Effects of allelic variation at *Rht-B1* and *Rht-D1* on grain yield and agronomic traits of southern US soft red winter wheat

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Abstract Semi dwarfism in hexaploid wheat (*Triticum aestivum* L.) is primarily governed by two loci, *Rht-B1* and *Rht-D1*. Cultivars adapted to the soft red winter wheat growing region of southeastern USA are predominantly *Rht-D1b* genotypes but report no significant grain yield advantage over *Rht-B1b* semi dwarfing cultivars. The objective of this study was to determine the effect of allelic variation at *Rht-B1* and *Rht-D1* on plant height, grain yield and additional yield components in a doubled haploid population consisting of 35 semi dwarfs with *Rht-B1b*, 50 semi dwarfs with *Rht-D1b*, eight wild type lines, and two lines with dwarfing alleles at both loci. *Rht* loci significantly affected plant height, with double dwarfs shorter than both single gene semi dwarfs and wild types. *Rht-D1b* semi dwarfs were significantly shorter than their *Rht-B1b* counterparts. *Rht* loci also had a significant effect on grain yield, with *Rht-D1b* lines having higher mean grain yield (4.03 t ha^{-1}) compared to *Rht-B1b* (3.83 t ha^{-1}) and wild type (3.49 t ha^{-1}) lines. A significant interaction between *Rht* loci and site-year was detected only for thousand kernel weight, indicating that the advantage of *Rht-D1b* over the other haplotypes was consistent across environments. Overall, their higher grain yield was due in part to higher thousand kernel weight that contributed to higher kernel weight spike^{-1} and likely influenced by a shorter stature. The results of this study will aid breeders in choice of semi dwarfing alleles for adaptation to the soft wheat growing region of the southern USA.

Keywords Green revolution · Semi dwarf · Reduced height · KASP

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Introduction

Wheat is a staple food crop that is grown on more than 17% of arable land and provides more than one fifth of the daily calorie needs around the world (FAOSTAT 2017). To meet future demands, increasing grain yield continues to be the major target for wheat breeding programs (Parry et al. 2010; Reynolds et al. 2009). Grain yield is a complex trait controlled by genetic and environmental factors (Ashfaq et al. 2003) and therefore a holistic approach that incorporates

agronomics (Wang et al. 2012), physiology, and genetics (Foulkes et al. 2010) is necessary for yield improvement.

The green revolution remains the most rapid period of genetic gain for agricultural crops. The architect of this revolution, Norman Borlaug, joined the International Wheat and Maize Improvement Center (CIM-MYT) in 1944 with the objective of making Mexico self-sufficient in wheat production (Rajaram 1995). After nearly 2 decades, his initial goal of developing rust resistant wheat varieties was coming to fruition, but the program struggled with poor straw strength and lodging (Lumpkin 2015). A solution was identified in the variety 'Norin 10-Brevor 14', developed at Washington State University by Orville Vogel. Vogel introduced 'Norin 10' (PI 156641) from Japan. Unknown at the time, it possessed dwarfing alleles at two height regulating loci, *Rht-B1* and *Rht-D1*, on chromosomes 4B and 4D, respectively (Hedden 2003). Borlaug hybridized Norin10-Brevor 14 with tall, rust resistant varieties to produce 'Sonora 64' and 'Lerma Rojo 64'. These varieties maintained lodging resistance despite increased application rates of nitrogen fertilizer (Lumpkin 2015).

The *Rht-B1* locus on chromosome 4B and the *Rht-D1* locus on chromosome 4D both have the possibility of a tall wild type (a) or reduced height dwarfing (b) allele. The dwarfing alleles *Rht-B1b* and *Rht-D1b* encode DELLA proteins that repress gibberellic acid (GA) signaling, resulting in GA insensitivity and reduced height (Peng et al. 1999). In total, there are four possible phenotypes in inbred wheat lines, including wild type, *Rht-B1b* semi dwarfs, *Rht-D1b* semi dwarfs, and double dwarfs. Most studies have observed a greater reduction in plant height due to *Rht-D1b* compared to *Rht-B1b*. For example, Gale and Youssefian (1985) showed the *Rht-B1b* and *Rht-D1b* alleles to cause a 15% reduction in plant height, while Flintham et al. (1997) observed reductions in plant height of 14 and 17%, respectively.

