



Dwarfing gene *Rht24* does not affect Fusarium head blight resistance in a large European winter wheat diversity panel

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Abstract Reduced height (*Rht*) genes are widely used in modern wheat breeding although some confer higher susceptibility to Fusarium head blight (FHB) caused by *F. graminearum* and other species. Our objective was to test whether the recently identified *Rht24b* dwarfing allele has a neutral effect on FHB response as reported previously from a single mapping population when unrelated winter wheat cultivars were analyzed. We artificially infected a panel of 420 cultivars divided into four genotypic groups (*Rht24a*+*Rht-D1a*, *Rht24b*+*Rht-D1a*, *Rht24a*+*Rht-D1b*, *Rht24b*+*Rht-D1b*) with *Fusarium culmorum* in five location-year combinations. High and significant ($P \leq 0.001$) genetic variance for FHB severity and plant height (PH) was found in the entire panel as well as within the four *Rht* groups and both traits showed high entry-mean heritabilities of 0.92 and 0.98, respectively. *Rht24b* had no significant effect on FHB severity whereas *Rht-D1b* increased FHB susceptibility by 37%. The 29 most resistant cultivars either had the tallness alleles of the above mentioned *Rht-D1* gene or *Rht24b* alone. The *Rht24b*+*Rht-D1b*

combination had no significantly higher FHB severity than *Rht-D1b* alone. However, *Rht24b* reduced average PH only by 6.8 cm, whereas *Rht-D1b* conferred a reduction of 13.6 cm. For breeding short, FHB-resistant germplasm the neutral *Rht24* gene must be complemented by further QTL or other FHB-neutral *Rht* genes.

Keywords Dwarfing genes · FHB · Head scab · Plant height · Reduced height genes · *Triticum aestivum*

Introduction

Fusarium head blight (FHB) caused by *Fusarium graminearum* Schwabe, *F. culmorum* (W.G.Smith) Sacc. and other *Fusarium* species is a devastating disease in wheat growing worldwide. The disease does not only reduce grain yield, but also contaminates the grain with mycotoxins, of which deoxynivalenol is one of the most frequently found in wheat (Palumbo et al. 2020). The most promising management of FHB is a combination of agronomic measures (like no maize as the previous crop, soil tilling) and resistance breeding. Resistance to FHB in current European winter wheat is quantitatively inherited based on a plethora of quantitative trait loci (QTL) with mostly small effects (Buerstmayr et al. 2020). From Asian sources, a few QTL with major effects are reported, like *Fhb1* and *Fhb5*.

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Dwarfing genes have had a tremendous influence on international wheat breeding since World War II and their use is not restricted to the Green Revolution that occurred in developing countries, but they were also widely used in other countries (Sanchez-Garcia and Bentley 2019; Worland and Angus 2001; Würschum et al. 2017). Although 25 *Rht* genes are named in wheat (McIntosh et al. 2013, 2017; Mo et al. 2018) and comprise more than 30 dwarfing alleles (Sanchez-Garcia and Bentley 2019), only a few of these genes/alleles are routinely used. The ‘a’ allele always refers to the wild type, ‘b’ and further letters to different dwarfing alleles. The most often used are the b alleles of homoeologous loci *Rht-B1* (syn. *Rht1*) and *Rht-D1* (syn. *Rht2*) (= *Rht-1* alleles) located on chromosomes 4B and 4D, respectively. These alleles are gibberellin-insensitive whereas the height reducing alleles of *Rht8* and *Rht24* are gibberellin-sensitive. *Rht24b* was first detected in Chinese wheat genotypes (Li et al. 2015; Tian et al. 2017), but it soon became evident that it was common in many varieties worldwide (Würschum et al. 2017). *Rht24* (*TaGA2ox-A9*), located on the long arm of chromosome 6A, encodes gibberellin (GA) 2-oxidase, and the *Rht24b* allele causes reduced gibberellin acid content in the stems. This allele was also detected in wild emmer wheat (*T. turgidum* var. *dicoccoides*), but not in 160 accessions of wild or domesticated einkorn wheat (Tian et al. 2021).

