

GENETIC EFFECTS OF *Rht-B1b* AND *Rht-D1b* DWARFING ALLELES ON PLANT HEIGHT AND AGRONOMIC TRAITS OF BREAD WHEAT (*Triticum aestivum* L.) BREEDING LINES

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Plant height is an important agronomic trait related to plant architecture and grain yield in wheat. We investigated the effects of the gibberellic acid (GA)-insensitive *Rht-B1b* and *Rht-D1b* semi-dwarfing alleles in a set of 599 F_{4:5} spring wheat breeding lines grown in rainfed and supplemental irrigation conditions at Setif semi-arid high plateaus region (Algeria). Genotyping of diagnostic markers was performed using Kompetitive Allele Specific PCR assays. The *Rht-B1b* mutant allele was present in 66% of the evaluated lines, while the *Rht-D1b* allele was found only in 8% of the lines. Relative to wild-type, *Rht-B1b* or *Rht-D1b* alone reduced plant height by 16.0 and 16.3% in rainfed, and by 20.7 and 21.8% in irrigated environments, respectively. The two dwarfing alleles when combined decreased height by 39.3 and 56.6% in rainfed and irrigated conditions, respectively. The semi-dwarf breeding lines generally outperformed the tall genotypes for

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yield and yield components including the number of grains per spike and harvest index irrespective of environment. Variation in heading date under the influence of dwarfing alleles has not been found. In addition, above-ground biomass was reduced in most of the short statured lines, compared to their tall counter parts across environments. We also demonstrate clear yield and yield components penalty for *Rht-B1b* + *Rht-D1b* double dwarf backgrounds.

Keywords: pleiotropic effects, plant height, reduced height genes, *Triticum aestivum*, yield components.

INTRODUCTION

In Algeria, bread wheat (*Triticum aestivum* L.) is the third most cultivated crop after durum wheat (*T. turgidum* L. var *durum*) and barley (*Hordeum vulgare* L.) with an annual sown area of 354,165 ha (MADRP-DSASI, 2020). Wheat is rainfed grown in areas where water availability is the major limiting factor for production. In these rainfed environments, where black fallow-wheat is the main cropping system adopted, plant height is an important agronomic characteristic. Wheat straw produced is balled, stocked and fed to livestock during the winter months (FILALI *et al.*, 2019). Local old varieties which are tall, late and low yielding are still largely adopted by farmers because of their stress resilience, high straw yield—and effective weeds competitiveness. Plant height is often reported as a beneficial characteristic under water deficit conditions. Tall cultivars develop deeper rooting system that promotes access to soil water and nutrients. Such cultivars are able to transfer appreciable amount of stem stored assimilates to the grain, to minimize grain yield reduction under terminal stress (AZIZ *et al.*, 2017; FRIEDLI *et al.*, 2019; FIGUEROA-BUSTOS *et al.*, 2020; JATAYEV *et al.*, 2020). At the beginning of the 1970s, new semi-dwarf wheat varieties were introduced from the International Maize and Wheat Improvement Center (CIMMYT) which were adopted on a large scale, replacing traditional cultivars. Under good crop management and less harsh environments, these new cultivars showed much higher grain yielding ability (BENBELKACEM, 2014).

Plant height is controlled by more than twenty genes (MCINTOSH *et al.*, 2017). *Rht-B1b* and *Rht-D1b* dwarfing alleles (known as *Rht1* and *Rht2*, respectively) are the most prevalent in wheat (JOBSON *et al.*, 2019; REYNOLDS and BRAUN, 2022). Originating from Japanese cultivar ‘Norin10’ they were transferred into a wide range of CIMMYT germplasm, defining the characteristics of the ‘Green Revolution’ (LUMPKIN, 2015; DREISIGACKER *et al.*, 2016). *Rht-B1b* and *Rht-D1b* alleles occur at homoeologous loci on the short arms of chromosomes 4B and 4D, respectively. Encoding DELLA proteins involved in gibberellic acid (GA) sensitivity, both are insensitive to exogenous GA, which is necessary for stem elongation (WILHELM *et al.*, 2013; REBETZKE *et al.*, 2021; SUKHIKH *et al.*, 2021). Both alleles exhibit pleiotropic effects on plant growth, morphology and physiology. Their influence depends on growth habit type (spring vs winter type), genetic background and environmental conditions (REBETZKE *et al.*, 2012; SUBIRA *et al.*, 2016; SUKHIKH *et al.*, 2021; INGVORSEN *et al.*, 2022; REYNOLDS and BRAUN, 2022).

Compared to the corresponding wild-type alleles (*Rht-B1a* and *Rht-D1a*), *Rht-B1b* and *Rht-D1b* mutant alleles each can reduce plant height in bread wheat by 10–47% through shortening the internodes length of wheat stem (WILHELM *et al.*, 2013). It has been reported that height-reducing alleles *Rht-B1b* and *Rht-D1b* are associated with yield and yield component

traits. Varieties carrying either *Rht-B1b* or *Rht-D1b* allele headed earlier and outperformed tall varieties for grain yield, number of grains per spike and harvest index, with no sizeable changes in above-ground biomass (CHAPMAN *et al.*, 2007; REBETZKE *et al.*, 2012; LIU *et al.*, 2017). However, their advantage is narrowed under drought and heat stresses where they exhibited smaller leaves, lower chlorophyll content, shorter coleoptile and root lengths, slower growth rate and eventually lower above-ground biomass and yield (REBETZKE *et al.*, 2007; WANG *et al.*, 2014). Several studies also demonstrated that the presence of dwarfing genes increased susceptibility to *Fusarium* head blight and decreased grain quality, including seed size, protein content, alpha amylase activity, grain Zinc and Iron contents (BUERSTMAYR and BUERSTMAYR, 2016; CASEBOW *et al.*, 2016; HE *et al.*, 2016; VELU *et al.*, 2017; JOBSON *et al.*, 2018, 2019). This study aimed to investigate the effects of *Rht-B1b* and *Rht-D1b* genes on plant height and a number of agronomic characteristics of bread wheat breeding lines derived from twenty bi-parental crosses involving nine parents, under field conditions in Algeria.