Rht loci significantly impact grain yield through pleiotropic mechanisms. The earliest reported was through increased partitioning of assimilates to the generative as opposed to vegetative parts of the plant in semi dwarfs (Flintham et al. 1997). Gale and Youssefian (1985) observed an association between semi dwarfing alleles and increased floret fertility. Grain yield increases of 16–24% have been reported for semi dwarfs compared to wild types (Allan 1986;

Blake et al. 2009; Chapman et al. 2007; Flintham et al. 1997; Singh et al. 2001). Butler et al. (2005) compared the performance of *Rht-B1b* and *Rht-D1b* semi dwarfs at three different moisture levels and reported that *Rht-B1b* semi dwarfs outperformed *Rht-D1b* semi dwarfs only under full irrigation. Other studies reported no significant ($P \leq 0.05$) difference between the two semi dwarf haplotypes (Knott 1986; McNeal et al. 1972).

The Uniform Southern Soft Red Winter Wheat Nursery, organized and administered by the USDA Agriculture Research Service in cooperation with nearly 40 public and private entities, tests the performance of breeding lines adapted to the Southeastern growing region of the United States. In this nursery, the frequency of entries homozygous for the dwarfing allele at the *Rht-D1* locus (*Rht-D1b*) from 2012 to 2018 exceeded 80% (data available at https://www.ars.usda.gov). In a historical panel, Guedira et al. (2010) reported 53% of southern US SRWW breeding lines were *Rht-D1b* semi dwarf whereas 31% had *Rht-B1b*. Given this high frequency and the pleiotropic impact of *Rht* loci on grain yield and adaptation, it was hypothesized that *Rht-D1b* provides a yield advantage over lines possessing *Rht-B1b* when grown in southeastern USA. The objective of this study was to determine the effects of allelic variation at *Rht-B1* and *Rht-D1* on plant height, grain yield and yield components in a doubled haploid population of soft red winter wheat lines adapted to the Southeastern region of the US. Specifically, it aimed to (1) evaluate the impact of *Rht* loci on plant height; (2) compare yield and agronomic traits between semi dwarf and wild type lines; and (3) compare yield and agronomic traits between *Rht-B1b* and *Rht-D1b* semi dwarf lines.

Materials and methods

Germplasm

The population under study consisted of 95 soft red winter wheat (SRWW) doubled haploid (DH) lines derived from a cross of two SRWW cultivars, 'Bess' (PI642794) and 'NC-Neuse' (PI633037). Bess was developed by the University of Missouri and released in 2005 (McKendry et al. 2007). Its pedigree is MO-11769/MADISON. Its extensive pedigree is available at http://wheatpedigree.net/sort/renderPedigree/83643). Bess is a semi dwarf and is homozygous for

the dwarfing allele *Rht-B1b* and for the wild-type allele at the *Rht-D1* locus (*Rht-D1a*).

NC-Neuse was developed by North Carolina State University and was released in 2003 (Murphy et al. 2004). Its pedigree is: COKER-86-29//STELLA/ CHD-756-80/3/COKER-9907. Its extensive pedigree is available at http://wheatpedigree.net/sort/ renderPedigree/82784. NC-Neuse is semi dwarf and is homozygous for the wild-type allele *Rht-B1a* and the dwarfing allele *Rht-D1b* (Petersen et al. 2016).

Both parents have the Norin10-Brevor 14 cultivar in their pedigree, historically the primary source of *Rht-B1b* and *Rht-D1b*. Both are well adapted to the southeastern US and are homozygous for *Ppd-D1b* (sensitivity) at the *Ppd-D1* locus on chromosome 2D.

Based on the genetic makeup of the parents, the DH population segregated for alleles at the *Rht-B1* and *Rht-D1* loci on chromosomes 4B and 4D, respectively. To confirm this, the DH population was genotyped for KASP markers diagnostic for both semi-dwarfing loci as previously reported by Petersen et al. (2016). At both loci there are two possible alleles, either dwarfing (designated by '*a*') or wild type tall (designated by '*b*'). Collectively there are four possible allelic combinations or haplotypes. In the population there were 35 semi dwarfs homozygous for *Rht-B1b* (dwarfing) and *Rht-D1a* (wild type) (referred to herein as *Rht-B1b* semi dwarf), 50 lines homozygous for *Rht-B1a* (wild type) and *Rht-D1b* (dwarfing) (*Rht-D1b* semi dwarf), eight lines homozygous wild type or tall at both loci (wild type), and two lines homozygous for the dwarfing alleles at both loci (double dwarf).

