.4	3.4	30.0	12.8	53.7	24.4	7.7	9.2	−0.6
QPht.nc-4A	2	4A	52.0	603.1	74.0	620.2	100.1	636.1	3.9	8.0	−1.8
QPht.nc-6A	2	6A	21.7	67.1	34.0	459.7	47.1	585.0	10.0	22.2	2.7

Note: Displayed is the name of the QTL, the chromosome upon which the QTL reside, the trait which the QTL affect, the centimorgan (cM) and megabase pair (Mbp) position of the flanking marker most proximal to the distal short arm of the chromosome, and the cM and Mbp position of the flanking marker most distal to the short arm of the chromosome. Effect size, standard error (SE), and percent variance accounted for calculated by drop-one analysis are also displayed. All effects are stated in reference to inheriting the resistant parent (NC13-20076) allele.

Abbreviation: LOD, Likelihood of odds.

[a]QTL designation: Pht: plant height; Hd: heading date.

[b]Number of environments where the QTL were observed.

[c]Chromosome name.

[d]Distance.

[e]Megabase pair position in reference to the Chinese Spring v1.0 reference genome.

[f]Percent variance calculated by drop-one analysis.

[g]Estimated effect: Pht: centimeters; Hd: number of days.

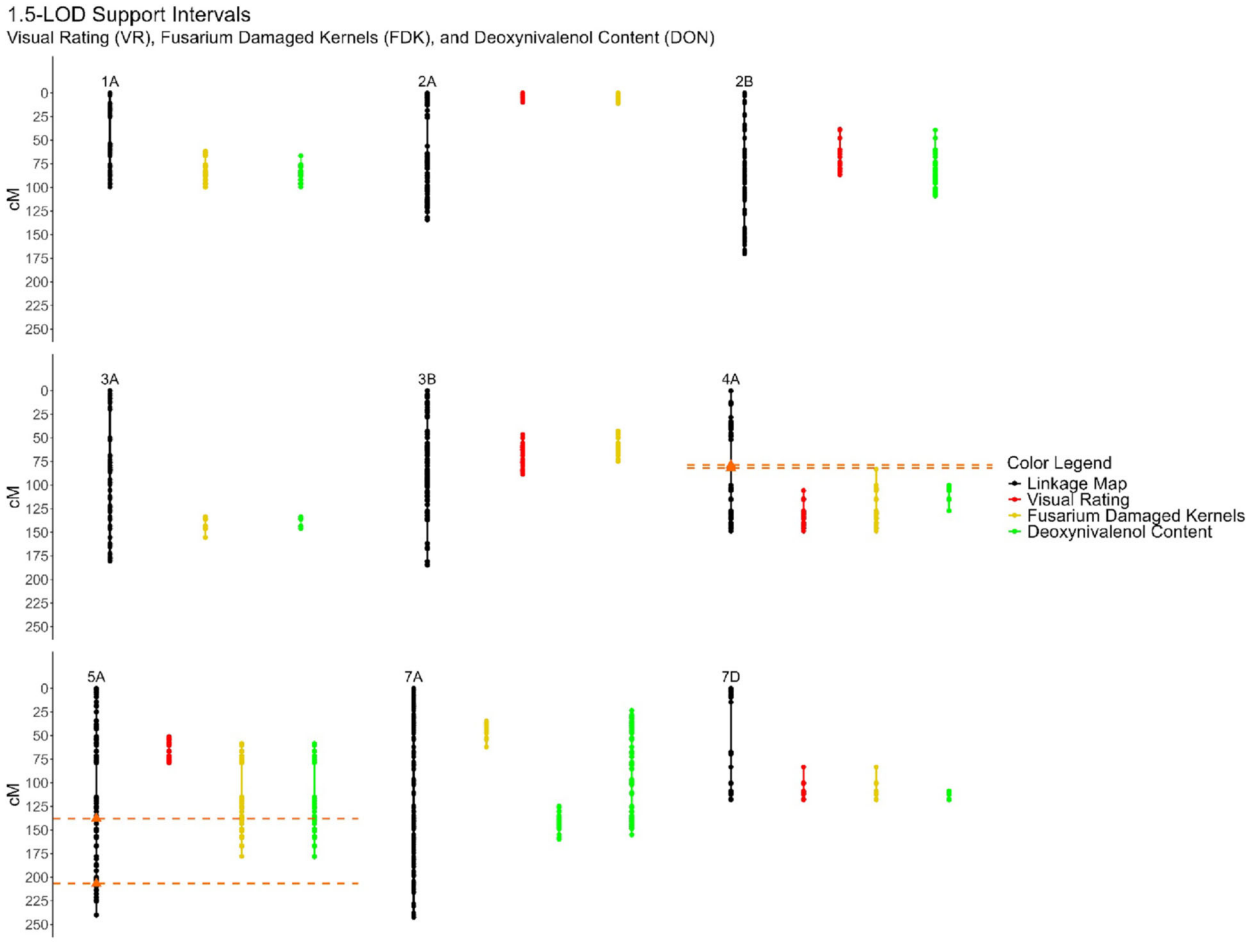

FIGURE 3 A visualization of linkage groups (chromosomes) with 1.5 likelihood of odds (LOD) quantitative trait loci (QTL) support intervals for the multi-environment scans of *Fusarium* head blight (FHB) reaction traits: visual rating, *Fusarium* damaged kernels, and deoxynivalenol (DON) content after the inclusion of peak markers for heading date and plant height as covariates. The *y*-axis displays the length of chromosomes in recombination-based centimorgan (cM) distance. Chromosomes are visualized as lines (demonstrating the length between markers) and dots (demonstrating the position of each marker). Each chromosome is denoted by the label at the top of each line graph. Each bar to the right of each chromosome denotes the length and general location of a 1.5-LOD support interval, and the color of the bar, as denoted by the figure legend on the right, indicates the trait to which the 1.5-LOD support interval belongs. Markers labeled with orange, enlarged triangles and dashed lines were used as covariates for scans displayed intervals.

