Euphytica **125:** 113–119, 2002.

Phosphorus use efficiency in tall, semi-dwarf and dwarf near-isogenic lines of spring wheat

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Received 20 November 1998; accepted 13 August 2001

Key words: dwarfing genes, phosphorus uptake, roots, spring wheat, utilization

Summary

The impact of the Rht dwarfing genes on P utilization efficiency (PUTE = grain dry matter per kg P in above-ground biomass), total P uptake (Pt) and related traits was studied in the varietal backgrounds of two tall wheat cultivars, Maringa and Nainari 60. Four sets of near-isogenic lines carrying different combinations of the alleles *Rht-B1b*, *Rht-D1b* and *Rht-B1c* for gibberellin-insensitive dwarfism in the hexaploid wheat (*Triticum aestivum* L.) were compared with tall controls in two field trials under conditions of adequate nutrient supply and irrigation in Northwest Mexico. The yield-increasing effect of the dwarfing genes *Rht-D1b* and *Rht-B1b* led to improved PUTE in Maringa and total P uptake in both cultivars. Also, the double dwarf line of Maringa had larger grain yields and P uptake compared to the tall control. The *Rht-B1c* genotypes showed low PUTE, thick roots and high P concentration in vegetative biomass indicating a surplus of assimilates and P, which could not be translocated into the grains. A similar problem could be observed in Nainari 60 with *Rht-B1b* and *Rht-D1b*, which produced the largest grain dry matter with the lowest P concentrations in grains although they showed high P accumulation in straw. Most of the net P uptake occurred before anthesis. P absorption after anthesis was more critical for the dwarf genotypes. For double dwarfs and *Rht-B1c*, respectively, only 3% and 21% of the total accumulated P at maturity was absorbed at post-anthesis. The grain P of the dwarf lines came more from P accumulated at pre-anthesis and translocated from the vegetative biomass into the grain. The pre-anthesis P accumulation was positively correlated with spikes per m^2 ($r = 0.91$), whereas post-anthesis P accumulation correlated better with grains per spike ($r = 0.72$), and thousand kernel weight ($r = 0.51$). P uptake efficiency played a secondary role under these non-P-limiting conditions, and differences in root length density were only slightly affected by Rht-genes.

Introduction

The dwarfing genes derived from Norin 10 provide lodging resistance in wheat, and also pleiotrophically affect grain yield by increasing biomass, the harvest index (Waddington et al., 1986) and/or spikelet fertility. The dwarfing genes *Rht-B1b* and *Rht-D1b* (with the former designation *Rht1* and *Rht2*, respectively), incorporated singly or together, are in the background of most of the successful wheat cultivars in use today. *Rht-B1c* (former *Rht3*) reduces culm length more than *Rht-B1b* and/or *Rht-D1b*, and is only used in physiological studies (Gent & Kiyomoto, 1998).

Wheat breeding is targeting the improvement of nutrient use efficiency, especially for the two main nutrients, nitrogen (Ortiz-Monasterio et al., 1997) and phosphorus (Batten, 1992; Manske et al., 2000). It is important to understand how the dwarfing genes affect nutrient use efficiency. This paper studies the effect of the *Rht*-genes on P uptake and P utilization efficiency (PUTE) and root growth in near-isogenic lines with different *Rht*-alleles in two different bread wheat cultivars.

Material and methods

Two field experiments were carried out during the crop cycles of 1994/95 and 1995/96 at the experimental station of CIMMYT, CIANO, in the Yaqui Valley, near Ciudad Obregon, Sonora, Northwest Mexico (27°N 109' W, 40 masl).