Experimental locations and design

The DH population and parents were evaluated over three growing seasons at Fayetteville, Arkansas in the years 2014–15, 2015–16, and 2016–17 and at Newport, Arkansas in the years 2015–16 and 2016–17 for a total of five site-years. The population was planted in a randomized complete block design with the two parents used as repeated checks. Each site-year consisted of two replications except for Fayetteville (2014–2015), which had a single replication. All locations were drill-seeded at ∼ 118 kg seed ha^{-1} with plot dimensions of 1.52 m wide and 4.26 m long. The sowing date for the 2014–2015 season was October 25, 2014 for Fayetteville. For the 2015–2016 season, sowing was October 21, 2015 at Fayetteville and November 10, 2015 at Newport. For the 2016–2017 season, sowing occurred on October 18, 2016 at both Fayetteville and Newport. Plots were harvested during May and June depending on physiological maturity at each location. Nitrogen in the form of urea was applied to both locations in a split application (100.87 kg ha^{-1} and 67.45 kg ha^{-1}) firstly at Feekes growth stage 5. For pest management, herbicides including Harmony® (DuPont™) for controlling winter annual weeds, Axial® (Syngenta Group Company) and Osprey® (Bayer) for controlling Italian ryegrass (*Lolium multiflorum Lam.*), Grizzly® (Winfield Solutions, LLC) for pest control, and fungicide Tilt® (Syngenta Group Company) for foliar disease control, were applied at recommended rates and growth stages.

Data collection

Plant height (in cm) was measured at physiological maturity twice per plot from the soil surface to the top of the canopy of each plot, excluding awns and averaged for one value per plot. Days to heading was measured in Julian days when approximately 50% of heads in a plot were completely emerged. Grain yield was determined at all locations by whole plot harvesting and adjusting to 13% moisture in metric tons ha^{-1} (t ha^{-1}). Thousand kernel weight was determined by counting one thousand kernels in a seed counter (Seedburo Equipment CO., Chicago, IL) and weighing. Other yield components including kernel weight $spike^{-1}$, kernel number $spike^{-1}$, and spikes m^{-2} were determined directly or using formulae after randomly harvesting and threshing 50 spike-bearing culms from each plot prior to whole-plot harvest (Reynolds et al. 2001).

Statistical and genotypic analyses

An analysis of variance was conducted using the PROC MIXED procedure in SAS 9.4 (SAS Institute Inc. 2011, Cary, NC) to determine the effect of allelic variation at *Rht-B1* and *Rht-D1* on grain yield and agronomic traits. Despite being located on different chromosomes, there was high level of linkage disequilibrium between the *Rht-B1* and *Rht-D1* loci, with 90% (85/95) of the DH lines homozygous for the dwarfing allele at one locus and the wild-type allele at the other. As such, the loci were analyzed as *Rht* haplotypes and not individual loci. The model included *Rht* haplotype, genotype nested within locus, location, the interaction of *Rht* and

location, replicate nested within location, and residual error (Balut et al. 2013). Genotype, *Rht* and their interaction were treated as fixed effects whereas location and replicate were treated as random. In addition, trait heritability was determined using TYPE 3 sums of squares with all factors treated as random effects and the following formula:

$$h^2 = \frac{\sigma^2_{genotype}}{\left(\sigma^2_{genotype} + \frac{\sigma^2_{genotype \times location}}{l} + \frac{\sigma^2_{residual}}{l \cdot r} \right)}$$

where $\sigma^2_{genotype}$ is the genotypic variance, $\sigma^2_{genotype \times location}$ is the interaction of genotype and location variance, and $\sigma^2_{residual}$ is the error variance; l and r are the number of locations and replicates, respectively. Multiple regression was used to determine the variation in grain yield explained by its components, with the independent variables (including all yield components, agronomic traits, and *Rht*) added and removed in a step-wise manner to determine contribution based on partial R^2. A minimum value of $P \leq 0.05$ was used for determining which traits were included in the final regression equation.

Results

Analysis of variance and correlation of traits

Bess (*Rht-B1b*) had a mean grain yield of 4.4 t ha^{-1} across all five site-years, compared to NC-Neuse (*Rht-D1b*) at 3.8 t ha^{-1} (Table 1). Overall, Bess had higher kernel number spike^{-1}, kernel weight spike^{-1} and spikes m^{-2}. The DH lines had a mean grain yield of 3.9 t ha^{-1} ranging from 1.8 to 5.4 t ha^{-1} (Table 1). Bess was on average 4 cm taller than the NC-Neuse

whereas the DH lines ranged from 71 to 98 cm. Both parents had similar days to heading, while the population ranged from 89 to 111 Julian days.