peak markers of all identified multi-environment BLUEs QTL scans for plant height and heading date (Figure 2) were used as covariates for new QTL scans involving FHB reaction traits.

3.3 | Regions associated with reaction to FHB infection

After inclusion of peak heading date and plant height markers as covariates, FHB reaction QTL, which co-occurred across and within environments, were detected on chromosomes 1A, 2A, 2B, 3A, 3B, 4A, 5A, 7A, and 7D (Table 3; Figure 3). Scan plots and tables for all FHB visual ratings, FDK, and DON QTL scans are provided for each environment-by-trait combination and the multi-environment BLUEs (Supporting Information S6). A visualization of all QTL 1.5-LOD support intervals identified across all environment-by-trait combinations and the multi-environment scans is also provided (Supporting Information S7).

Note that the consistent QTL on chromosome 1A were identified for *Fusarium* damaged kernel (*QFdk.nc-1A*) over three environments and for DON (*QDon.nc-1A*) in all six environments assessed. This region shared a nearly identical support interval among the two traits (Table 3) and accounted for 8.2% and 10.3% of the total variance for DON and FDK, respectively. The region encompassing both FHB QTL was delimited to a wide region of nearly 241 Mbp (Table 3). The unadjusted estimated effect of this region suggests that inheriting the resistant haplotype of the locus results in a reduction of 2.4 ppm DON and 6.7% FDK.

The FHB QTL located on the distally (39.6–45.1 Mbp) on the short arm of chromosome 2A (*QFvr.nc-2A*, *QFdk.nc-2A*)

TABLE 3 Table of *Fusarium* head blight (FHB) resistance quantitative trait loci (QTL).