Tian et al. (2021) found that 75% of 1000 wheat genotypes from a worldwide collection contained *Rht24b*. Also, *Rht24b* was detected in many Central European cultivars (Würschum et al. 2017). In Germany, for example, 70% of the tested winter wheat genotypes released after 1990 contained *Rht24b*, about 60% of the number with *Rht-D1b*, and 2% of the number with *Rht-B1b*. This implied that the combination of *Rht24b*+*Rht-D1b* occurred quite frequently. This was even more pronounced in modern Swedish, Danish, French, and British cultivars released after 1990 where up to 98% contained one or both of these dwarfing alleles. *Rht24b* occurred at a higher frequency (84.2%) than the other dwarfing alleles in Chinese elite cultivars, usually together with *Rht-D1b* or a reduced height allele of *Rht8* (Tian et al. 2019). This worldwide distribution of *Rht24b* in breeding materials was explained by presence in the donors of the reduced height alleles of the *Rht-1* genes and *Rht8*, namely, Japanese

cultivars ‘Norin 10’ and ‘Akakomugi’, respectively (Tian et al. 2019).

Active and passive resistance mechanisms contribute to FHB resistance (Mesterhazy 1995). Among the passive factors plant height is among the most prominent. Generally, plant height in wheat is governed by many genes, the *Rht* genes have the largest effects, but there are many other loci conferring small effects (Mao et al. 2010). It is well established that *Rht-D1b*, and to a lesser extent *Rht-B1b* and reduced height alleles of *Rht8* increase susceptibility to FHB (Draeger et al. 2007; Gosman et al. 2008; Voss et al. 2008; Srinivasachary et al. 2009; Lu et al. 2013). Miedaner and Voss (2008) reported that *Rht-B1b*, *Rht-D1b* and *Rht8c* increased FHB by 19%, 52%, and 19% averaged across two backgrounds of near-isogenic lines, respectively. These effects were significant, but only for *Rht-D1b* in the Mercia background. Nevertheless, these genes reduced progress in breeding for FHB resistance because selection of short, quantitatively FHB-resistant entries with one of these dwarfing alleles requires a much larger population size (Voss et al. 2008). Marker-assisted introgression of one non-adapted QTL (*Fhb1* or *Fhb5*) counterbalanced the negative effect of *Rht-D1b* on FHB response (Miedaner et al. 2019). This, however, again leads to an increased effort in selection. Therefore, it was important to find that *Rht24b* had no negative effect on FHB response in a segregating population derived from a cross of German winter wheat cultivars Solitär and Bussard (Herter et al. 2018). However, it was unknown if the finding also applied to other winter wheat genotypes containing *Rht24b*. Given the high frequency of this allele and the problem of FHB this question is of eminent importance and was analyzed in this study. We artificially infected a panel of 420 winter wheat cultivars comprising four *Rht* groups: *Rht24a*+*Rht-D1a* (hereafter ‘none’), *Rht24b*+*Rht-D1a*, *Rht24a*+*Rht-D1b*, *Rht24b*+*Rht-D1b* across five location-year combinations.

Materials and methods

Plant material and field trials

A diversity panel of 420 European winter wheat cultivars (*Triticum aestivum*) from 15 countries was selected on the basis of their *Rht* alleles