The effects of genotype and *Rht* were significant ($P \leq 0.05$) for all traits and location was significant ($P \leq 0.05$) for all traits except kernel weight spike^{-1} (Table 2). A significant ($P \leq 0.05$) *Rht* by location interaction was observed only for thousand kernel weight, indicating that the effects of *Rht* alleles were generally consistent across site-years. Trait heritability was high and ranged from $h^2 = 0.41$ for days to heading to $h^2 = 0.94$ for plant height, with the lower heritability for days to heading due to fewer replicates with datapoints. The heritability of grain yield was $h^2 = 0.82$ across the five site-years. Grain yield was positively correlated with all measured yield components and days to heading (Table 3). A negative correlation was observed between grain yield and plant height (r = − 0.30, $P \leq 0.01$) and between plant height and all yield components excluding thousand kernel weight.

Stepwise regression was used to explore the ability of allelic variation at *Rht* loci, yield components, and agronomic traits to explain grain yield. Kernel number spike^{-1}, spikes m^{-2}, thousand kernel weight, and *Rht* were the only factors significantly associated ($P \leq 0.05$) with grain yield based on simple regression (Table 4). The total grain yield variation explained (R^2) by these factors in a multiple regression was 0.85. The percent contribution of individual factors ranged from 1.7% for *Rht* to 54% for kernel number spike^{-1}.

Comparison of *Rht* haplotypes for plant height and days to heading

As expected, *Rht-B1b* (81.0 cm) and *Rht-D1b* (83.0 cm) semi dwarfs were significantly ($P \leq 0.05$) shorter than wild type (87.3 cm) (Fig. 1). Double

Table 1 Summary of trait means measured for NC-Neuse, Bess and 95 doubled haploid lines across five site-years in Arkansas, 2014–2017

	Parents		Doubled haploids		
	NC-Neuse	Bess	Mean	Min	Max
Grain yield (t ha^{-1})	3.8	4.4***	3.9	1.8	5.4
Plant height (cm)	84	88**	83	71	98
Days to heading (days)	98.4	98.5	103	89	111
Thousand kernel weight (g)	32.2	30.5*	31.3	26.0	39.4
Kernel number spike^{-1}	27.4	37.3***	29.5	19.7	44.2
Kernel weight spike^{-1} (g)	0.90	1.2***	0.92	0.51	1.28
Spikes m^{-2}	422	489**	384	221	550

*, **, ***Significantly different from NC-Neuse at $P = 0.05$, $P = 0.01$, and $P = 0.001$, respectively

Table 2 Analysis of variance for 95 doubled haploid lines evaluated across five site-years in Arkansas, 2014–2017

Trait	Site-years	h^2	Mean squares					
			Entry	*Rht*	*Rht* by location interaction	Rep (location)	Location	Residual
Grain yield (t ha^{-1})	5	0.82	1.98***	6.58***	0.49	24.53***	68.67***	0.44
Days to heading (Julian)	2	0.41	37.87***	122.47***	21.65	91.70*	6677.00**	16.82
Plant height (cm)	5	0.94	271.38***	831.30***	51.86	18.25	1925.81***	38.38
Thousand kernel weight (g)	2	0.69	24.21***	58.83***	26.95**	266.66***	157.99***	5.75
Kernel weight spike^{-1}	2	0.60	0.046***	0.15***	0.012	0.30***	0.53	0.017
Kernel number spike^{-1}	2	0.81	46.18***	139.27***	8.29	860.73***	1162.59***	10.70
Spikes m^{-2}	2	0.63	10,128***	13,517***	2508	536,987***	212,439	3483

*, **, ***Significantly different at $P = 0.05$, $P = 0.01$, and $P = 0.001$, respectively

Table 3 Pearson's correlation coefficients for 95 doubled haploid lines evaluated across five site-years in Arkansas, 2014–2017

	Grain yield	Days to heading	Plant height	Thousand kernel weight	Kernel number spike^{-1}	Kernel weight spike^{-1}
Days to heading	0.20*					
Plant height	− 0.30**	− 0.16				
Thousand kernel weight	0.09	− 0.28**	0.25*			
Kernel number spike^{-1}	0.63***	0.26**	− 0.31**	− 0.31**		
Kernel weight spike^{-1}	0.67***	0.07	− 0.14	0.35***	0.77***	
Spike m^{-2}	0.60***	0.05	− 0.20*	0.00	0.05	0.02