The gibberelline-insensitive dwarfing genes formerly described as *Rht1*, *Rht2* and *Rht3* form a partial homoeoallelic series, with *rht1* (=*rht3*), *Rht1* and *Rht3* alleles at a locus on the short arm of chromosome 4B, *rht2* and *Rht2* alleles at a homoeolocus on the short arm of 4D. Recently, these gene symbols have been re-named, because they did not follow the systematic rules recommended in the wheat gene catalogue (McIntosh et al., 1998). The revised designations of the genes *rht1*, *Rht1* and *Rht3* at the chromosome 4B are *Rht-B1a*, *Rht-B1b*, and *Rht-B1c*, respectively, and for the genes *rht2* and *Rht2* at the chromosome 4D are *Rht-D1a* and *Rht-D1b*, respectively. The dwarfing genes *Rht-B1b, Rht-D1b* and *Rht-B1c* were introduced into the gibberelline-sensitive cultivars Maringa (a Brazilian cultivar adapted to acid soils) and Nainari 60 (from Mexico) (both *Rht-B1a* and *Rht-D1a* genotypes) by seven backcrosses from CIMMYT lines followed by selfing to produce lines carrying single dwarfing alleles, two-allele combinations and tall controls in each varietal background. Each varietal background was thus represented by the following five genotypes: tall line (*Rht-B1aRht-B1a Rht-D1aRht-D1a*), three near-isogenic semi-dwarfs (*Rht-B1bRht-B1b Rht-D1aRht-D1a*), (*Rht-B1aRht-B1a Rht-D1bRht-D1b*) and (*Rht-B1cRht-B1c Rht-D1aRht-D1a*) and one double dwarf (*Rht-B1bRht-B1b Rht-D1bRht-D1b*). These lines will now be referred to as tall control, *Rht-B1b*, *Rht-D1b* and *Rht-B1c* for semi-dwarfs, and double dwarfs, respectively.

The climate at the CIANO experimental station is semiarid, and the wheat was grown under full irrigation during the winter seasons. The soil was a coarse sandy clay mixed montmorillonitic Typic Caliciorthid (Aridisol), calcareous with 5% extractable calcium in the soil. Plant available P (Olsen) was 4.8 mg P kg^{-1} soil. The plots were fertilized with 35 kg P ha^{-1} as triple super phosphate, and 250 kg N ha^{-1} as urea. All fertilizers were applied as basal broadcast, and incorporated prior to seeding. Broadleaved weeds were controlled with bromoxynil (3,5-dibromo-4-hydroxybenzonitrile) at 1L ha^{-1} applied at 20 days after emergence and by additional hand weeding. The crop was sprayed twice against rust pathogens with Propiconazole.

The genotypes were completely randomised in three blocks. The wheat was planted on 80-cm beds with three rows per bed, four beds 5 m long in each plot. Wheat was seeded within the optimum sowing window (December 4 in 1994 and November 16 in 1995) at a seeding rate of 120 kg ha^{-1}. At maturity, which occurred between April 5–15, the plants were harvested from the centre 3 m of the two centre beds. The harvest area was 4.8 m^2.

Plant height measurements were made from the soil surface to the top of the spike in three randomly chosen areas within the plot. Biomass of the harvested area was measured in the field by cutting off the crop by hand at ground level. A subsample of 100 stems was taken from the harvest area and dried in an oven at 75 °C for 48 hrs. After threshing, fresh grain weight was determined, sub-samples of grain and straw were taken, weighed, dried, and weighed again to adjust grain dry matter (GDM) and straw weight (SW) to 0% moisture. The yield components, grains per spike and spikes m^{-2} were determined from the hundred stems. Thousand kernel weight (TKW) was obtained from the dry weight of 400 grains. The P-concentrations in grain (PCg) and straw (PCs) were obtained from the mean of two representative subsamples (each 250 mg) from the ground and carefully mixed dry material of straw or grains) and analyzed colorimetrically for P concentration with the vanadate-molybdate method (Kitson & Melon, 1944). A third subsample was taken, when the first two deviated more than 5%. The following variables were then calculated: dry matter of total above ground biomass (B = GDM+SW), harvest index in% (HI = GDM/B∗100), total P in grain at maturity (Pg = PCg∗GDM), total P in straw at maturity (Ps = PCs∗SW), total P in total above-ground biomass at maturity (Pt = Pg+Ps), P concentration in total biomass (PCt = Pt/B), and P harvest index in% (PHI = Pg/Pt∗100).

