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The allelic state at the major semi-dwarfing genes in a panel of Turkish bread wheat cultivars and landraces

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Abstract

Dwarfing genes play an important role in improving yield and adaptability of wheat cultivars in most production environments. Understanding the allelic distribution at dwarfing loci is very important for any wheat-breeding programmes. In this study, we reported the allelic constitution at microsatellite locus *Xgwm261* and the two major height-reducing genes *Rht-B1* and *Rht-D1* among a set of 56 bread wheat cultivars and nine landraces, based on diagnostic polymerase chain reaction assays. With respect to *Rht-B1,* 37% of the accessions carried the dwarfing allele *Rht-B1b*, while at *Rht-D1,* only one accession carried the dwarfing allele *Rht-D1b*. The allelic state at *Rht8* was assayed indirectly by genotyping for the linked microsatellite locus *Xgwm261*. About 26% of the accessions carried the 192 bp allele (linked with *Rht8* gene in some cases), whereas 35 and 12% genotypes carried 165 and 174 bp allele at the microsatellite locus *Xgwm261*. Cultivars released from 1980 onwards increasingly carried either *Rht-B1b* or *Rht8*. This information should allow for a more rational use of this collection for the purpose of wheat improvement in Turkey.

Keywords: bread wheat; dwarfing genes; *Rht*; *Triticum aestivum*

Introduction

In bread wheat (*Triticum aestivum* L.), at least 21 major genes dispersed over a number of chromosomes determine the overall height of plant. The Green Revolution semi-dwarfing genes *Rht-B1b* and *Rht-D1b* have widely been used for cultivar development (Knopf *et al.*, 2008). Both of these semi-dwarfing alleles are insensitive to exogenous gibberellic acid (GA_3; McIntosh *et al.*, 1995) and were sourced from the Japanese cultivar 'Norin-10', from which they were transferred to the Green Revolution wheat bred at CIMMYT, and thereafter to an estimated 70% of commercial cultivars grown across the whole range of wheat production containing at least one of them (Evans, 1998). While the dwarfing effect of the *Rht-1* alleles cannot be reversed by the provision of exogenous GA_3, a number of other dwarfing genes are sensitive to GA application. Different GA_3-sensitive genes such as *Rht4* have been mapped on chromosomes 2BL, *Rht5* on 3BS, *Rht8* on 2DS, *Rht9* and *Rht12* on 5AL, and *Rht13* on 7BS (Ellis *et al.*, 2005), while the GA-insensitive *Rht-B1* and *Rht-D1* genes reside on the short arms of, respectively, chromosomes 4B and 4D (Gale and Marshall, 1975; McVittie *et al.*, 1978; Börner

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et al., 1997). Following the isolation of the latter genes by Peng *et al.* (1997, 1999), it became clear that both semi-dwarfing alleles derive from a single base pair mutation that abolishes the plant's ability to respond to GA, and this difference soon led to the elaboration of diagnostic polymerase chain reaction (PCR)-based assays for their presence (Ellis *et al.*, 2002).

Both *Rht-B1b* and *Rht-D1b* reduce plant height and increase yield under favourable climatic conditions (Worland *et al.*, 1998; Petsova *et al.*, 2008), but they are not beneficial in the Mediterranean environment, where high temperatures and drought are commonly encountered in the period between anthesis and grain filling (Worland and Sayers, 1995). As a result, alternative dwarfing genes, such as the GA-sensitive *Rht8*, have become widespread among cultivars grown in the Mediterranean basin and Southern Europe. This gene, along with *Ppd-D1*, another important gene associated with adaptation, is located on the short arm of chromosome 2D. When favourable alleles are present at both *Rht8* and *Ppd-D1*, as in the Japanese cultivar 'Akakomugi', plant height is reduced by 10 cm, flowering is accelerated by 8 d and spikelet fertility is markedly improved (Worland *et al.*, 1998; Zhang *et al.*, 2006). These genes were introduced to the European wheat gene pool by the Italian breeder Nazareno Strampelli in the early 1940s, who used them to avoid heat stress during grain filling. Since then, *Rht8* has been exploited throughout the Mediterranean basin (Worland *et al.*, 1998) and has more recently been spread to Australia, where it is favoured in some wheat-growing areas as it is not associated with the poor seedling emergence in impacted soils that do affect carriers of the *Rht-1* (*Rht-B1b* and *Rht-D1b*) semi-dwarfing alleles (Rebetzke and Richards, 2000; Bonnett *et al.*, 2001; Ellis *et al.*, 2005, 2007). Mapping experiments have established that *Rht8* is closely linked to the microsatellite locus *Xwgm261* (Korzun *et al.*, 1998), specifically, the 192 bp allele of *Xgwm261* is associated with the dwarfing allele of *Rht8*. However, Ellis *et al.* (2007) reported that 192 bp allele at *Xgwm261* is not always associated with *Rht8* dwarfing gene in wheat. They further explained that wide spread use of Norin-10-derived germplasm from the CIMMYT green revolution germplasm introduced a second haplotype into international germplasm, in which *Xgwm261* has no association with *Rht8*.