*, **, ***Significantly different at $P = 0.05$, $P = 0.01$, and $P = 0.001$, respectively

Table 4 Multiple regression of grain yield (GY) with *Rht* and yield components in 95 doubled haploid lines evaluated across five site-years in Arkansas, 2014–2017

Treatment	R^{2a}	% Contribution[b]
GY = − 3.31318 + 0.09475 KNS + 0.00540 Sm2 + 0.04953 TKW + 0.08785 Rht	0.845***	
Kernel number spike^{-1} (KNS)	0.456***	54.0
Spikes m^{-2} (Sm^{-2})	0.302***	35.7
1000 kernel weight (TKW)	0.074***	8.8
Rht	0.014**	1.7

[a]Coefficient of variation of each independent variable using linear regression

[b]Percent of the total R^2 contributed by each independent variable based on partial R^2 values

dwarfs were the shortest of the four *Rht* haplotypes (80.3 cm) but were not significantly ($P \leq 0.05$) different from *Rht-D1b* lines. *Rht-D1b* semi dwarfs were significantly ($P \leq 0.05$) shorter than *Rht-B1b* and this trend was consistent across environments (data not shown). Wild type lines were earlier heading (99 days) compared to both semi dwarfs and the double dwarf ($P \leq 0.05$). No significant ($P \leq 0.05$) differences were observed for days to heading between *Rht-B1b* (104 days), *Rht-D1b* (104 days), and double dwarf (103 days) lines.

Comparison of *Rht* haplotypes for grain yield and yield components

Rht-D1b semi dwarfs had significantly ($P \leq 0.05$) higher mean grain yield (4.03 t ha^{-1}) compared to both *Rht-B1b* (3.83 t ha^{-1}) and wild type (3.49 t ha^{-1}, Fig. 2) and this trend was consistent across individual site-years (data not shown). The wild type had significantly ($P \leq 0.05$) lower grain yield, kernel number spike^{-1}, kernel weight spike^{-1}, and spike density compared to other *Rht* haplotypes. Comparing the two semi dwarf haplotypes, *Rht-D1b* lines had higher thousand kernel weight (3.3%) and kernel weight spike^{-1} (3.7%) than *Rht-B1b* lines, which contributed to the 5.3% higher grain yield.

Discussion

Impact of *Rht* loci on plant height

As expected, *Rht* loci had a significant effect on plant height, with *Rht-B1b* and *Rht-D1b* semi dwarfs 5.1%

and 7.2% shorter than the wild type, respectively. Differences in plant height were less than previously reported, keeping in mind that wild types occurred at a very low frequency in the population. Robbins (2009) observed 20.5 and 22.4% lower plant heights for *Rht-B1b* and *Rht-D1b*, respectively, compared to wild type in spring wheat near-isogenic lines. Similar results were reported in other studies (Blake et al. 2009; Flintham et al. 1997; Gale and Youssefian 1985; Trethowan et al. 2002). Overall, plant height was negatively correlated with grain yield (r = − 0.30), thousand kernel weight (r = − 0.24), and kernel number spike^{-1} (r = − 0.31), indicating shorter stature was favorable for grain yield in agreement with previous studies (Rebetzke and Richards 2000).

Comparison of semi dwarf to wild type

In addition to reducing plant height, it is well documented that semi dwarfism imparts a grain yield advantage over wild type (Butler et al. 2005; Flintham et al. 1997; Kuchel et al. 2007; Robbins 2009) with differences in magnitude differs likely caused by genetic backgrounds (Addisu et al. 2010). In this study, the grain yield advantage of the semi dwarf over wild type was 9.7 and 15.5% for *Rht-B1b* and *Rht-D1b*, respectively. This trend was in agreement with, but lower than, previous studies with a range from 16 to 24% (Allan 1986; Blake et al. 2009; Chapman et al. 2007; Flintham et al. 1997; Singh et al. 2001). All yield components except spikes m^{-2} were also significantly affected by the *Rht* loci. Kernel number spike^{-1} was significantly lower for the wild type, in agreement with Miralles and Slafer (1995) and Kertesz et al. (1991). Rebetzke and Richards (2000)
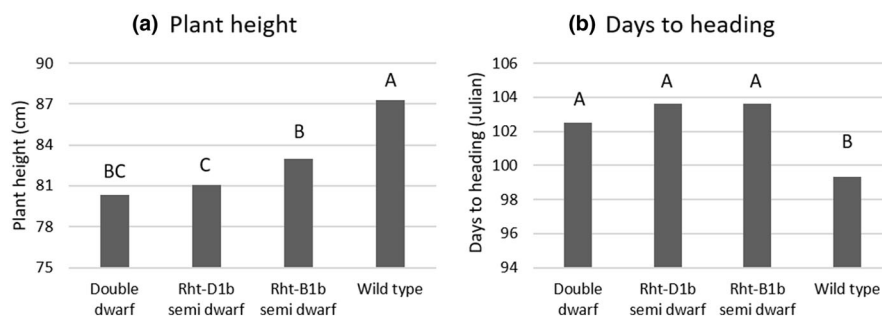