(Supplementary Table 1). The panel was grown at three locations in Germany in 2020: Hohenheim (HOH) near Stuttgart (9.12 °E, 48.42 °N; 400 m above sea level [a.s.l.]), Oberer Lindenhof (OLI) near Reutlingen (9.18 °E, 48.28 °N; 700 m a.s.l.) in southern Germany and Wohlde (WOH) near Bergen (9.98 °E, 52.80 °N; 80 m a.s.l.) in northern Germany. In 2021, the experiment was performed at HOH and OLI only, thus comprising five environments (location × year combinations). We used an incomplete lattice design with two replications at each location. Entries were planted as 0.9 m double rows at WOH and as 1.2 m single rows at HOH and OLI with seeding rates of 40 kernels (WOH) and 60 kernels per row (HOH, OLI), respectively. Agronomic measures followed standard procedures at the respective locations. The *Rht* status of each cultivar was identified by a customized wheat 25 K Illumina Infinium Array that is proprietary to SGS, Institute Fresenius, TraitGenetics Section (<http://www.traitgenetics.com/index.php/contact>, Gatersleben, Germany). Markers *TGWA25K.TG0011* and *BS00022120_51* were used for genotyping the tall and reduced height alleles at the *Rht-D1* and *Rht24* loci, respectively. Marker *Tdurum_contig64772_417* was used to genotype *Rht-B1*. Based on the sequence of the SNPs we figured out that *TGWA25K-TG0011* (*Rht-D1*) was gene-based, *Tdurum_contig64772_417* is in close linkage to the *Rht-B1* locus, and *BS00022120_51* and nine other completely associated markers were in significant LD with *Rht24*, but not diagnostic. However, we compared our results with that of another SNP marker published by Würschum et al. (2017) in common cultivars and found 96% agreement among 389 genotypes.

Inoculation and resistance traits

The highly aggressive single-spore isolate of *F. culmorum* FC46 (=IPO 39-01; Snijders and Perkowski 1990) was used for inoculum production. Inoculum was prepared on autoclaved wheat kernels as described by Miedaner et al. (1996). The FHB suspension was diluted to 200,000 spores ml⁻¹ and dispersed with a field sprayer (Hege 75, Waldenbuch, Germany) at about 100 ml m⁻². To ensure that all genotypes were inoculated at least once at mid-anthesis, inoculations started at the beginning of anthesis

of early entries and were repeated four or five times at intervals of 2 or 3 days.

Entries were analyzed for FHB severity, heading stage (HS), anthesis date (FD), and plant height (PH), but anthesis date was not recorded at WOH. FHB severity was rated visually at a minimum of three assessment dates as the percentage of infected spikelets (0–100%) per plot. Ratings began with the onset of symptom development about 15 to 20 days post inoculation and continued in intervals of three to five days until the beginning of yellow ripening. The arithmetic mean of the ratings was used for statistical analyses. Heading stage was recorded plotwise as a single assessment date as the respective BBCH stage 51 to 59 (Meier 2001). Anthesis date was also recorded plotwise in days after May 1, when 75% of the heads had reached anthesis, observed as extruded anthers. Plant height was measured after anthesis at all locations.

Statistical analyses

The data was analyzed using the following linear mixed model:

$$y_{ijkn} = \mu + g_i + l_j + (gl)_{ij} + r_{jk} + b_{jkn} + e_{ijkn}$$

y_{ijkn} is the single phenotypic observation (plot), μ is the intercept, g_i the effect of the i th genotype, l_j the effect of the j th environment, $(gl)_{ij}$ the genotype-environment interaction, r_{jk} the effect of the k th replicate, b_{jkn} the effect of the n th block nested within the k th replicate and e_{ijkn} is the error term. For calculation of best linear unbiased estimates (BLUEs) of genotypes all effects except genotype were fitted randomly; for estimation of variance components all effects were fitted random. Separate variances for each environment were fitted for the replicate, block and residual effects (heterogenous variance). The residual variances reported in the tables were calculated by the simple mean of environment-specific residual variance. The significances of the corresponding variances were tested by calculating chi-squared statistics for a likelihood ratio test (Stram and Lee 1994).

To account for the effect of anthesis date on FHB (Fusarium infection starts at anthesis and early cultivars tend to be more susceptible) we used FD and HS as (fixed) linear cofactors in our statistical analysis (Emrich et al. 2008). As no FD