MATERIALS AND METHODS

Plant materials, experimental details and phenotyping

A total of 602 bread wheat genotypes, including 599 F_{4.5} breeding lines and three checks namely Hidhab, Rmada, and El-Wifak were used as plant materials. The breeding lines were selected offspring from crosses made between nine divergent parents coming from local wheat breeding programs (FELLAHI *et al.*, 2013). Checks were released cultivars grown at large scale in the eastern high plateaus of Algeria. Plant materials were planted and evaluated at the Setif Research Unit (36°15'N; 5°87'E; 1,081 masl) belonging to the National Agronomic Research Institute of Algeria (INRAA). Field experiments were conducted during the 2014/15 cropping season under rainfed and supplemental irrigation conditions and arranged in a type III randomized incomplete block design (augmented blocks) with three replications. Seeds were sown in a single 1-m row, with row spacing of 20 cm and a target planting density of 350 seeds m⁻². Supplemental irrigation included nearly 60 mm of water applied (3 doses of 30 mm each at 7 days interval) at heading. Under both environmental conditions, natural rainfall recorded during the growing season reached 343.6 mm from September to June. Plant materials under both environmental conditions were fertilized with 100 kg ha⁻¹ of 46% superphosphate (N: 0%, P: 46%, K: 0%) fertilizer before sowing and 75 kg ha⁻¹ of urea (N: 46%, P: 0%, K: 0%) at the tillering stage. Herbicide applications were made as necessary to control weeds. Data were recorded for heading date (HD, days), plant height (PH, cm), number of spikes (NS, spikes m⁻²), thousand-grain weight (TGW, g), number of grains per spike (NGS, No), above-ground biomass (BIO, g m⁻²), grain yield (GY, g m⁻²) and harvest index (HI, %).

Genotyping

Fresh leaves of 2- to 3-week-old greenhouse-grown plants were collected, frozen in liquid nitrogen and stored at -80°C until use. After samples grinding, genomic DNA was extracted using CTAB (Cetyl Trimethyl Ammonium Bromide) following SAGHAI-MAROOF *et al.* (1984), method with minor modifications as described by DREISIGACKER *et al.* (2016). DNA quality and quantity were determined by spectrophotometer (NanoDrop 8000, Thermo Scientific, USA) at 260 and 280 nm. PCR reactions for molecular analyses were performed in a total volume of 5µl

containing 2.5 µl, 2 x KASPar Reaction mix, 0.07 µl Assay mix, 30 ng of genomic DNA and 2.5 µl of H₂O (DREISIGACKER *et al.*, 2016). Two KASP (Kompetitive Allele-Specific PCR) assays, *wMAS000001* and *wMAS000002*, from published sequences of causal genes were used to distinguish alleles at *Rht-B1* and *Rht-D1* loci in wheat breeding lines (Table 1; ELLIS *et al.*, 2002).

Table 1. KASP assays associated with plant height used in this study.

Gene	<i>Rht-B1</i>	<i>Rht-D1</i>
SNP id	<i>wMAS000001</i>	<i>wMAS000002</i>
Marker name	<i>Rht-B1_SNP</i>	<i>Rht-D1_SNP</i>
FAM primer	CCCATGGCCATCTCSAGCTG	CATGGCCATCTCGAGCTRCTC
VIC primer	CCCATGGCCATCTCSAGCTA	CATGGCCATCTCGAGCTRCTA
Common primer	TCGGGTACAAGGTGCGGGCG	CGGGTACAAGGTGCGGGCC
Dominance	Co-dominant	Co-dominant
FAM Allele	Wild-type (Tall)	Wild-type (Tall)
VIC Allele	Semi-dwarf	Semi-dwarf

Krichauff (*Rht-B1b* + *Rht-D1a*) and Pavon F76 (*Rht-B1a* + *Rht-D1b*) were used as controls. Program used for thermocycling was ramp consisted of 1) 94°C for 15 min; 2) 94° for 20 s; 3) 65°C for 60 s; 4) 72°C for 30 s; 5) 57°C for 60 s; 6) 72°C for 20 s; 7) 72°C for 2 min. All amplified products were analyzed and read by the Pherastar Plus (BMG Labtech) that allowed to cluster the genotypes into FAM, VIC or HET (heterozygote) in *Rht-B1* and *Rht-D1* semi-dominant height regulating genes. In this case, dominant and recessive alleles are associated with VIC and FAM fluorophores, respectively (DREISIGACKER *et al.*, 2016). Genotyping was done at the Bioscience Laboratory of CIMMYT.

Statistical analysis

Shapiro-Wilk test was initially used to fit data normality for each trait. Whenever a normal distribution was observed, combined analysis of variance (ANOVA) over the two environments was performed for all traits using Genes software (CRUZ, 2013). Breeding line source of variation was considered as fixed effect, while the replications within environment and environments were considered as random effects. Heritability estimate for multiple environments, was calculated using the formula: $H^2 = \sigma_G^2 / (\sigma_G^2 + \frac{\sigma_{GE}^2}{e} + \frac{\sigma_e^2}{re})$; where σ_G^2 represents the genetic variance, σ_{GE}^2 genotype x environment variance, σ_e^2 error variance, e is the number of environments, and r for the number of replications (Acquaah, 2012). In presence of lack of normality in the allele combinations dataset (Shapiro-Wilk test), the significance of difference between *Rht-B1* and *Rht-D1* was assessed by the non-parametric Kruskal-Wallis test followed by a Wilcoxon post hoc pairwise comparison of mean ranks for all groups. Linear/quadratic regressions were fitted to data with alleles varying at the *Rht-B1* and *Rht-D1* loci in order to examine the responses of measured traits to plant height variation mediated through GA-insensitivity. Whenever, both were significant, we used the partial F -test to compare them formally and decide if squared y variable significantly improved the regression model. Heterozygote lines at *Rht-B1* and *Rht-D1* loci as well as lines where their DNA was not

amplified and/or their polymorphism was not identified were excluded from the analysis. Data were analyzed using R package (R Development Core Team, 2020). All statistical tests were performed at a 95% confidence level.