Fig. 1 Plant heights for *Rht* haplotypes (double dwarf, *Rht-B1b* semi dwarf, *Rht-D1b* semi dwarf and wild type) (**a**) and days to heading (**b**) in 95 doubled haploid lines evaluated across five

site-years in Arkansas, 2014–2017. Means were separated using Fishers LSD at an alpha value of 0.05
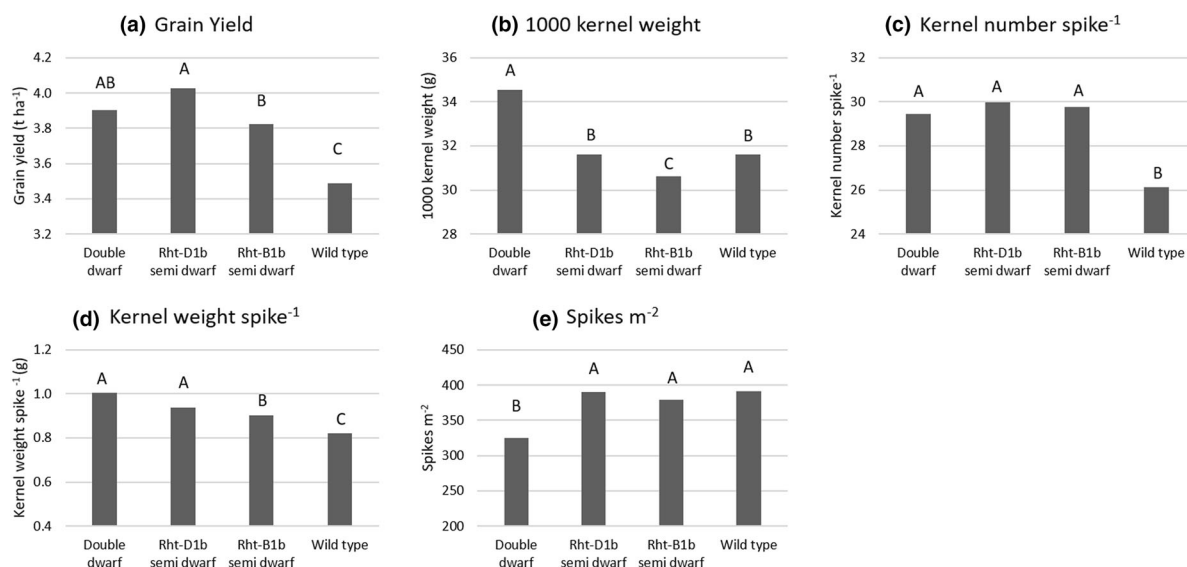
Fig. 2 Performance of *Rht* haplotypes (double dwarf, *Rht-B1b* semi dwarf, *Rht-D1b* semi dwarf and wild type) for grain yield (**a**) 1000 kernel weight (**b**), kernel number spike^{-1} (**c**), kernel weight spike^{-1} (**d**) and spikes m^{-2} (**e**) in 95 doubled haploid lines evaluated across five site-years in Arkansas, 2014–2017. Means were separated using Fishers LSD at an alpha value of 0.05

also showed a linear correlation between semi dwarfing in wheat and kernel number and harvest index.