was recorded in WOH we fitted an additional effect with two levels (HS+FD, FD) for the correction method. Due to this correction the coefficient of correlation between FHB severity and HS dropped from $r=0.29$ to $r=0.13$ and the correlation between FHB severity and FD from $r=-0.33$ to $r=-0.17$. Here, we report only the corrected values. Because the experiments included filler and some very early and late genotypes we used a dummy (0,1) variable to exclude those genotypes for estimating effects of correction variables and variances for genotype and genotype-environment interaction. The dummy variables were fitted as interactions and if dummy=0 the respective factor level of the interaction effect was not used to derive effect estimates in model calculation. The respective genotypes were not dropped from the analysis because they made the experimental design less imbalanced and helped to better estimate effects of replicates and blocks. Outliers were removed following the Bonferroni–Holm method in Bernal-Vasquez et al. (2016). Residuals were standardized by the environment-specific standard deviation (studentized residuals). Broad-sense heritability was calculated following Piepho and Möhring (2007):

$$h^2 = \frac{\sigma_g^2}{\sigma_g^2 + \frac{\bar{v}_{BLUE}}{2}}$$

with \bar{v}_{BLUE} being the mean variance of the difference of two BLUEs and σ_g^2 being the genetic variance. The determination of Pearson's correlation coefficients and all other further analyses were performed based on the BLUEs for the specific trait and genotype. Group-specific means were calculated based on BLUEs and tested for significant differences between the *Rht* groups using a Tukey test ($p=0.05$).

Pearson's coefficients of phenotypic correlation between the different traits were calculated by using the BLUEs. Genetic correlation of PH and FHB was calculated by extending the mixed model to a bivariate form and fitting unstructured variance–covariance (corh-option) for genotype, environment and genotype-environment interaction effects and diagonal variance–covariance for replicate and block effects. All statistical analyses were performed using the package ASReml-R 3.0 (Gilmour et al. 2009)

in the statistical software R Studio 3.6.2 (R Core Team 2019).

Results

FHB severities among cultivars ranged from 12.45 to 70.74% across environments (Table 1). This large range resulted in high genetic variance and a high entry-mean heritability of 0.92. High or even higher heritabilities were achieved for the other traits. Plant height ranged from 71.0 to 129.9 cm. There was wide variation in FHB severity within each *Rht* group. Variance components for plant height were considerably smaller in the short *Rht* groups compared to the tall groups.

Both *Rht* genes had significant effects on plant height as expected; *Rht24b* reduced plant height by 6.8 cm and reduction due to *Rht-D1b* was 13.6 cm (Fig. 1a). Cultivars with both reduced height alleles were 19.4 cm shorter than those with the respective alleles for tallness. Whereas *Rht24b* had no significant effect on FHB severity, *Rht-D1b* enhanced FHB severity significantly by 11.42% (Fig. 1b). The simultaneous presence of *Rht24b* did not significantly affect FHB severity. Boxplots (Fig. 1) and the scatter plot (Suppl. Fig. 1) illustrate the large genetic variance for FHB severity within each *Rht* group. There was a moderate, significant ($P \leq 0.001$) phenotypic correlation between FHB severity and plant height across all genotypes ($r = -0.61$) and the genetic correlation was negligibly higher (Table 2). Similar, although somewhat lower coefficients of phenotypic correlation were found within each of the four *Rht* groups with the highest genetic correlation in the tall allele group.

A comparison of the ten most resistant and ten most susceptible accessions in the 420 cultivar panel (Table 3) showed that the resistant cultivars had no dwarfing allele at either locus or had *Rht24b*; indeed, the 29 most resistant cultivars followed this trend (Supplementary Table 1). All 10 of the most susceptible cultivars carried *Rht-D1b* (Table 3). Accordingly, genotypes of the resistant group were, on average, much taller than those of the susceptible group (103.8 vs. 78.4, Table 3).