			Left flanking position		Peak position		Right flanking position					
QTL[a]	N[b]	Chr[c]	cM	Mbp[d]	cM	Mbp	cM	Mbp	LOD	PV[e]	Effect[f]	Unadjusted effect[g]
QDon.nc-1A	6	1A	66.4	369.1	86	514.1	99.6	544.5	7.1	8.2	−0.14	−2.4
QDon.nc-2B	3	2B	39.3	34.6	84	159.5	109	700.4	4.8	5.4	−0.11	−2.4
QDon.nc-3A	3	3A	133.7	703	135.8	708	146.1	716.1	8.3	9.9	−0.15	−2.7
QDon.nc-4A	2	4A	100.1	634.8	108	645.7	127.2	703.9	6.0	6.9	−0.13	−2.2
QDon.nc-5A	1	5A	58.5	455.3	75.7	494.4	178.3	653.3	8.5	10.1	−0.19	−3.0
QDon.nc-7A.1	2	7A	23.4	12.5	48	29.3	155	637.3	4.4	4.9	−0.11	−1.5
QDon.nc-7A.2	1	7A	124.7	101.3	137.8	365.1	159.8	652.5	4.4	4.9	−0.10	−2.3
QDon.nc-7D	2	7D	108.6	194.1	117.2	517.5	118	527.7	4.8	5.4	0.11	2.4
QFdk.nc-1A	3	1A	61.8	303.7	88.1	530.3	99.6	544.9	9.1	10.3	−0.13	−6.7
QFdk.nc-2A	2	2A	0	39.6	0.8	42.2	11	45.1	5.6	6.0	−0.10	−5.5
QFdk.nc-3A	3	3A	133.7	703	140	714.4	155.4	717.3	7.1	7.8	−0.12	−5.6
QFdk.nc-3B	2	3B	42.9	42.9	52	62.4	74.9	581.3	3.9	4.1	−0.09	−4.9
QFdk.nc-4A	2	4A	83.2	618.3	112	695.7	148.6	744.4	5.3	5.7	−0.10	−4.2
QFdk.nc-5A	1	5A	58.5	455.3	62	458.5	177.9	650.5	7.8	8.7	−0.12	−6.7
QFdk.nc-7A	2	7A	34.7	20.2	50	30.9	62.1	36.5	6.5	7.0	−0.11	−5.6
QFdk.nc-7D	1	7D	83.3	78.9	117.2	517.5	118	527.7	5.6	6.1	0.10	5.7
QFvr.nc-2A	1	2A	0	39.6	2	42.5	9.8	45.1	3.0	4.1	−0.06	−0.5
QFvr.nc-2B	2	2B	38.4	32.1	66	74.2	86.5	164	4.6	6.5	−0.08	−0.6
QFvr.nc-3B	2	3B	46.4	58.8	58.7	252.4	88.6	678.5	4.4	6.1	−0.08	−0.4
QFvr.nc-4A	2	4A	105.8	645.7	114.9	693.4	148.6	744.4	3.0	4.0	−0.06	−0.4
QFvr.nc-5A	2	5A	50.9	400.5	60.4	458.5	78.7	503.9	7.5	10.8	−0.10	−0.7
QFvr.nc-7D	1	7D	83.3	78.9	118	527.7	118	527.7	5.2	7.3	0.09	0.6

Note: Displayed is the name of the QTL, the chromosome upon which the QTL reside, the trait which the QTL affect, the centimorgan (cM) and megabase pair (Mbp) position of the flanking marker most proximal to the distal short arm of the chromosome cM and Mbp position, the peak marker of the QTL, and the flanking marker most distal to the distal short arm of the chromosome. Likelihood of odds (LOD), percent variance (PV), and effect were calculated by drop-one analysis are also displayed. Unadjusted effects were calculated via multiple marker regression on unadjusted observations. All effects are stated in reference to inheriting the resistant (NC13-20076) form of the FHB resistance QTL.

[a]QTL designation: Don: deoxynivalenol content; Fdk: *Fusarium* damaged kernels; Fvr: *Fusarium* head blight visual rating.

[b]Number of environments where the QTL were observed.

[c]Chromosome name.

[d]Megabase pair position in reference to the Chinese Spring v1.0 reference genome.

[e]Percent variance calculated by drop-one analysis.

[f]Estimated effect scaled to adjusted best linear unbiased estimates.

[g]Unadjusted estimate in the scale of the raw observations: Don—parts per million, Fdk—percent *Fusarium* damaged kernels, Fvr—ordinal scale from 0 to 9.

affect both visual ratings (−0.5 points) and FDK (−5.5%) while accounting for a relatively small portion of the total variance (4.1%–6.0%). The support intervals for FHB QTL identified on 2B (*QFvr.nc*-2B, *QDon.nc*-2B) differ vastly between FHB visual ratings (38.4–164 Mbp) and DON (39.3–700.4 Mbp). When referring to scan plots of the multi-environment QTL scans for FHB visual ratings versus DON (Supplementary Information 5), the peak of the multi-environment QTL scan for FHB visual ratings was narrower than that of the DON scans, resulting in a smaller region for FHB visual ratings. Regardless, both *QFvr.nc-2B* and *QDon.nc-2B* account for a relatively small portion of the percent variance explained (6.5% and 5.4%, respectively) and have limited effect size (−0.6 points and −2.4 ppm, respectively).