Comparison of grain yield for *Rht-B1b* and *Rht-D1b* semi-dwarfs

In this study, *Rht-D1b* semi dwarfs were 5.3% higher yielding compared to *Rht-B1b*, resulting from increased thousand kernel weight and kernel weight spike^{-1}. This finding provides explanation for the high selection pressure on *Rht-D1b* in the US southern soft wheat germplasm (Guedira et al. 2010). Lozada et al. (2017) also reported that *Rht-D1b* was present at a higher frequency (60%) compared to *Rht-B1b* (40%) in high yielding soft red winter wheat lines. This advantage was however dependent on genetic background and environment. For example, the performance of the parental lines was contrary to the population, with Bess (*Rht-B1b*) outperforming NC-Neuse (*Rht-D1b*) in total grain yield and nearly all yield components. The same population was also used by Petersen et al. (2016) to identify QTL associated with resistance to *Fusarium* head blight (FHB), a disease caused by the fungal pathogen *Fusarium graminearum*. The authors identified *Qfhb.nc-4D.1* which spanned the *Rht-D1* region and concluded *Rht-D1b* to be associated with susceptibility FHB.

Although FHB did not occur at site-years reported in this study, FHB susceptibility associated with *Rht-D1b* should be taken into consideration by breeders targeting environments with a high incidence of FHB. Flintham et al. (1997) showed a significant grain yield advantage for *Rht-B1b* over *Rht-D1b* in only one of four near-isogenic backgrounds. Butler et al. (2005) reported a grain yield advantage for *Rht-B1b* of 8.1% under full irrigation, with no difference in partially irrigated or rain-fed conditions.

Conclusions and implications for breeding

The results of this study show a clear grain yield advantage (on average) for lines possessing the chromosome 4D dwarfing allele (*Rht-D1b*) as oppose to the 4B (*Rht-B1b*) allele and this was consistent over five site-years, with no significant *Rht* by location interaction. This is in agreement with observations by Lozada et al. (2017) and Guedira et al. (2010) noting the high frequency of *Rht-D1b* in lines adapted to southeastern US. While the contribution to variation in total grain yield was small (1.7%) in comparison to yield components (8.8–54%), breeders in this region should continue to use *Rht-D1b* for management of plant height in their breeding material to develop lines adapted to this soft wheat growing region.

References

Addisu M, Snape JW, Simmonds JR, Gooding MJ (2010) Effects of reduced height (Rht) and photoperiod insensitivity (Ppd) alleles on yield of wheat in contrasting production systems. Euphytica 172:169–181. https://doi.org/10.1007/s10681-009-0025-2

Allan RE (1986) Agronomic comparisons among wheat lines nearly isogenic for three reduced-height genes 1. Crop Sci 26:707–710. https://doi.org/10.2135/cropsci1986.0011183X002600040014x

Ashfaq M, Khan AS, Ali Z (2003) Association of morphological traits with grain yield in wheat (Triticum aestivum L.). Int J Agric Biol 5:262–264

Balut AL, Clark AJ, Brown-Guedira G, Souza E, Van Sanford DA (2013) Validation of Fhb1 and QFhs.nau-2DL in several soft red winter wheat populations. Crop Sci 53:934–945. https://doi.org/10.2135/cropsci2012.09.0550

Blake N, Lanning S, Martin J, Doyle M, Sherman J, Naruoka Y, Talbert L (2009) Effect of variation for major growth habit genes on maturity and yield in five spring wheat populations. Crop Sci 49:1211–1220

Butler JD, Byrne PF, Mohammadi V, Chapman PL, Haley SD (2005) Agronomic performance of Rht alleles in a spring wheat population across a range of moisture levels. Crop Sci 45:939–947

Chapman S, Mathews K, Trethowan R, Singh R (2007) Relationships between height and yield in near-isogenic spring wheats that contrast for major reduced height genes. Euphytica 157:391–397

FAOSTAT (2017) Statistical data. Food and Agriculture Organization of the United Nations, Rome

Flintham J, Börner A, Worland A, Gale M (1997) Optimizing wheat grain yield: effects of Rht (gibberellin-insensitive) dwarfing genes. J Agric Sci 128:11–25

Foulkes MJ, Slafer GA, Davies WJ, Berry PM, Sylvester-Bradley R, Martre P, Calderini DF, Griffiths S, Reynolds MP (2010) Raising yield potential of wheat. III. Optimizing partitioning to grain while maintaining lodging resistance. J Exp Bot 62:469–486

Gale MD, Youssefian S (1985) Dwarfing genes in wheat. Prog Plant Breed 1:1–35

Guedira M, Brown-Guedira G, Van Sanford D, Sneller C, Souza E, Marshall D (2010) Distribution of Rht genes in modern and historic winter wheat cultivars from the eastern and central USA. Crop Sci 50:1811–1822. https://doi.org/10.2135/cropsci2009.10.0626