P utilization efficiency (PUTE) was defined analogously to nitrogen utilization efficiency by Moll et al. (1982) as PUTE = GDM/Pt. P accumulation was determined at three stages of plant development, at tillering (Zadok's decimal code = DC 23-25, Zadok et al., 1974), early anthesis (DC 61) and maturity. Above-ground biomass was sampled (0.24 m^2 per plot), dried, its P concentration determined and P accumulation at each sampling date calculated. P translocation of pre-anthesis P into grain was calculated by subtracting post-anthesis P accumulation from Pg at

Table 1. The effect of dwarfing genes (*Rht-B1b*, *Rht-D1b*, double dwarfs of the two genes; *Rht-B1c*; tall controls) on grain dry matter, P utilization efficiency (PUTE), total P uptake into above-ground biomass (Pt). P harvest index, and P concentration at maturity in total above-ground biomass, straw and grain in the bread wheat cultivars Nainari and Maringa, averaged over two crop cycles in Mexico

	Grain dry matter [kg ha^{-1}]		PUTE [kg grain kg^{-1} P]		Pt [kg P ha^{-1}]	
	Nainari	Maringa	Nainari	Maringa	Nainari	Maringa
Tall control	4193 b	3045 a	240 c	214 a	17.2 a	12.8 a
Rht-B1b	4394 bc	3646 bc	235 c	230 b	19.1 b	14.4 b
Rht-D1b	4454 c	3850 c	255 c	235 b	18.5 b	15.0 b
Double dwarf	4143 b	3882 c	217 b	216 a	18.2 ab	17.5 c
Rht-B1c	3404 a	3542 b	182 a	204 a	17.2 a	17.2 c
Means	4117*	3593	226 ns	220	18.1*	15.4

	P harvest index [%]		P concentration [mg P kg^{-1}] in			
			Total above-ground biomass	Straw	Grains	
	Nainari	Maringa	Mean	Mean	Nainari	Maringa
Tall control	75 c	73 b	1439 a	545 a	3162 b	3434 a
Rht-B1b	70 ab	77 c	1579 a	671 ab	2994 a	3354 a
Rht-D1b	72 bc	80 c	1531 a	588 a	2849 a	3410 a
Double dwarf	74 bc	70 a	1770 b	768 b	3410 bc	3233 a
Rht-B1c	66 a	70 a	1884 b	937 c	3616 c	3423 a

a<b for $p = 0.05$, LSD, separately calculated for each column (cultivar or mean).
* significant differences between cultivar means, $p = 0.05$, LSD; ns = not significant.

maturity, because Pg is equivalent to net P accumulation after anthesis plus net translocation of P stored in the vegetative tissue prior to anthesis (Moll et al., 1982).

In the field, roots from a defined volume of soil were extracted in the form of monoliths from the upper soil layer (0–20 cm soil depth), and in the form of soil cores from the deeper soil layer (20–40 cm depth). The soil monoliths were collected by driving a metal frame (root box) into the soil. The root box was 20 cm deep, 30 cm long and 15 cm wide (9000 cm^3 volume). The root box was placed length-wise into the centre row of a bed. Two boxes per plot were taken from the ends of two different beds, leaving the central part of the plot undisturbed for grain harvest. A root auger (diameter 8 cm, length 15 cm, volume 750 cm^3) was used to collect the two soil cores from the 20 – 35 cm soil layer, where the monoliths had been extracted (4 soil cores per plot). The roots from the monolith were separated from the soil by a jet of water aided by hand manipulation over sieves, the root cores from the root auger by a root-washing machine (hydropneumatic elutriation device, Smucker et al., 1982). Total root length was assessed by the line-intercept method of Tennant (1975). Root length density (RLD) was calculated by the root length divided by the volume of the monoliths or cores.

Analysis of variance was performed with the SAS statistical package (SAS Institute, 1985). Pearson correlation coefficients for phenotypic correlation (r) were based on individual genotypic means.