Turkey is a major producer of wheat, with some 9Mha sown annually leading to an annual production of 20 Mt (Altintas *et al.*, 2008). Modern breeding in Turkey started in 1925 with the goal to select well-adapted lines from local landraces for wheat improvement. In 1967, the national wheat release and training project was established, and international organizations contributed by introducing several cultivars from foreign countries (Braun *et al.*, 2001). Large parts of Turkey are located within the Fertile Crescent, the region where wheat originated and where wheat was brought in cultivation and domestication (Kilian *et al.*, 2009). It is essential to have information about allelic variations at agricultural important loci in Turkish wheat collections at hand. Some characterization of Turkish germplasm has been undertaken, in particular with respect to the presence of the important 1B/1R and 1A/1R wheat–rye translocations (Yediay *et al.*, 2010) and the allelic constitution at the major vernalization and photoperiod requirement genes (Andeden *et al.*, 2011). In this study, we report the allelic constitution at the major semi-dwarfing genes of the Turkish bread wheat core collection.

Material and methods

Plant material, DNA extraction and PCR analysis

The bread wheat core collection consists of 65 accessions, comprising 56 cultivars released for cultivation in Turkey over the past 70 years and nine landraces (Supplementary Table S1, available online only at http://journals.cambridge.org). As controls, four isogenic lines in 'Norin-10' (*Rht1* + *Rht2*; *Rht1* + *rht2*; *rht1* + *Rht2* and *rht1* + *rht2*) were included. From each accession, eight plants were grown under greenhouse conditions, from which young leaf was collected from 10-d-old seedlings. DNA was extracted from snap-frozen leaf material from four seedlings per accession individually, following the Doyle and Doyle (1987) Cetyl trimethylammonium bromide method, as modified by Ozkan *et al.* (2005). We applied six PCR primer pairs diagnostic for the *Rht-B1* and *Rht-D1* alleles (Ellis *et al.*, 2002; Zhang *et al.*, 2006) to obtain allele calling at these two loci. Experimental details relating to these assays are given in Table 1. As the *Rht-B1* targeted primer combinations BF-WRI and BF-MRI (Ellis *et al.*, 2002) were not fully diagnostic when tested on the control plants, the Zhang *et al.* (2006) procedure was preferred, in which the relevant primer combinations were NH.BF2-MR1.2 and NH.BF2-MR1. Gradient PCR experiments were used to determine an optimum annealing temperature of 66°C. For *Rht-D1*, the Ellis *et al.* (2002) primers DF-WR2 and DF2-MR2 were effective. All amplicons were electrophoretically separated through 2% agarose gels and visualized by ethidium bromide staining. All experiments were repeated three times. For *Rht8* typing, amplicon length at the *Xwgm261* locus was obtained following the methods described by Korzun *et al.* (1998). All PCR were performed according to Cömertpay *et al.* (2011). The amplicons were separated by capillary electrophoresis on an ABI 3130xl Genetic Analyser

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Table 1. Specific DNA molecular markers for three dwarfing gene considered in this study