RESULTS AND DISCUSSION

A combined analysis of 602 genotypes over two environments showed significant difference among genotypes for days to heading, plant height and biomass. The ‘environment’ source of variation was highly significant for all the traits while the ‘genotype x environment’ was only significant for plant height and above-ground biomass (Table 2). For all traits, variance components for environment were larger than those for genetic background and genetic background by environment.

Table 2. Mean squares of the combined analysis of variance of the eight traits across two environments.

Source of variation	Genotype	Environment	Genotype x Environment	Error
df	598	1	598	8
HD	6.6*	863.0**	3.7 ^{ns}	1.6
PH	133.4**	39233.5**	50.0*	11.1
NS	20029.6 ^{ns}	1319211.9**	13371.4 ^{ns}	11230.6
TGW	34.8 ^{ns}	29126.8**	34.2 ^{ns}	18.9
NGS	99.6 ^{ns}	3056.2**	25.1 ^{ns}	47.6
BIO	280651.0**	55778651.5**	149356.1*	33402.8
GY	55439.7 ^{ns}	20238116.0**	33887.2 ^{ns}	24443.6
HI	46.7 ^{ns}	14081.9**	31.6 ^{ns}	114.8

HD: heading date (days), PH: plant height (cm), NS: number of spikes (spikes m⁻²), TGW: thousand-grain weight (g), NGS: number of grains per spike (No), BIO: above-ground biomass (g m⁻²), GY: grain yield (g m⁻²), HI: harvest index (%). ns, * and **: non-significant and significant effects at 0.05 and 0.01 probability levels, respectively.

Even though the results of combined environment analysis of variance showed non-significant ‘genotype’ effect for some traits, the ANOVA of each environment individually revealed, respectively, significant and highly significant differences for grain yield and harvest index in irrigated; and globally the breeding lines exhibited a wide range of variation in all cases (Table 3). While comparing the data of the two environments, it appears there was a shift to the right in all the data distribution, which is explained by realizing that all of the measured traits have significantly increased under irrigation conditions. When considering the two environments, number of grains per spike exhibited the highest heritability followed by plant height (Table 3). The lowest heritability was found for thousand-grain weight, while the remaining traits showed intermediate estimates (Table 3).

The screening with the KASP markers revealed that 398 lines (66%) carried the *Rht-B1b* allele whereas the *Rht-D1b* was present in only 46 lines (8%), suggesting that the B genome mutant allele was the most abundant height-reducing gene within the assessed genetic material (Figure 1). The frequency of the *Rht-B1b* and *Rht-D1b* semi-dwarfing alleles is well documented, their relative proportion depends on geographical distribution and year of variety release. According to WÜRSCHUM *et al.* (2015), the *Rht-B1b* mutant allele was present at a

relatively low frequencies in Central Europe compared to *Rht-D1b* allele. While Eastern European and Turkish varieties carry mostly the *Rht-B1b* height-reducing allele (WÜRSCHUM *et al.*, 2015). CIMMYT lines almost all carry the *Rht-B1b* mutant allele (VAN BEEM *et al.*, 2005).

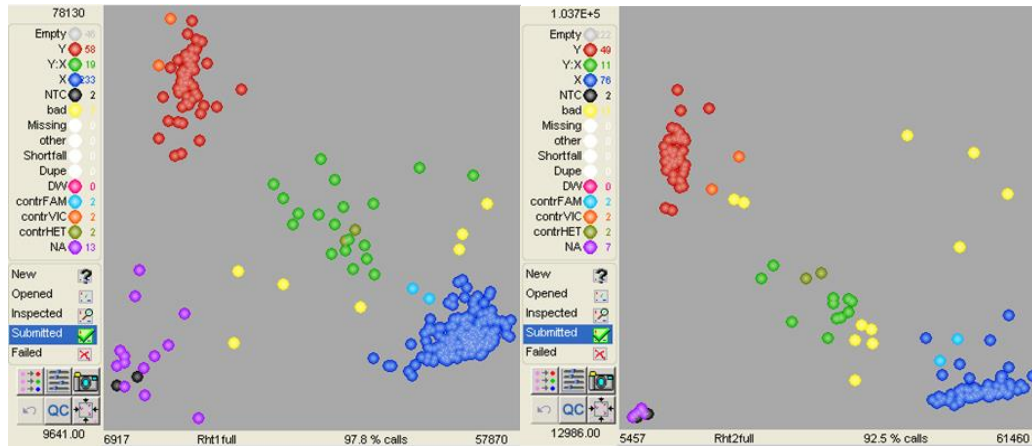


Figure 1. Polymorphism generated by the KASP SNPs height reducing genes *Rht-B1_SNP* (left) and *Rht-D1_SNP* (right) markers in the wheat breeding lines studied. Each dot represents one genotype: red for dominant, blue for recessive, green for heterozygote individuals. Black, purple and yellow dots symbolize water, not amplified and bad DNA quality, respectively. Other three paired dots represent the positive, negative and heterozygote controls.

Table 3. Means, range and heritability of the eight traits measured in wheat breeding lines in rainfed and irrigated environments.