When PH was analyzed according to year of cultivar release it was clearly evident that older cultivars were taller and that breeding had reduced PH

Table 1 Summary statistics of Fusarium head blight (FHB) severity, plant height, and heading stage for four genotypic *Rht* groups across five environments and anthesis date across four environments

Parameter	FHB severity (%) ± SE	Plant height (cm) ± SE	Heading stage (BBCH) ± SE	Anthesis date (days) ± SE
BLUES				
Minimum	12.45	71.0	47.5	38.3
Mean	37.91	90.9	53.6	43.5
Maximum	70.74	129.9	62.1	47.4
LSD _{5%}	8.74	4.2	1.9	1.3
Variance components				
σ^2_G	121.26 ± 9.04	102.04 ± 7.21	8.60 ± 0.63 ns	2.95 ± 0.22
None	102.64 ± 16.99	230.53 ± 34.66	9.56 ± 1.44 ns	3.37 ± 0.51 ns
<i>Rht24b</i>	99.61 ± 14.38	80.02 ± 11.55	10.24 ± 1.39 ns	3.31 ± 0.45 ns
<i>RhtD1b</i>	127.06 ± 25.18	35.28 ± 6.86	8.18 ± 1.57 ns	2.77 ± 0.53 ns
<i>Rht24b + RhtD1b</i>	152.50 ± 20.41	74.88 ± 10.59	6.72 ± 0.86 ns	2.42 ± 0.31 ns
σ^2_{GL}	36.10 ± 1.68	6.22 ± 0.42	1.45 ± 0.09 ns	0.41 ± 0.03
σ^2	20.23 ± 1.44	9.74 ± 0.66	1.83 ± 0.13 ns	0.62 ± 0.04
H ²	0.92	0.98	0.95	0.93

SE, standard error, days = Days after May 1

σ^2_G , genetic variance for all genotypic *Rht* groups together and separately, σ^2_{GL} genotype-environment interaction variance, σ^2 , error variance, H², broad-sense heritability

All variance components are significant at $p \leq 0.001$, except ns = not significant

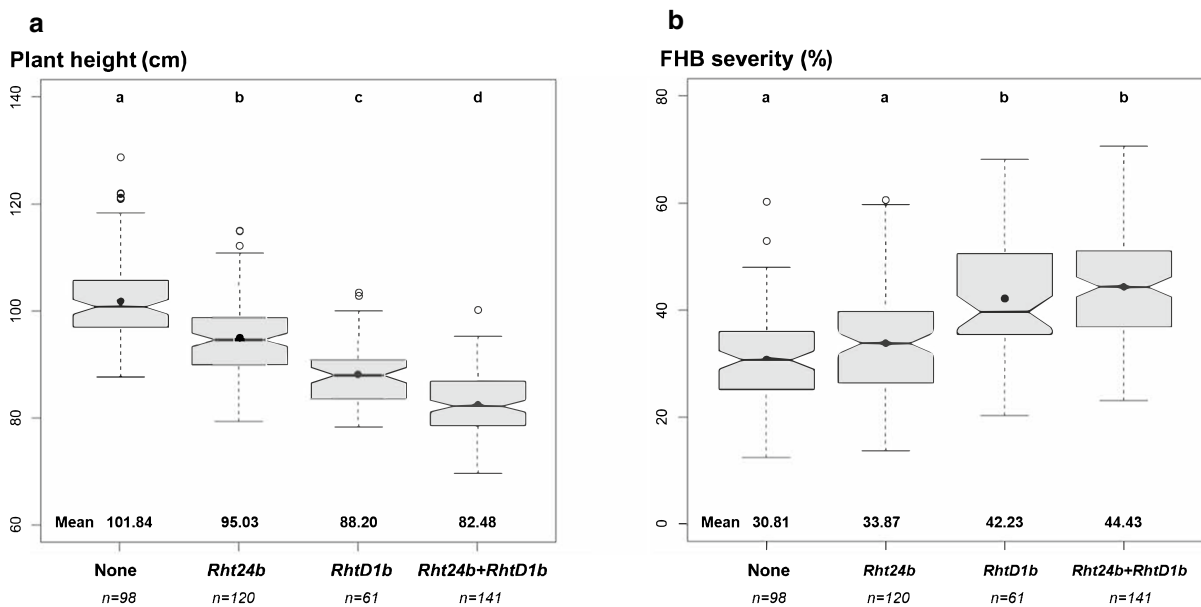


Fig. 1 Box plots and means of **a** plant height and **b** Fusarium head blight (FHB) severity for four genotypic groups of winter wheat cultivars possessing either none of the two dwarfing alleles (none) or the dwarfing alleles *Rht24b* or *Rht-D1b* or both across five environments; boxes represent 50% and

whiskers 95% of trial observations, filled dots indicate mean, horizontal lines within boxes median, and open dots outliers; *n* = number of cultivars; different letters indicate significance at $p = 0.05$ (Tukey test)