The FHB QTL identified on the long arm of 3A (*QFdk.nc-3A* and *QDon.nc-3A*) were observed over three environments each and were delimited to a region of 703–717 Mbp. *QFdk.nc-3A* had an unadjusted estimated effect of −5.6% FDK, and *QDon.nc-3A* had an unadjusted estimated effect of −2.7 ppm DON content. Both *QFdk.nc-3A* and *QDon.nc-3A* accounted for a moderate proportion of variance (7.8% and 9.9%, respectively). The FHB QTL on 3B (*QFdk.nc-3B, QFvr.nc-3B*) were delimited to the pericentric region

(42.9–678.5 Mbp) of chromosome 3B, and those QTL affect both visual ratings (−0.4 points) and FDK (−4.9%) while accounting for 4.1%–6.1% of the total variance.

The FHB QTL located on the long arm (618.8–744.4 Mbp) of chromosome 4A affect FHB visual ratings (*QFvr.nc-4A*, estimated effect = −0.2 points), FDK (*QFdk.nc-4A*, estimated effect = −4.1%), and DON (*QDon.nc-4A*, estimated effect = −2.5 ppm) and account for a relatively small portion of the total variance (4.0%–6.9%). Interestingly, this region was found near the *QHd.nc-4A* and *QPht.nc-4A* QTL for heading date and plant height (Figure 2). Likewise, FHB QTL were identified on chromosome 5A for FHB visual ratings (*QFvr.nc-5A)*, FDK (*QFdk.nc-5A)*, and DON (*QDon.nc-5A*). The region for the QTL identified on 5A is delimited between 458.5 and 653.3 Mbp and accounts for a relatively large percentage of the total variance (8.7%–10.8%). This QTL region encompassed the *QHd.nc-5A.1* QTL identified for heading date.

On chromosome 7A, two separate FHB QTL were identified for DON (*QDon.nc-7A.1* and *QDon.nc-7A.2*) and one for FDK (*QFdk.nc-7A*). Both *QDon.nc-7A.1* and *QDon.nc-7A.2* are delimited to a region that spans the centromere and covers much of the 7A chromosome (12.5–652.5 Mbp). In contrast, the *QFdk.nc-7A* region is contained in a region on the short arm of 7A (20.2–36.5 Mbp).

When looking at the scan graphs for both the DON and FDK scan plots (Supporting Information S6), it appears that *QDon.nc-7A.1* was identified in the first round of multiple QTL mapping and *QDon.nc-7A.2* was identified in the second round of multiple QTL mapping. Furthermore, it appears that both *QDon.nc-7A.1* and *QDon.nc-7A.2* may have been originally delimited to separate regions without overlap; however, the position optimization algorithm in the "fitqtl()" function led to the two QTL being co-located. This implies that there is more than one QTL at play in this vast region of nearly 650 Mbp, and attempting to separate these QTL with the present phenotypic data yields poor results. These QTL account for a relatively small portion of the total variance (4.9%) and have limited estimated effect (−1.5 ppm and −2.3 ppm, respectively).

In contrast, the region on 7A associated with FDK, *QFdk.nc-7A*, is delimited to a shorter region on the distal short arm of 7A (20.2–36.5 Mbp). *QFdk.nc-7A* also accounts for a higher percent variance (7%) than either of the DON QTL on 7A and is estimated to have a relatively large effect on FDK (−5.6%). This implies that FDK is affected by QTL on the short arm of 7A, and DON may also be affected by these QTL (e.g., *QDon.nc-7A.1*) and separate QTL (e.g., *QDon.nc-7A.2*) on the distal part of the long arm of the 7A.

Lastly, FHB QTL identified on the long arm of 7D were found for FHB visual ratings (*QFvr.nc-7D*), FDK (*QFdk.nc-7D*), and DON (*QDon.nc-7D*). From the estimated effects of this locus, it appears that inheriting the NC13-20076 allele of this locus may confer "susceptibility." The unadjusted estimated effects for FHB visual ratings, FDK, and DON are +0.6 points, +5.7%, and +2.4 ppm, respectively. The long arm of the 7D chromosome was not complete in the final linkage map due to filtration parameters (Supplementary Information 2), and when referencing the scan plots for the multi-environment QTL scans (Supplementary Information 5), it appears that the QTL peak is located on the terminus of the long arm of the 7D linkage group. This implies that this 7D locus lies somewhere else further on the distal end of the 7D linkage group, but this cannot be tested in this population due to the lack of markers in the region.