Results and discussion

Grain yield, harvest index and yield components

The single-gene dwarfs, *Rht-B1b* and *Rht-D1b*, and the double dwarfs reduced the plant height by 30 cm and 40 cm, respectively, and *Rht-B1c* by another 10 cm to a plant height of only 50 cm. The effects of the dwarfing genes on grain dry matter (GDM), harvest index and yield components were consistent with observations known from the literature. Final biomass was reduced by the double dwarfs and *Rht-B1c,* but was not affected by Rht-*B1b* or *Rht-D1b* as reported also by Miralles & Slafer (1995). The tall line of Maringa had lower GDM due to lodging which occurred two weeks before physiological maturity. Thus, all dwarfing genes in Maringa increased the GDM in comparison to the control, whereas in Nainari it was

Table 2. Straw P and grain P at maturity [kg P ha^{-1}]; grain P separated into pre- and post-anthesis net-absorbed P, details in Table 1

	Straw P		Grain P		Grain P absorbed pre-anthesis	Grain P absorbed post-anthesis
	Nainari	Maringa	Nainari	Maringa	Mean	Mean
Tall control	5.5 a	4.5 ab	11.7 b	8.3 a	3.9 a	6.1 c
Rht-B1b	7.3 bc	3.5 ab	11.8 b	10.9 b	5.7 b	5.7 c
Rht-D1b	6.9 bc	3.3 a	11.6 b	11.7 b	6.1 bc	5.5 bc
Double dwarf	6.5 ab	6.4 c	11.7 b	11.1 b	7.7 c	3.7 b
Rht-B1c	7.8 c	6.3 c	9.5 a	10.9 b	9.7 d	0.5 a
Means	6.8*	4.8	11.3 ns	10.6		

a<b for $p = 0.5$, LSD, separately calculated for each column (cultivar).
* significant differences between cultivar means, $p = 0.5$, LSD; ns = not significant.

only *Rht-D1b*. In contrast, *Rht-B1c* reduced GDM in Nainari as observed earlier by Hoogendoorn et al. (1988) (Table 1). The improved GDM through the introduction of *Rht-B1b* and/or *Rht-D1b* was associated with a rise in harvest index as found by Bush and Evans (1988) in other cultivars. All dwarfing genes reduced TKW by about 10%, but the lower TKW did not affect GDM in *Rht-B1b* and *Rht-D1b* singly or in combination, because higher number of grains per m^2 compensated for smaller grains.

The near-isolines of Maringa were between 5–10 cm taller, flowered five days earlier and initially had higher growth rates than Nainari 60, but the cultivars did not differ in the length of the grain-filling phase and in the total above-ground biomass at maturity.

Table 3. Total P accumulated in above-ground biomass [kg P ha^{-1}] at tillering, anthesis and total P at anthesis / total P in% at maturity, details in Table 1

	PT [kg P ha^{-1}]		Preanthesis P/ total P at maturity in %
	Tillering	Anthesis	
Tall control	6.9 a	8.3 a	55%
Rht-B1b	9.0 b	11.1 b	66%
Rht-D1b	8.9 b	10.6 b	63%
Double dwarf	7.8 ab	14.1 c	79%
Rht-B1c	7.9 ab	16.8 d	97%

a<b for $p = 0.5$, LSD, separately calculated for each column.

P utilization efficiency

The combined analysis of variance revealed significant differences in PUTE between the two growing seasons and cultivar × *Rht*-alleles interactions but no interactions year × cultivar, year × *Rht*-alleles nor 3-way interactions (not shown) were found. Grain yield can be explained as a function of P utilization efficiency (PUTE) and total P uptake (Pt) (GDM = PUTE ∗ Pt). On average, PUTE (GDM/Pt) was 16.6% higher in the 1995/96 season, because GDM was increased more (26.4%) than total P uptake (7.8%). Nainari 60 isolines had higher GDM and Pt than the isogenic lines of Maringa, on average. PUTE was not different between those cultivars (Table 1).