Traits	Rainfed		Irrigated		H^2
	Range	Mean \pm SE	Range	Mean \pm SE	
HD	124.0–136.0	125.9 \pm 0.06	125.0–139.0	127.6 \pm 0.11	0.44
PH	42.0–100.0	65.6 \pm 0.34	45.0–121.0	77.0 \pm 0.43	0.62
NS	80.0–850.0	442.5 \pm 5.16	110.0–920	508.8 \pm 5.37	0.33
TGW	19.0–51.0	36.4 \pm 0.19	30.0–61.0	46.3 \pm 0.28	0.18
NGS	9.3–56.8	25.0 \pm 0.32	10.8–63.6	28.2 \pm 0.33	0.75
BIO	150.0–2420.0	1099.2 \pm 17.36	320.0–4340.0	1530.5 \pm 20.31	0.47
GY	43.0–921.0	404.8 \pm 7.34	102.0–1434.0	664.7 \pm 9.71	0.39
HI	12.6–70.0	36.6 \pm 0.27	14.0–81.3	43.4 \pm 0.23	0.33

HD: heading date (days), PH: plant height (cm), NS: number of spikes (spikes m^{-2}), TGW: thousand-grain weight (g), NGS: number of grains per spike (No), BIO: above-ground biomass (g m^{-2}), GY: grain yield (g m^{-2}), HI: harvest index (%).

ZANKE *et al.* (2014) observed the opposite pattern as obtained in our study when analyzing a set of 372 modern European winter and spring wheat varieties; *Rht-D1b* was present

in 58% of the investigated varieties and the *Rht-B1b* allele was found in only 7%. CHEN *et al.* (2016) reported that these two semi-dwarfing alleles were only found in cultivars registered after 1990 in Canada. In the US, about 90% of recent wheat cultivars contain either *Rht-B1b* or *Rht-D1b* allele (GUEDIRA *et al.*, 2010). Similarly, VIJAYARAGHAVAN *et al.* (2018) reported that more than 95% of improved wheat cultivars in Nepal contains one of these two allelic forms. CHO *et al.* (2016) studied the frequency of dwarfism genes in Korean wheat cultivars and concluded that 70.4% of cultivars carry the *Rht-B1b*, and 51.9% contain the *Rht-D1b* allele. Screened more than 300 Chinese dwarf mutant wheat lines, XIONG *et al.* (2016) identified that *Rht-D1b* and *Rht-B1b* were present in 17.49% and 1.37% of the evaluated plant materials. TOŠOVIĆ-MARIĆ *et al.* (2008) investigated the genetic architecture of plant height in 172 wheat genotypes originating from more than 20 countries, they found that *Rht-B1b* and *Rht-D1b* existed in 40% and 22% of this genetic material and that only 4% of the investigated varieties carry both height reducing alleles. Cultivars with or without the *Rht-B1b* allele, differed significantly for most of the studied traits except for days to heading and grain yield under rainfed conditions, and for days to heading and number of spikes under supplemental irrigation conditions (Table 4).

In this study, the highest differences in the irrigated environment were a -13.14% reduction in plant height and a 17.93% increase of number of grains per spike for lines carrying the B genome mutant allele. Considering both growth conditions, cultivars with *Rht-B1b* were, on average, shorter, having reduced number of spikes, smaller grains and lower biomass. Conversely, they demonstrated higher spikes fertility, grain yield and harvest index (Table 4). This result suggested that *Rht-B1b* increased the yield by increasing spike fertility and harvest index or biomass partitioning. Similarly, cultivars with and without *Rht-D1b* significantly differed for number of spikes in rainfed environment, for days to heading in the irrigated environment, and for plant height, thousand-grain weight and number of grains per spike in both environments (Table 5).

Table 4. Allelic variation of *Rht-B1* locus in the wheat breeding lines.

Traits	Rainfed				Irrigated			
	<i>Rht-B1a</i> †	<i>Rht-B1b</i> †	Difference	Effect (%)	<i>Rht-B1a</i> †	<i>Rht-B1b</i> †	Difference	Effect (%)
HD	126.0	125.9	-0.1 ^{ns}	-0.1	127.6	127.6	0.0 ^{ns}	-0.3
PH	70.5	63.3	-7.2**	-11.4	84.5	73.4	-11.1**	-5.9
NS	463.0	431.0	-32.0**	-7.4	517.9	501.8	-16.1 ^{ns}	7.4
TGW	38.3	35.6	-2.7**	-7.6	48.2	45.2	-3.0**	4.7
NGS	22.4	26.2	3.8**	14.5	25.1	29.6	4.5**	-9.1
BIO	1145.7	1072.8	-72.9*	-6.8	1578.6	1495.1	-83.5*	-0.8
GY	398.7	406.1	7.4 ^{ns}	1.8	626.3	676.7	50.4**	3.9
HI	34.7	37.4	2.70**	7.2	39.9	45.1	5.2**	4.7

HD: heading date (days), PH: plant height (cm), NS: number of spikes (spikes m⁻²), TGW: thousand-grain weight (g), NGS: number of grains per spike (No), BIO: above-ground biomass (g m⁻²), GY: grain yield (g m⁻²), HI: harvest index (%). †: values in columns represents the mean values of measured traits, A *t*-test was used for comparing means of the different between the wild-type and mutant alleles at *Rht-B1* locus. ns, * and **: non-significant and significant effects at 0.05 and 0.01 probability levels, respectively. Effect (%) = 100 [(semi-dwarf mean_{TRAIT} - tall mean_{TRAIT})/semi-dwarf mean_{TRAIT}].

Table 5. Allelic variation of *Rht-D1* locus in the wheat breeding lines.