4 | DISCUSSION

In the present study, we developed and sequenced a biparental, doubled haploid QTL mapping population developed from a cross between the moderately FHB-resistant line NC13-20076 and the highly FHB susceptible line GA06493-13LE6. We collected phenotypic information for FHB avoidance traits (plant height and heading date) as well as FHB reaction traits (visual ratings, FDK, and DON). We performed interval and multiple QTL mapping on heading date and plant height and used the peak markers from identified QTL as covariates in QTL scans for FHB reaction traits. Consequently, we observed in this population that resistance to FHB is polygenic and a result of many small-to-moderate effect QTL.

A plethora of FHB reaction QTL studies have been reported, and it is estimated that there are nearly 500 FHB QTL identified across the wheat germplasm (M. Buerstmayr et al., 2020). Among these studies, around 20% of the QTL were identified by the authors as "major" (M. Buerstmayr et al., 2020). One of the first "major-effect" FHB resistance QTL to be mapped, *Fhb1*, accounted for 30%–56% (expressed as R^2) of the total phenotypic variance of its mapping population (Bai et al., 1999). Using the *Fhb1* locus as a reference for a "major-effect QTL," we may state that the QTL contributing to the resistance identified in NC13-20076 are "minor to moderate effect."

In the wheat germplasm relevant to the eastern United States, there have been several FHB reaction QTL studies performed (Carpenter et al., 2020; M. S. Islam et al., 2016; Petersen et al., 2016, 2017). The sources of resistance QTL for FHB are found across many soft red winter wheat cultivars, which are often used as parents, such as NC-Neuse, Bess, and Tribute (Ghimire et al., 2020). FHB reaction QTL can be found in lines relevant to the southeastern soft red winter wheat germplasm on 1A, 2A, 3A, 4A, 5A, 6A, 1B, 2B, 3B, 4B, 6B, 2D, 3D, and 4D (Ghimire et al., 2020). Among the eastern soft wheat QTL reviewed by Ghimire et al. (2020), FHB reaction QTL on 7A are not presented.

The FHB reaction QTL identified on 4A (*QFvr.nc-4A*, *QFdk.nc-4A*, and *QDon.nc-4A*) co-occur on the same chromosome as the identified plant height (*QPht.nc-4A*) and heading date (*QHd.nc-4A*) QTL; this is despite the use of these FHB avoidance trait QTL peak markers as covariates in scans for FHB reaction traits. The inclusion of marker covariates from the heading date and plant height in the multi-environment scans for FHB reaction traits resulted in peak marker positions for *QFvr.nc-4A* (693.4 Mbp), *QFdk.nc-4A* (695.7 Mbp), and *QDon.nc-4A* (645.7 Mbp) just distal to *QHd.nc-4A* (618.4 Mbp) and *QPht.nc-4A* (620.2 Mbp) on the same linkage group. These results indicate that while the FHB reaction trait QTL on 4A may differ from the plant height and heading date QTL, they should be further investigated for their relationship to those traits.

The FHB reaction QTL identified in the NC-Neuse background on chromosome 4A, referred to as *Qfhb.nc-4A* by Petersen et al. (2016), encompass a region of 544.8–581.9 Mbp. This region determination is based on the top results from basic local alignment search tool of markers utilized to haplotype the *Qfhb.nc-4A* region by the USDA-ARS Eastern Regional Small Grains Genotyping Lab, aligned to version 1.0 of the Chinese Spring reference genome (data not shown). This region identified by Petersen et al. (2016) is nearly 60 Mbp away from *QDon.nc-4A* identified in this study. Considering the linkage disequilibrium in a doubled haploid population, these QTL could be related, yet the data presented in this work cannot directly support this claim. Nonetheless, it would be prudent to validate these QTL in a separate population, perhaps one related to NC-Neuse, to identify if *QFhb.nc-4A* is related to the NC-Neuse QTL and if the *QFhb.nc-4A* QTL are confounded with plant height and heading date.

The highest percent variance FHB reaction QTL identified in this study reside on chromosome 1A (*QFdk.nc-1A* and *QDon.nc-1A*), 3A (*QFdk.nc-3A* and *QDon.nc-3A*), and 5A (*QFvr.nc-5A*, *QFdk.nc-5A*, and *QDon.nc-5A*). All three regions identified in this study overlap with known resistance QTL reviewed by Ghimire et al. (2020) and identified in the meta-QTL analysis performed by Venske et al. (2019), indicating precedent for these regions' association with FHB reaction. The QTL identified on chromosome 1A (303–544 Mbp) were identified in both the multi-environment scans and six single environment scans for DON and three for FDK. Moreover, no heading date or plant height QTL were identified on chromosome 1A, indicating that this locus may be an appropriate target for introgression via MAS.