Locus	Allele	Marker name	Primer pair sequence (5′ → 3′)	Reference
Rht-B1	*Rht-B1a* (tall type)	BF WR1	GGTAGGGAGGCGAGAGGCGAG CATCCCCATGGCCATCTCGAGCTG	Ellis *et al.* (2002)
	Rht-B1b (dwarf type)	BF MR1	GGTAGGGAGGCGAGAGGCGAG CATCCCCATGGCCATCTCGAG CTA	Ellis *et al.* (2002)
Rht-D1	*Rht-D1a* (tall type)	DF WR2	CGCGCAATTATTGGCCAGAGATAG GGCCATCTCGAGCTGCAC	Ellis *et al.* (2002)
	Rht-D1b (dwarf type)	DF MR2	CGCGCAATTATTGGCCAGAGATAG CCCCATGGCCATCTCGAGCTGCTA	Ellis *et al.* (2002)
Rht-B1	*Rht-B1a* (tall type)	NH-BF.2 WR1.2	TCTCCTCCCTCCCCACCCCAAC CCATGGCCATCTCGAGCTGC	Zhang *et al.* (2006)
	Rht-B1b (dwarf type)	NH-BF.2 MR1	TCTCCTCCCTCCCCACCCCAAC CATCCCCATGGCCATCTCGAGCTA	Zhang *et al.* (2006)
Rht8		WMS261-F WMS261-R	CTC CCT GTA CGC CTA AGG C CTC GCG CTA CTA GCC ATT G	Korzun *et al.* (1998)

(Applied Biosystems, Foster City, USA) platform, and the output was handled by GeneMapper software v3.7 (Applied Biosystems).

Results

The allelic state at *Rht-B1* and *Rht-D1* for each of the accessions is given in Supplementary Table S1 (available online only at http://journals.cambridge.org). At *Rht-B1*, 41 of the 65 accessions carried a 372 bp NH.BF2-WR1.2 fragment, diagnostic for the wild-type (non-dwarfing) *Rht-B1a* allele, while the remaining 24 accessions were presumed to carry *Rht-B1b* because no product was amplified. The presence of *Rht-B1b* in these accessions was confirmed by amplification profiles obtained using the primer pair NH.BF2-MR1.2, since a 380 bp fragment was present in all of them but was absent from each of the 41 lines typed as carrying *Rht-B1a*. With respect to the allelic status at *Rht-D1*, the only accession from which the 264 bp fragment diagnostic for *Rht-D1b* was amplified was cultivar 'Pandas'. The other 64 accessions produced a 220 bp fragment when their DNA was amplified with the DF-MR2 primer pair diagnostic for *Rht-D1a*. Amplification profiles for *Rht-B1a* and *Rht-B1b* for some bread wheat genotypes are shown in the Fig. 1. Finally, for *Rht8*, at least seven distinct *Xgwm261* amplicon lengths were represented in the core collection (Fig. 2). At microsatellite *Xgwm261* locus, 17 bread wheat cultivars and landraces (26%) carried 192 bp allele; 35% (23 entries) carried 165 bp allele, whereas only 12% (8 entries) carried 174 bp allele. Of the 65 accessions, 48 carried either the 165 bp, the 174 bp or the 192 bp alleles, while six carried the 202 bp allele, five carried the 211 bp allele, three carried the 196 bp allele and one carried the 169 bp allele. The 192 bp allele diagnostic for *Rht8* was present in 18 accessions (Supplementary Table S1, available online only at http://journals.cambridge.org).

Discussion

Dwarfing genes have been credited with an important contribution to yield improvement, both because they permit a more efficient utilization of assimilate and reduce the extent of lodging-induced yield loss. In warm humid environments, taller plants tend to produce less leaf area, and therefore are less effective as photosynthesizers and assimilators (Ahmad and Sorrells, 2002). The various dwarfing genes vary with respect to their effect on height, grain yield and other aspects of agronomic performance (Worland *et al.*, 1998; Ahmad and Sorrells, 2002; Ganeva *et al.*, 2005; Zhang *et al.*, 2006; Ellis *et al.*, 2007; Knopf *et al.*, 2008; Pestsova *et al.*, 2008; Guedira *et al.*, 2010).