Traits	Rainfed				Irrigated			
	<i>Rht-D1a</i> †	<i>Rht-D1b</i> †	Difference	Effect (%)	<i>Rht-D1a</i> †	<i>Rht-D1b</i> †	Difference	Effect (%)
HD	126.0	125.6	-0.4 ^{ns}	0.0	127.7	127.1	-0.6*	-0.5
PH	65.9	62.2	-3.7**	-15.1	77.5	72.0	-5.5**	-7.6
NS	440.3	475.7	35.4*	-3.2	508.4	506.5	-1.9 ^{ns}	-0.4
TGW	36.2	38.0	1.8*	-6.6	45.9	49.4	3.5**	7.1
NGS	25.2	23.1	-2.1*	15.2	28.6	25.6	-3.0**	-11.7
BIO	1104.8	1096.1	-8.7 ^{ns}	-5.6	1534.2	1507.6	-26.6 ^{ns}	-1.8
GY	405	421.5	16.5 ^{ns}	7.4	669.2	636.2	-33.0 ^{ns}	-5.2
HI	36.4	38.2	1.8 ^{ns}	11.5	43.6	42.1	-1.5 ^{ns}	-3.6

HD: heading date (days), PH: plant height (cm), NS: number of spikes (spikes m⁻²), TGW: thousand-grain weight (g), NGS: number of grains per spike (No), BIO: above-ground biomass (g m⁻²), GY: grain yield (g m⁻²), HI: harvest index (%). †: values in columns represents the mean values of measured traits, A *t*-test was used for comparing means of the different between the wild-type and mutant alleles at *Rht-D1* locus. ns, * and **: non-significant and significant effects at 0.05 and 0.01 probability levels, respectively. Effect (%) = 100 [(semi-dwarf mean_{TRAIT} - tall mean_{TRAIT})/semi-dwarf mean_{TRAIT}].

These effects varied from -10.49% for number of grains per spike in the irrigated environment to 8% for number of spikes per unit area under rainfed conditions (Table 5). *Rht-D1b* had significant negative effects for heading time, plant height, spikes number, number of grains per spike, above-ground biomass, grain yield and harvest index in the irrigated environment. Significant positive effect of this allele was expressed for thousand-grain weight (Table 4). Breeding lines carrying *Rht-D1b* (*Rht-B1b* and *Rht-B1a* included) were earlier and had reduced height, lower spikes fertility and above-ground biomass under rainfed conditions. A much higher number of spikes, bigger grain size and higher yield and harvest index (Table 5) were also recorded, indicating that yield increase in this environment was the consequence of increasing number spikes, grain weight and declined plant height.

Among the plant material studied, 22% were tall carrying both wild type alleles (*Rht-B1a* + *Rht-D1a*) and 1% were double dwarf carrying the *Rht-B1b* + *Rht-D1b* combination. The Kruskal-Wallis test showed that the observed variation between the four possible combinations (*Rht-B1a* + *Rht-D1a*, *Rht-B1b* + *Rht-D1a*, *Rht-B1a* + *Rht-D1b*, *Rht-B1b* + *Rht-D1b*) were significant for most of the studied traits, except for grain yield under rainfed, number of spikes under irrigated and heading time in both growth environmental conditions (Table 6).

The effects of different *Rht*-allele combinations on the eight recorded traits are given in figure 2. Variation in heading date based on any, *Rht-B1b* and *Rht-D1b* dwarfing allele, has not been observed irrespective of environment, due to the close divergence of the parents for major flowering genes loci and/or the small sample size of the plant material evaluated. In southern Australia, CANE *et al.* (2013) reported a negligible change between the two reduced-height loci for heading time in wheat. In the literature, it is well documented that flowering time in wheat is mainly controlled by the three groups of genes including vernalization (*Vrn*), photoperiod (*Ppd*) and earliness *per se* (*Eps*) (ROUSSET *et al.*, 2011).