The *Rht-D1b* genotypes had the highest PUTE in both varietal backgrounds due to high GDM (Table 1). In Nainari 60, the short double dwarfs and extremely short *Rht-B1c* genotypes showed reduced PUTE compared to the tall control. In the double dwarfs, this was related to higher Pt because GDM was the same as the tall control. The *Rht-B1c* genotypes had reduced yields and the same Pt as the tall control (Table 1). The same trend could be observed in Maringa, except that lodging reduced GDM in the tall line and PUTE was not different among the tall control, double-dwarfs and *Rht-B1c* (Table 1).

PUTE is arithmetically dependent on harvest index (HI), P harvest index (PHI) and P concentration in grain (PCg) and total biomass (PCg), (PUTE = GY/Pt = HI / PCt, or GY/Pt = PHI / PCg), so that an increased HI or PHI, and reduced PCt or PCg would result into an increase of PUTE. *Rht* dwarfing genes cause large changes in stem height and weight, which influence the partitioning of assimilates and the distribution of P between vegetative parts (Sherchand & Paulsen, 1985) and grain, and consequently may affect P harvest index.

The cultivars and dwarfing genes affected the P harvest index and P concentrations (Table 1). In

Table 4. Root length density at 0–20 soil depths at tillering and anthesis and at 20–35 soil depth at tillering, details in Table 1

	Root length density [cm.cm^{-3} soil]					
	0–20 cm depth				20–35 cm depth	
	Tillering		Anthesis		Tillering	
	Nainari	Maringa	Nainari	Maringa	Nainari	Maringa
Tall control	3.7 b	3.1 b	4.5 a	4.9 a	1.9 b	1.2 ab
Rht-B1b	2.9 a	2.0 a	5.4 a	4.7 a	0.8 a	1.0 ab
Rht-D1b	2.7 a	3.0 b	4.2 a	4.2 a	1.4 b	0.9 a
Double dwarf	3.3 b	2.6 a	4.1 a	5.4 a	0.9 a	1.3 ab
Rht-B1c	2.7 a	2.1 a	4.8 a	5.0 a	1.0 ab	1.7 b
	3.1*	2.6	4.6	4.8 ns	1.2	1.2 ns

a<b for $p = 0.5$, LSD, separately calculated for each column (cultivar).
* significant differences between cultivar means, $p = 0.5$, LSD; ns = not significant.

Maringa, high P harvest index was responsible for improved PUTE in *Rht-D1b*, whereas in Nainari 60 it was lower P concentration in grains (Table 1). Also *Rht-B1b* reduced the grain P concentration in Nainari 60. The P concentrations in total above-ground biomass and straw were not significantly influenced by the single introduction of *Rht-B1b* or *Rht-D1b*, but were increased in the double dwarfs and even more with *Rht-B1c* (Table 1). The latter had lower PUTE than the double dwarfs, because high P concentration in total above-ground biomass was combined with low GDM. The double dwarfs showed only high P concentrations but no reduced yields (Table 1).

P uptake

Total P uptake showed significant effects of varietal background and *Rht*-alleles, but no significant two- or three-way interactions. On average for all *Rht*-alleles, Nainari had accumulated about 17% more P in the above-ground biomass at maturity than Maringa (Table 1), which was related to more P in the straw (Table 2). The P accumulation in grains did not differ between cultivars (Table 2).

Almost all *Rht*-alleles increased the total P uptake in both cultivars, only *Rht-B1c* and the double dwarf had no effect in Nainari 60 (Table 1). Lodging led to the lowest Pt in the tall line of Maringa (Table 1). All dwarfing genes increased grain P in Maringa (Table 2). In the higher yielding Nainari 60, grain P did not differ between the tall controls, *Rht-B1b* and/or *Rht-D1b*, but *Rht-B1c* had less P accumulated in the grain. *Rht-B1c* exhibited large P accumulation in straw in both varietal backgrounds (Table 2).