The FHB reaction QTL identified on 5A identified in this study were delimited to a region of approximately 400–650 Mbp. The regions of the two QTL identified for heading date in this population, *QHd.nc-5A.1* and *QHd.nc-5A.2*, have support intervals that encompass this region (Table 2). This indicates that the FHB reaction QTL on 5A may be confounded with the large effect heading date gene *Vrn-A1* and should be further investigated for their interaction with heading date.

The two QTL regions for FHB reaction traits that were identified on chromosome 7A (*QDon.nc-7A.2* vs. *QDon.nc-7A.1* and *QFdk.nc-7A*) appear not to be in regions previously associated with resistance in southern United States soft red winter wheat germplasm (Ghimire et al., 2020). In meta-QTL studies of FHB reaction traits in diverse germplasm, which attempt to synthesize previously identified QTL into consensus regions, the short arm of chromosome 7A is often indicated as containing several FHB reaction QTL (Löffler et al., 2009; Venske et al., 2019). Venske et al. (2019) identified several meta-QTL sites ranging from 27 to 36 cM, 66 to 71 cM, 79 to 85 cM, and 108 to 164 cM. These meta-QTL regions potentially overlap with the regions reported for FHB reaction trait QTL on 7A, which in this study encompass much of the chromosome. However, from the review conducted by Ghimire et al. (2020), it appears that this region may be novel to southeastern United States soft red winter wheat germplasm.

5 | CONCLUSION

Resistance to FHB in wheat is polygenic and is primarily determined by the combined influence of many small to moderate effect FHB reaction QTL. Some moderate to large effect loci, like *Fhb1* or the QTL identified on chromosome 1B in Jamestown, have been widely used in breeding programs and have been found to provide durable FHB resistance in soft red winter wheat. In this study, we mapped FHB reaction QTL in a biparental, doubled haploid population and identified several small to moderate effect QTL. While mapping such QTL may be useful in development of FHB-resistant varieties, it is prudent to also test the founders of such populations for known genes, which affect photoperiodism, vernalization requirement, and height. Furthermore, when diagnostic markers are unavailable to assess unidentified plant height and heading date QTL, it is best practice to perform some type of experimental correction for these confounding factors.

While the QTL identified in the current work are not novel in wheat germplasm overall, their identification in soft red winter wheat germplasm of the southeastern United States is novel, and the source germplasm is immediately accessible to wheat breeding programs via the USDA-ARS Germplasm Resource Information Network (GRIN; Accession ID—PI 700335). Future research should focus on the efficacy of these QTL, particularly *QFdk.nc-1A* and *QDon.nc-1A*, which may be related to QTL identified by Petersen et al. (2016) in the cultivar NC-Neuse. Development of markers diagnostic for the resistant QTL haplotypes may allow for validation of these moderate-effect loci in other populations. Once validated, these markers can be utilized to further investigate their

effectiveness and usefulness in developing and maintaining FHB resistance in soft red winter wheat.

AUTHOR CONTRIBUTIONS

Z. L. Winn: Conceptualization; data curation; formal analysis; investigation; methodology; project administration; supervision; validation; visualization; writing—original draft; writing—review and editing. **R. Acharya**: Conceptualization; data curation; investigation; methodology; resources; writing—review and editing. **B. Ward**: Data curation; investigation; methodology; writing—review and editing. **J. Lyerly**: Data curation; formal analysis; writing—review and editing. **C. Griffey**: Data curation; methodology; project administration; resources. **J. Fitzgerald**: Data curation; methodology. **Y. Dong**: Data curation; formal analysis. **C. Cowger**: Data curation; investigation; methodology; project administration; writing—review and editing. **J. P. Murphy**: Conceptualization; data curation; funding acquisition; investigation; methodology; project administration; resources; supervision; writing—review and editing. **G. Brown-Guedira**: Funding acquisition; supervision; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All data, code, and referenced statistics mentioned in this publication is available at https://github.com/zjwinn/NC13-20076-FHB-QTL-Mapping.

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SUPPORTING INFORMATION

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