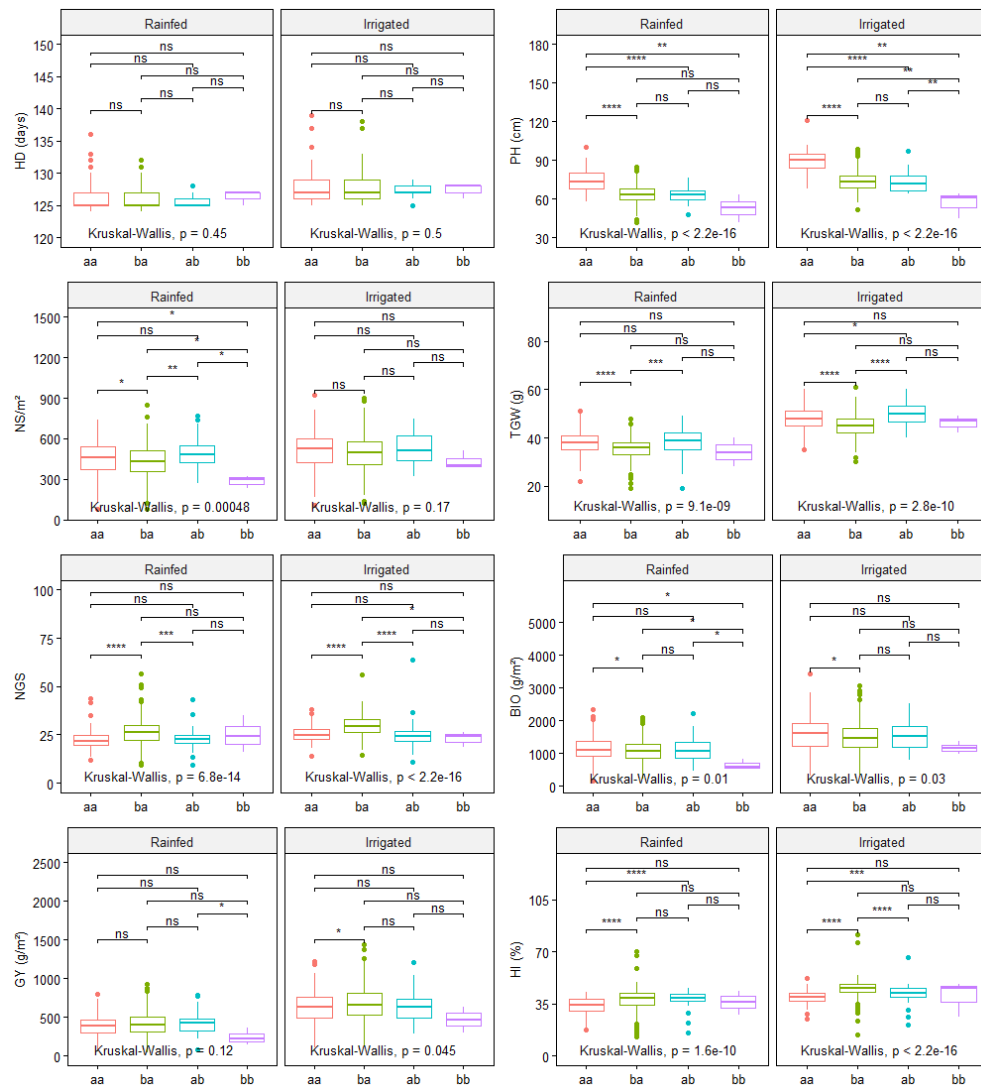


Figure 2. Box plots showing the effects of the effects of *Rht*-alleles on height and agronomic traits of wheat breeding lines across all environments, as well as the pairwise mean comparison between the genetic background. Letters in x-axis correspond to *Rht*-alleles (aa = *Rht-B1a* + *Rht-D1a*, ba = *Rht-B1b* + *Rht-D1a*, ab = *Rht-B1a* + *Rht-D1b*, bb = *Rht-B1b* + *Rht-D1b*). Medians with inter quartile ranges are indicated. *p* values (ns > 0.05; * < 0.05; ** < 0.01; *** < 0.001; **** < 0.0001) were determined by Kruskal-Wallis test followed by a Wilcoxon post hoc test.

Table 6. Summary of results for the Kruskal-Wallis test of *Rht-B1* and *Rht-D1* combination effects on height and agronomic traits of wheat breeding lines in rainfed and irrigated environments.

Traits	Rainfed		Irrigated	
	Kruskal-Wallis value	<i>p</i> value	Kruskal-Wallis value	<i>p</i> value
HD	2.66	0.45	2.35	0.50
PH	147.48	<0.001	211.81	<0.001
NS	17.83	<0.001	4.97	0.17
TGW	40.32	<0.001	47.42	<0.001
NGS	64.37	<0.001	102.48	<0.001
BIO	11.34	0.01	8.96	0.03
GY	5.75	0.12	8.03	0.04
HI	48.53	<0.001	142.07	<0.001

HD: heading date (days), PH: plant height (cm), NS: number of spikes (spikes m⁻²), TGW: thousand-grain weight (g), NGS: number of grains per spike (No), BIO: above-ground biomass (g m⁻²), GY: grain yield (g m⁻²), HI: harvest index (%).

The estimated plant height for the *Rht-B1b* + *Rht-D1a* genotypes were 63.3 and 73.6 cm and for the *Rht-B1a* + *Rht-D1b* genotypes were 63.1 and 72.9 cm in the rainfed and irrigated environment, respectively. In both environments these two combinations did not significantly differ from each other but both were significantly shorter than the tall (*Rht-B1a* + *Rht-D1a*) lines with a -16.0 and -16.3% reduced height in the rainfed and a -20.7 and -21.8% reduced height under irrigation, respectively. In the irrigated environment the semi-dwarf genotypes were taller than the double dwarf line (56.7 cm), but with only a negligible effect under rainfed conditions (52.7 cm). The two dwarfing genes together, contributed a -39.3 and -56.6% height reduction in rainfed and irrigated environments, respectively. ZHANG *et al.* (2013) investigated the effects of interaction of height-reducing alleles *Rht-B1* and *Rht-D1* on yield-components in 225 double haploid wheat lines and concluded that average height of semi-dwarf lines with *Rht-B1a* + *Rht-D1b* and *Rht-B1b* + *Rht-D1a* was not different, but significantly varied from the *Rht-B1a* + *Rht-D1a* wild-type and the *Rht-B1b* + *Rht-D1b* double dwarf classes. HAYAT *et al.* (2019) reported that the presence of the height-reducing *Rht-B1b* or *Rht-D1b* alleles alone reduced plant height up to 20%, while the combination of both alleles resulted in a short plant stature among the four *Rht* haplotypes analyzed. In addition, lines carrying *Rht-D1b* allele were significantly shorter than *Rht-B1b* semi dwarfs across all environments. In the same context, double dwarf cultivars usually result in large height reduction, less biomass, poor emergence and leaf area development. However, their harvest index is notably improved and lodging risk is reduced, especially under high water and nitrogen availability (WANG *et al.*, 2014; CASEBOW *et al.*, 2016). The magnitude of the gene effects is variable depending on the genetic material studied and the target environment; their advantage is less important in dryland farming, due to decreased seedling emergence (REBETZKE *et al.*, 2012). No difference in spikes number between the four different gene combinations were observed under the irrigated conditions. In the rainfed environment, the *Rht-B1a* + *Rht-D1b* genotypes (488.2 spikes m⁻²) showed the highest trait values, followed by tall lines (459.5 spikes m⁻²), *Rht-B1b* + *Rht-D1a* semi-dwarf lines (488.2 spikes m⁻²) and double dwarf lines (283.3 spikes m⁻²). Tiller number is positively correlated to spikes m⁻². For thousand-grain weight, the lines with the wild-type alleles (38.2 g) and *Rht-B1a* + *Rht-D1b* semi-dwarf lines (38.1 g) exhibited elevated grain sizes in the both environments. While no significant