Hedden P (2003) The genes of the green revolution. Trends Genet 19:5–9

Kertesz Z, Flintham JE, Gale MD (1991) Effects of Rht dwarfing genes on wheat grain yield and its components under eastern European conditions. Cereal Res Commun 19:297–304

Knott D (1986) Effect of genes for photoperiodism, semi-dwarfism, and awns on agronomic characters in a wheat cross 1. Crop Sci 26:1158–1162

Kuchel H, Williams K, Langridge P, Eagles H, Jefferies S (2007) Genetic dissection of grain yield in bread wheat. I. QTL analysis. Theor Appl Genet 115:1029–1041

Lozada DN, Mason RE, Babar MA, Carver BF, Guedira G-B, Merrill K, Arguello MN, Acuna A, Vieira L, Holder A, Addison C, Moon DE, Miller RG, Dreisigacker S (2017) Association mapping reveals loci associated with multiple traits that affect grain yield and adaptation in soft winter wheat. Euphytica 213:222. https://doi.org/10.1007/s10681-017-2005-2

Lumpkin TA (2015) How a gene from Japan revolutionized the world of wheat: CIMMYT's quest for combining genes to mitigate threats to global food security. In: Ogihara Y, Takumi S, Handa H (eds) Advances in wheat genetics: from genome to field. Springer, Tokyo, pp 13–20

McKendry A, Tague D, Wright R, Tremain J (2007) Registration of 'Bess' wheat. J Plant Regist 1:21–23

McNeal F, Berg M, Stewart V, Baldridge D (1972) Agronomic response of three height classes of spring wheat, Triticum aestivum L., compared at different yield levels 1. Agron J 64:362–364

Miralles D, Slafer G (1995) Yield, biomass and yield components in dwarf, semi-dwarf and tall isogenic lines of spring wheat under recommended and late sowing dates. Plant Breed 114:392–396

Murphy J, Navarro R, Leath S, Bowman D, Weisz P, Ambrose L, Pate M, Fountain M (2004) Registration of 'NC-Neuse' wheat. Crop Sci 44:1479–1481

Parry MA, Reynolds M, Salvucci ME, Raines C, Andralojc PJ, Zhu X-G, Price GD, Condon AG, Furbank RT (2010) Raising yield potential of wheat. II. Increasing photosynthetic capacity and efficiency. J Exp Bot 62:453–467

Peng J, Richards DE, Hartley NM, Murphy GP, Devos KM, Flintham JE, Beales J, Fish LJ, Worland AJ, Pelica F (1999) 'Green revolution' genes encode mutant gibberellin response modulators. Nature 400:256–261

Petersen S, Lyerly JH, McKendry AL, Islam MS, Brown-Guedira G, Cowger C, Dong Y, Murphy JP (2016) Validation of Fusarium head blight resistance QTL in US winter wheat. Crop Sci 57:1–12

Rajaram S (1995) Wheat germplasm improvement: historical perspectives, philosophy, objectives, and missions. In: Rajaram S, Hettel GP (eds) Wheat breeding at CIMMYT: commemorating 50 years of research in Mexico for global wheat improvement. CIMMYT, Mexico, pp 1–10

Rebetzke G, Richards R (2000) Gibberellic acid-sensitive dwarfing genes reduce plant height to increase kernel number and grain yield of wheat. Crop Pasture Sci 51:235–246

Reynolds MP, Ortiz-Monasterio JI, McNab A (eds) (2001) Application of physiology in wheat breeding. CIMMYT, Mexico

Reynolds M, Foulkes MJ, Slafer GA, Berry P, Parry MA, Snape JW, Angus WJ (2009) Raising yield potential in wheat. J Exp Bot 60:1899–1918

Robbins AM (2009) Dwarfing genes in spring wheat: an agronomic comparison of *Rht-B1*, *Rht-D1*, and *Rht8*. Master of Science Dissertation, Montana State Univ., Bozeman Montana

Singh R, Huerta-Espino J, Rajaram S, Crossa J (2001) Grain yield and other traits of tall and dwarf isolines of modern bread and durum wheats. Euphytica 119:241–244

Trethowan RM, van Ginkel M, Rajaram S (2002) Progress in breeding wheat for yield and adaptation in global drought affected environments. Crop Sci 42:1441–1446

Wang J, Wang E, Yang X, Zhang F, Yin H (2012) Increased yield potential of wheat-maize cropping system in the North China plain by climate change adaptation. Clim Change 113:825–840