In both cultivars, only the dwarfing genes *Rht-B1b* and *Rht-D1b* showed higher P uptake at tillering. At anthesis, all dwarfing genes enhanced P uptake (Table 3). Most of the net P uptake occurred before anthesis. The extremely short *Rht-B1c* isolines had the largest amount of P accumulated at anthesis (97% of the total P accumulated at maturity), followed by the double dwarfs (79% of the total P) (Table 3). The tall control plants absorbed only 55% of all P before anthesis, on average (Table 3). Parts of the pre-anthesis accumulated P is translocated from vegetative plant organs into the grain, and net-post-anthesis P uptake goes directly to grain. Plant height was negatively correlated with the translocation of pre-anthesis accumulated P into grain (r = –0.67). Averaged for both cultivars, as much as 39%, 50%, 52%, 67% and 95% of the total P in grains came from pre-anthesis absorbed P, for tall controls, *Rht-B1b*, *Rht-D1b*, double dwarfs and *Rht-B1c*, respectively (Table 2). The highest P uptake at post-anthesis was found in the tall control of Nainari 60. P absorption at post-anthesis seems to be more critical for dwarf wheat than for tall wheats (Sherchand & Paulsen, 1985).

The pre-anthesis P accumulation was enhanced by more spikes per m^2 (r = 0.91), whereas the post-anthesis P accumulation was related to more grains per spike (r = 0.72), higher thousand kernel weight (r = 0.51) and higher growth rate during post-anthesis (r = 0.68). PUTE was negatively correlated with pre-anthesis P accumulation (r = –0.58) and positively with post-anthesis P accumulation (r = 0.72).

Root length density

Previous studies (Pepe & Welsh, 1979; McCaig & Morgan, 1993; Siddique et al., 1990; Miralles et al., 1997) showed contradicting effects of the dwarfing genes on root growth, because the root growth varies with genetic background, growing conditions and stage of development (Bush & Evans, 1988). Also our study showed no clear effects. Only, the analysis of RLD in the upper soil layer (0–20 cm depth) suggested some effects of the *Rht*-alleles (Table 4). At the stage of tillering, the introduction of *Rht-B1b* or *Rht-B1c* were associated with lower RLD in both cultivars. In addition, *Rht-D1b* reduced RLD in Nainari 60. At anthesis, no differences between *Rht* alleles were present in both cultivars (Table 4). Only in Nainari 60, the tall control and *Rht-D1b* near-isolines had more RLD in the deeper soil (20–35 cm depth), and in Maringa this was true for *Rht-B1c* (Table 4). The *Rht-B1c* genotypes showed thick roots (data not shown), which is related to a surplus of assimilates during stem elongation, which are translocated to the roots due to the lack of alternative sinks (Miralles et al., 1997).

Conclusion

The goal is to breed wheat cultivars for high grain yields and efficient use of P fertilizer input, i.e. high PUTE (grain yield / kg P fertilizer) and high P fertilizer recovery (kg P in the crop / kg P applied). *Rht-B1b* and *Rht-D1b* in Nainari 60 produced the largest GDM with the lowest P concentration in grains resulting in high PUTE (Table 1). Across all genotypes, grain dry matter and grain P concentration were negatively correlated (r = –0.80). Although low grain P concentration may be a desirable trait, reducing P-removal from the soil and contributing to sustainable land use (Schulthess et al., 1997), a minimum amount of P in the grain is needed for nutritional reasons, and for good germination. High yields without reducing grain P concentration can be achieved by improved translocation of P into grains and increased P uptake. The high P accumulation in straw and low P harvest index of the high yielding *Rht-B1b* and *Rht-D1b* isolines of Nainari 60 (Table 1 and 2) indicated that P was not always efficiently translocated into grain. A similar observation could be made with the *Rht-B1c* genotypes, which could not use the absorbed P efficiently for grain formation. However, considering that between 70 and 80% of the total P in the wheat plants is usually found in the grain at harvest, the possibilities to raise P translocation from vegetative biomass into grain are limited. Given the little room to breed for higher P harvest index, the selection for high grain yield potential in wheat will further reduce grain P concentration due to an effect of dilution, if the P uptake efficiency is not improved.

Acknowledgements

The authors thank Ing J. Lopez-Cesati for the phosphorus determinations and Ing Guadalupe Ruiz I. for the excellent technical assistance. This research was funded by BMZ, Germany, under contract 223-K8064 CIMMYT-2/93.

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