differences of both gene combinations were observed to the double dwarf lines, significant differences were observed to the *Rht-B1b* + *Rht-D1a* semi-dwarf lines (Figure 2). Our results are in line with findings of ZHANG *et al.* (2013) who demonstrated neutral and negative effects of the *Rht-B1b* dwarfing allele on grain size and, therefore, on grain yield. They reported that the wild-type *Rht-B1a* and *Rht-D1a* alleles are associated with higher thousand-grain weight and grains number per spike, respectively. The same authors also recommended incorporating one of these two alleles when selecting wheat varieties for drought stress environments. In China, YU *et al.* (2017) genotyped 188 F_{6:7} Recombinant Inbred Lines and concluded that tall lines had higher grain yield with lower grain weight and sedimentation volume across over 2 years in replicated trials. For the number of grains per spike, the *Rht-B1b* + *Rht-D1a* semi-dwarfs show a higher spike fertility in comparison to all other gene combinations (allele effect equal to 18%), while not significant to double dwarfs in the rainfed environment. There was a reduction in the above-ground biomass, compared with the tall cultivars (1170.2 and 1616.9 g m⁻²) in all trials. A significant decrease was observed in the *Rht-B1b* + *Rht-D1a* semi-dwarf genotypes (1076.9 and 1498.3 g m⁻²) and especially compared to the *Rht-B1b* + *Rht-D1b* double dwarf lines (650.0 and 1166.7 g m⁻²). By contrast, no adverse effect was detected for the other *Rht-B1a* + *Rht-D1b* semi-dwarf combination (1127.7 and 1512.1 g m⁻²), suggesting that *Rht-D1b* allele could be associated to higher biomass, even though cultivars with *Rht-B1b* + *Rht-D1a* did not differ from lines with *Rht-B1a* + *Rht-D1b* allelic combination. Tall cultivars may be desirable for reasons other than high grain yield, including high above-ground biomass, longer straw lengths and larger leaf area (AFZAL *et al.*, 2017). By analyzing the figure 2, it appears that the *Rht-B1b* + *Rht-D1a* (37.4 and 45.1%) and *Rht-B1a* + *Rht-D1b* (38.1 and 41.9%) semi-dwarfs realized a higher harvest index when compared to tall (33.5 and 39.3%) and dwarf (35.9 and 39.9%) backgrounds irrespective of environment. Even though the difference observed was not significant for grain yield under rainfed conditions, the allele combination ranked as follows: *Rht-B1a* + *Rht-D1b* > *Rht-B1b* + *Rht-D1a* > *Rht-B1a* + *Rht-D1a* > *Rht-B1b* + *Rht-D1b*, with estimated means of 430.6, 408.0, 392.4 and 241.0 g m⁻², respectively. This was different under irrigation conditions where the ranking became: *Rht-B1b* + *Rht-D1a* (678.9 g m⁻²) > *Rht-B1a* + *Rht-D1b* (632.2 g m⁻²) > *Rht-B1a* + *Rht-D1a* (632.0 g m⁻²) > *Rht-B1b* + *Rht-D1b* (465.3 g m⁻²). The yield advantage of the semi-dwarf was 3.8 and 8.9% for *Rht-B1* locus and 6.9 and 0.0% at *Rht-D1* locus across rainfed and irrigated environments, respectively.

This result elucidates previous findings of wild-type plants performing better in water-limited environments (CHAPMAN *et al.*, 2007; SANAD *et al.*, 2016; JATAYEV *et al.*, 2020). In this context, LANNING *et al.* (2012) stated that tall and semi-dwarf lines had similar adaptation to stressed environments, but semi-dwarfs yielded more in favorable environments. Some studies highlighted the importance to breed “tall dwarfs” for a better adaptation to dry conditions (MOHAN *et al.*, 2017; WÜRSCHUM *et al.*, 2017; MO *et al.*, 2018). Conversely, other research supported the theory to breed for “short tall” to produce acceptable yields in these growing conditions (HYLES *et al.*, 2020). Indeed, it must be remembered that the *Rht-B1b* and *Rht-D1b* alleles are associated with some negative aspects in these environments. Under such growing conditions, where backgrounds carrying either *Rht-B1b* or *Rht-D1b* did not seem to perform well, other alternatives height reduced genes such as *Rht8* and *Rht24* with less negative effects

on yield components are suggested to be used in wheat breeding programs (REBETZKE *et al.*, 2012; WÜRSCHUM *et al.*, 2017).

Figure 3 shows the significant quadratic response ($p < 0.05$) of the recorded traits to plant height in the interval from 52.7 cm for *Rht-B1b* + *Rht-D1b* in rainfed to 88.8 cm for *Rht-B1a* + *Rht-D1a* in irrigated environments, as modified by allele combinations. For grain yield ($R^2 = 0.99$) and harvest index ($R^2 = 0.98$) in rainfed, and heading date ($R^2 = 0.85$ and $R^2 = 0.62$), number of spikes m^{-2} ($R^2 = 0.98$ and $R^2 = 0.98$), thousand-grain weight ($R^2 = 0.74$ and $R^2 = 0.13$) and above-ground biomass ($R^2 = 0.99$ and $R^2 = 0.99$) in both environments, the optimum height was achieved by incorporating the *Rht-D1b* to the tall backgrounds.