Table 2 Coefficients and standard errors (SE) of phenotypic (r_p) and genetic (r_g) correlations between Fusarium head blight (FHB) severity and plant height for four genotypic *Rht* groups and all genotypes across five environments; n=number of cultivars within each group

<i>Rht</i> group	n	$r_p \pm SE$	$r_g \pm SE$
None	98	-0.42 ± 0.09	-0.73 ± 0.05
<i>Rht24b</i>	120	-0.36 ± 0.09	-0.52 ± 0.07
<i>RhtD1b</i>	61	-0.45 ± 0.12	-0.52 ± 0.10
<i>Rht24b + RhtDb1</i>	141	-0.49 ± 0.07	-0.70 ± 0.05
All	420	-0.61 ± 0.04	-0.64 ± 0.03

All phenotypic coefficients of correlation are significant at $P \leq 0.01$

(Fig. 2a). For FHB severity, the trend was not so clear (Fig. 2b). Only the newest cultivars had a lower mean. Analysis of the frequency of the height-reducing alleles of *Rht24* and *Rht-D1* relative to year of registration revealed that selection for *Rht24b* had started prior to the introgression of *Rht-D1b*. *Rht-D1b* and especially the combination of *Rht24b + Rht-D1b* increased considerably in the 1990s (Fig. 2c). The frequency of cultivars with no height-reducing allele at these loci dramatically decreased after year 2000.

Discussion

The most effective reduced height genes are *Rht-B1b* and *Rht-D1b*, which have been used in wheat breeding worldwide since the 1960s. These alleles not only reduced plant height, but also increased spikelet fertility under optimal environmental conditions (Worland 2001). However, they also had negative effects, and increased FHB susceptibility was among the most important. The report that *Rht24b* conferred no negative effect on FHB response in one segregating population (Herter et al. 2018) motivated the present research. Würschum et al. (2017) reported that about 40% of a 1110 cultivars comprising a worldwide collection carried *Rht24b*. The worldwide use of *Rht24b* indicated that this allele conferred advantages that possibly extended to natural habitats because it was also present in more than half of a panel of 98 wild emmer wheat accessions from Turkey, Lebanon, and Syria (Tian et al. 2021).

The extent of plant height reduction by *Rht24b* averaging 6.8 cm in the present study was consistent with previous studies (-6 to -8 cm (Tian et al. 2017); -9 cm (Herter et al. 2018)) and was about half of the effect conferred by *Rht-D1b* (-13.6 cm). The additive effect of *Rht24b* and *Rht-D1b* for PH was confirmed and both genes are frequently found together (Würschum et al. 2017; Tian et al. 2019). Indeed, in our wheat material it was difficult to find cultivars with only *Rht-D1b* alone indicating that the additional plant height reduction conferred by *Rht24b* was essential in obtaining maximum yield level in Central Europe.

The higher FHB susceptibility of cultivars with *Rht-D1b* has been reported many times (for review see Buerstmayr et al. 2020). In this study cultivars with this allele had a 11.4% higher FHB severity than those without dwarfing *Rht* alleles. This corresponds to 37% higher susceptibility and is consistent with reports of Voss et al. (2008), Herter et al. (2018) and many other studies. One factor that might contribute to the higher susceptibility is anther extrusion. Buerstmayr and Buerstmayr (2015) showed that *Rht-D1b* genotypes had lower anther extrusion and higher FHB susceptibility with a significant correlation between both traits ($r=0.70$). *Rht24b* had no effect on this trait (Würschum et al. 2018).

There was wide variation in plant height (PH) within each *Rht* group that might be explained by additional segregating genes or QTL. Mao et al. (2010) projected 133 PH QTL onto a reference map and condensed them to 27 meta-QTL including the known *Rht* genes.

The large genetic variation in FHB response detected within each *Rht* group could also be caused by several factors. Many cultivars with tall *Rht* alleles are older, i.e., they were released before 1989 (Fig. 2). Many cultivars released after 2010 contained *Rht-D1b* and breeding for FHB resistance became more important as a consequence of its effect on FHB response. Generally, the frequently found colocalization of PH and FHB QTL (Buerstmayr et al. 2020; Mao et al. 2010) might favor taller cultivars within a dwarfing group (*Rht24b*, *Rht-D1b*, *Rht24b + Rht-D1b*) as being more resistant. Interestingly, two of the most resistant cultivars in the *Rht-D1b* group (Faktor, Event) were relatively tall with a plant height exceeding 100 cm. According to Buerstmayr et al. (2020) among 24 of

Table 3 Results of the ten most resistant and ten most susceptible winter wheat cultivars and their *Rht* group sorted after Fusarium head blight (FHB) severity

Rank	FHB severity (%)	Plant height (cm)	<i>Rht</i> group	Cultivar
Most resistant cultivars				
1	12.45	109.0	None	Carimulti
2	12.83	101.8	None	Helmond
3	13.66	95.1	<i>Rht24b</i>	Viki
4	14.17	101.6	None	Argument
5	15.16	103.2	<i>Rht24b</i>	Vitus
6	16.57	98.7	<i>Rht24b</i>	Muza
7	16.67	105.3	<i>Rht24b</i>	Arina
8	16.68	121.1	None	Karat
9	16.99	97.2	<i>Rht24b</i>	Monty
10	17.41	105.3	None	Wiwa
Mean	15.26	103.8		
Most susceptible cultivars				
1	61.14	78.3	<i>Rht-D1b</i>	Avalon
2	62.64	73.4	<i>Rht24b + Rht-D1b</i>	Kampana
3	63.01	80.9	<i>Rht-D1b</i>	Hobbit
4	64.65	78.5	<i>Rht24b + Rht-D1b</i>	Muszelka
5	65.14	80.1	<i>Rht24b + Rht-D1b</i>	Macro
6	67.41	72.1	<i>Rht24b + Rht-D1b</i>	Timber
7	68.29	78.3	<i>Rht-D1b</i>	Hobbit_Rht2
8	68.81	82.4	<i>Rht24b + Rht-D1b</i>	Longbow
9	70.46	81.8	<i>Rht24b + Rht-D1b</i>	Norman
10	70.74	77.7	<i>Rht24b + Rht-D1b</i>	Brigand
Mean	66.23	78.4		

32 mapping populations and in all of three analyzed association panels at least one FHB-resistance QTL overlapped with a PH QTL for tallness. Even when the *Rht-1* loci are excluded such overlaps occurred on 13 wheat chromosomes. Thus, tall cultivars might be more FHB resistant for reasons other than absence of dwarfing alleles. Micro-climatic effects such as lower humidity, shorter wetness duration or lower temperatures at ear height in reducing FHB susceptibility were discussed (Hilton et al. 1999; Jones et al. 2018). Field experiments with artificial spray inoculation from above as in this study or as reviewed by Burstmayr et al. (2020) or with PH dependent randomization structure (Voss et al. 2008) support this hypothesis as they also detected a significant correlation between FHB severity and PH. In our study, the highest genetic correlation between FHB severity and PH was found in the group without both dwarfing alleles (Table 2) illustrating the large effect of PH QTL on FHB response. However, this could also be affected by the much

higher genetic variance for PH in this group. We also need to consider the genetic background concerning FHB QTL. In modern cultivars with *Rht-D1b*, FHB-resistant alleles were probably enriched by (recurrent) selection to meet critical thresholds for variety registration, that in Germany, for example, is ≤ 6 on the 1–9 scale (with 1=healthy, 9=fully susceptible).