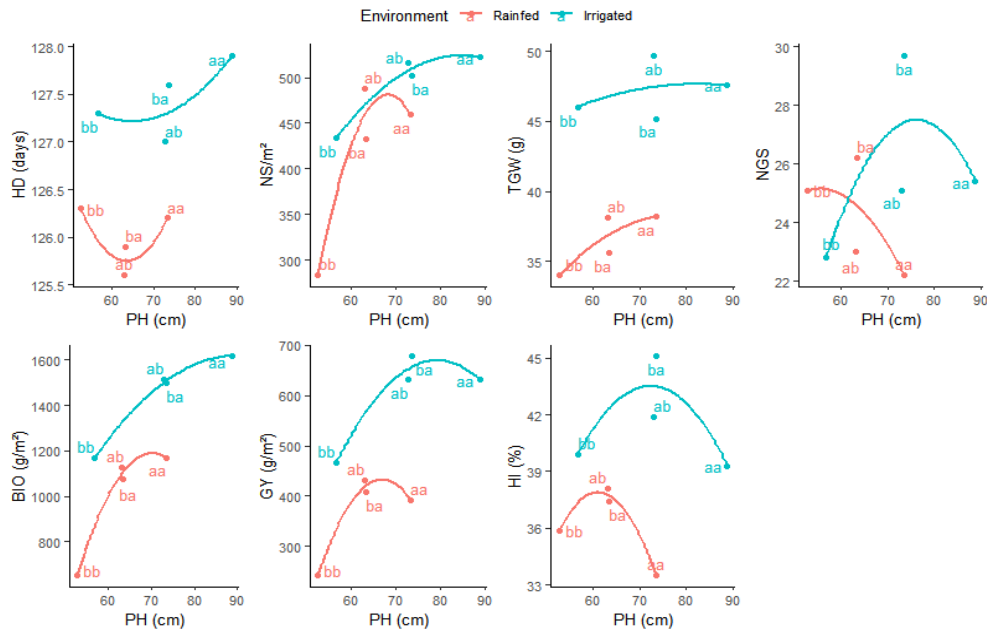


Figure 3. Regression by environment between plant height and agronomic traits of wheat breeding lines. Open symbols in panels correspond to *Rht*-alleles (aa = *Rht-B1a* + *Rht-D1a*, ba = *Rht-B1b* + *Rht-D1a*, ab = *Rht-B1a* + *Rht-D1b*, bb = *Rht-B1b* + *Rht-D1b*). Points are means from lines with same allelic combinations in each environment. Fits are quadratic for all traits.

The effects of *Rht*-alleles on heading time were the opposite of the other traits. On the other hand, to achieve the highest grain yield ($R^2 = 0.96$) and harvest index ($R^2 = 0.75$) in less stressed environment, and spikes fertility irrespective of environment ($R^2 = 0.49$ in rainfed and $R^2 = 0.58$ in irrigated), the optimum plant height was achieved by incorporating the *Rht-B1b* allele. Effects of different alleles and background combinations, in favorable environment (irrigation), on spikes number m^{-2} were constant at similar heights, except for dwarfs, suggesting no penalty for heights beyond 73.6 cm. The data were more variable between *Rht-B1b* + *Rht-*

D1a and *Rht-B1a* + *Rht-D1b* semi-dwarf genotypes when compared to each other. *Rht-D1b* caused the largest reduction in mean grain weight and spikes fertility. The penalty of incremental dwarfing becoming more exaggerated as height declined in all datasets.

CONCLUSION

We analyzed the pleiotropic effects of the gibberellin (GA)-insensitive alleles *Rht-B1b* and *Rht-D1b* mutant alleles on yield components traits of 599 wheat breeding lines. Our results demonstrate that the effect of the dwarfing alleles varies depending on the environment, the trait and the genetic background. We demonstrated that wheat lines with either the *Rht-B1b* or *Rht-D1b* allele performed equal to, or better than all other gene combinations for grain yield components in both environments (rainfed and irrigated) studies. The highest yield advantages (8.9 and 6.9%) were recorded in the lines carrying the *Rht-D1b* mutant allele in the irrigated environment and *Rht-B1b* semi-dwarf lines in rainfed conditions. The lines carrying the wild-type alleles usually produced more above-ground biomass and a bigger grain size depending on the environment. Double dwarf lines were significantly shorter, late and less productive than semi-dwarf and tall lines. Heading time did not vary between the four allele combinations irrespective of environment. Cultivars with *Rht-B1b* + *Rht-D1a* significantly differed for thousand-grain weight, number of grains per spike from cultivars with *Rht-B1a* + *Rht-D1b* allelic combination. Wheat genotypes with *Rht-B1b* + *Rht-D1a* showed, however, a higher harvest index under water supply. Owing to the lack of significant variation between these classes for plant height, factors other than *Rht-B1* and *Rht-D1* genes and/or other traits must cause these significant differences. Quadratic relationships between different yield contributing traits and crop height were investigated. We concurred that the *Rht1* and *Rht1* genes together with other 'Post-green Revolution' dwarf genes such as *Rht8*, *Rht11*, *Rht12*, and *Rht24* can be used for marker-assisted selection to fine-tune wheat plant height in local breeding programs to have good breeding value in adapted commercial wheat varieties with increased yield, improved disease resistance and end-use quality characteristics.

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**GENETIČKI EFEKTI *Rht-B1b* I *Rht-D1b* PATULJASTIH ALELA NA VISINU BILJKE
I AGRONOMSKA SVOJSTVA OPLEMENJIVAČKIH LINIJA HLEBNE PŠENICE
(*Triticum aestivum* L.)**

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Izvod

Visina biljke je važna agronomska osobina vezana za arhitekturu biljke i prinos zrna kod pšenice. Istraživali smo efekte polu-patuljastih alela *Rht-B1b* i *Rht-D1b* neosetljivih na giberelinsku kiselinu (GA) u setu od 599 F4:5 linija za oplemenjivanje jare pšenice uzgajanih u kišovitim uslovima i uslovima dodatnog navodnjavanja u regionu polusušne visoravni Setif. (Alžir). Genotipizacija dijagnostičkih markera je izvršena korišćenjem kompetitivnih alel specifičnih PCR testova. *Rht-B1b* mutantni alel je bio prisutan u 66% ispitivanih linija, dok je alel *Rht-D1b* pronađen samo u 8% linija. U odnosu na divlji tip, *Rht-B1b* ili *Rht-D1b* sami su smanjili visinu biljke za 16,0 i 16,3% u kišnim, odnosno za 20,7 i 21,8% u navodnjavanim sredinama. Dva patuljasta alela kada su kombinovana smanjila su visinu za 39,3 i 56,6% u kišnim uslovima i u navodnjavanju, respektivno. Polupatuljaste linije za uzgoj su generalno nadmašile visoke genotipove u pogledu prinosa i komponenti prinosa, uključujući broj zrna po klasu i indeks žetve, bez obzira na okruženje. Pored toga, nadzemna biomasa je smanjena u većini niskih linija, u poređenju sa njihovim visokim genotipovima u različitim sredinama. Takođe demonstrirana je jasno smanjenje prinosa i komponenti prinosa za *Rht-B1b* + *Rht-D1b* kod linija sa dvostruko patuljastim poreklom.

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