In conclusion, breeders of modern cultivars must not only consider the *Rht* status of candidates, but also the presence of additional QTL for PH, FHB resistance, and morphological traits such as degree of anther extrusion. The complex interactions between these traits and their molecular basis must be critically examined. In breeding FHB resistant semi-dwarf cultivars there are two approaches: (1) the higher FHB susceptibility conferred by *Rht-1* homoeoloci must be counterbalanced by additional FHB genes (such as *Fhb1* or *Fhb5*, Miedaner et al. 2019; Lu et al. 2011) or QTL (Burstmayr et al. 2020); (2) the FHB-neutral *Rht24b* could be complemented with

Fig. 2 a Plant height and **b** Fusarium head blight (FHB) severity in cultivars from different decades and **c** frequencies of genotypes possessing either no dwarfing allele (None) or the dwarfing alleles *Rht24b* or *Rht-D1b* or both in relation to the year of registration; n = number of cultivars within each group

additional dwarfing alleles of *Rht* genes or QTL that reduce PH with no effect on FHB response.

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Author contributions TM and SK designed the experiment. ML, JG and SK performed the phenotypic evaluations for all traits in HOH and OLI, SK and PG analyzed the data. TM wrote the draft manuscript, PG revised the draft manuscript. All authors read and approved the manuscript.

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Data availability All datasets supporting the conclusions of this article are included within the article and its supporting information files provided as accompanying supplementary materials.

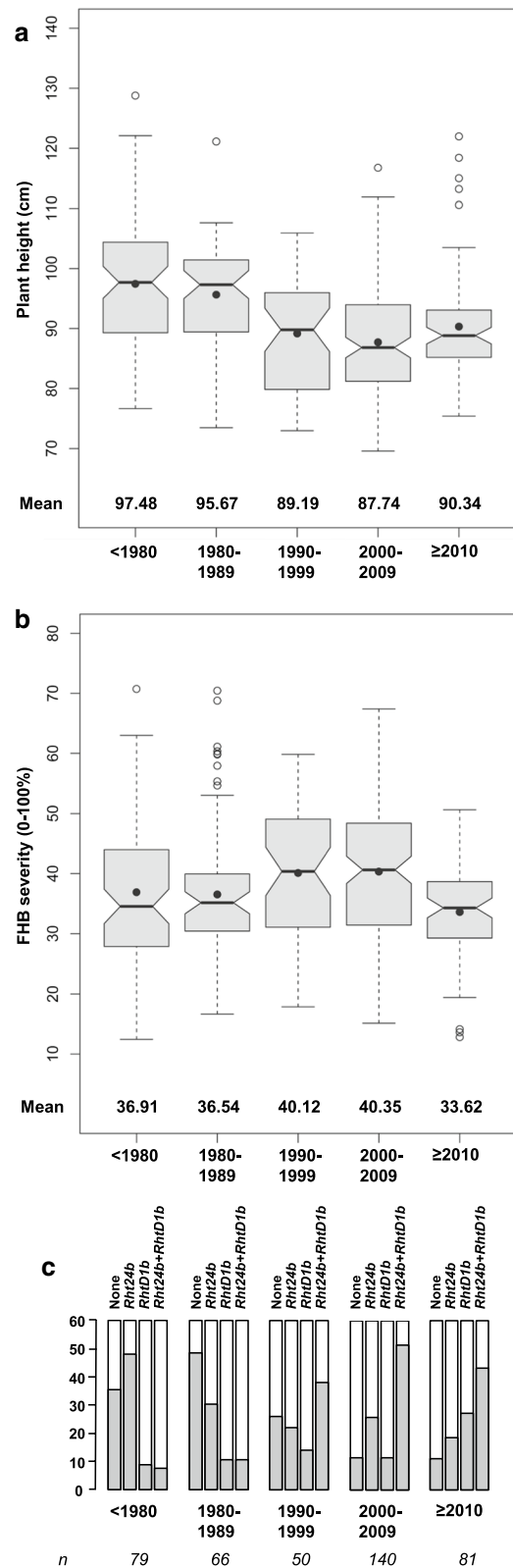
Declarations

Conflict of interest The authors declare no conflicts of interest.

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