The presence of dwarfing genes can be monitored directly from the behaviour of the seedling (Pestsova *et al.*, 2008; Tang *et al.*, 2009), but these techniques can be rather time and labour intensive, and sometimes are also influenced by the testing environment. The use of exogenously supplied GA is very effective for discriminating between semi-dwarf and tall types but is unable to differentiate between the *Rht-B1b* and *Rht-D1b* alleles. The acquisition of the DNA sequence of these two key genes now permits their unambiguous monitoring by marker technology (Korzun *et al.*, 1998; Ellis *et al.*, 2002; Zhang *et al.*, 2006), while the presence of *Rht8* can be fairly reliably predicted by the allelic state of a tightly linked microsatellite locus. However, Ellis *et al.* (2007) report that the 192 bp allele at the Xgwm261 locus is not always associated with the *Rht8* dwarfing gene in wheat.

In the Turkish bread wheat core collection, 37% of the accessions (24 entries) carried *Rht-B1b*, and the rest carried the wild-type *Rht-B1a* allele (Supplementary Table S1, available online only at http://journals.cambridge.org). Correspondingly, the *Rht-D1b* allele was carried by only one Turkish cultivar, which was released within the last 10 years. *Rht-B1b* is rather uncommon in German

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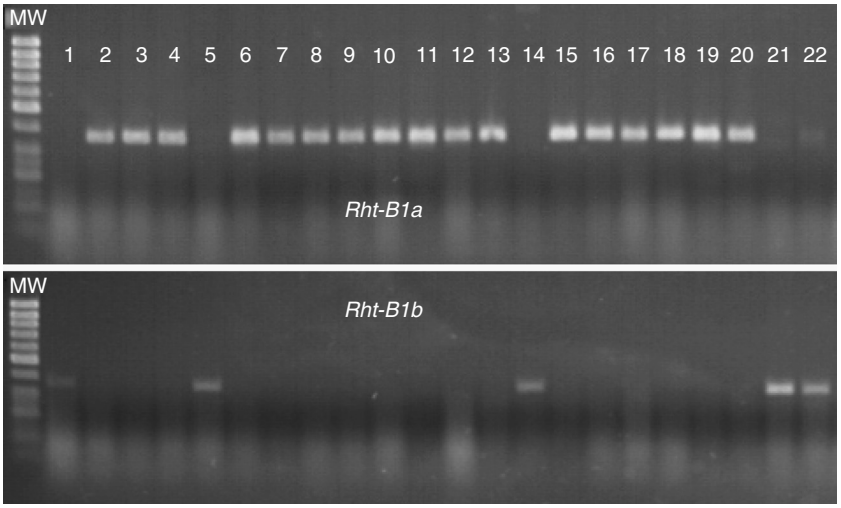

Fig. 1. Amplification profiles derived from primer combination NH-BF.2-WR1.2 diagnostic for *Rht-B1a* and primer combination NH-BF.2-MR2 diagnostic for *Rht-B1b*. 1, Atay-85; 2, Melez13; 3, Yektay; 4, Gerek 79; 5, Doğankent-1; 6, Kate A-1; 7, Kutluk-94; 8, İkizce-96; 9, Palandöken 97; 10, Süzen 97; 11, Demir 2000; 12, Bayraktar 2000; 13, Pandas; 14, Bağcı-2002; 15, Nenehatun; 16, Pehlivan; 17, Türkmen; 18, Yıldız 98; 19, Cumhuriyet 75; 20, Sertak 52; 21, Kırmızı başak; 22, Adana99. MW, molecular weight.

wheat germplasm (Knopf *et al.*, 2008), while it dominates Chinese wheat (Yang and Liu, 2006; Zhang *et al.*, 2006). *Rht-D1b* appears to be rather more frequent than *Rht-B1b* among semi-dwarf US soft winter wheat (Guedira *et al.*, 2010). Nearly, all Turkish cultivars released after 1967 were bred directly and/or indirectly from materials provided by the CIMMYT (Altintas *et al.*, 2008; Yediay *et al.*, 2010), but although the CIMMYT programme exploited both *Rht-B1b* and *Rht-D1b*, the percentage of *Rht-B1* is remarkably small and *Rht-D1b* has been found in only one line. Low frequency of *Rht-B1b* and the nearly absence of *Rht-D1b* in Turkish wheat might be also correlated with higher temperature during ear emergence and drought conditions especially in the Mediterranean and South-east Anatolian regions. Worland and Law (1985) reported that the distribution of GA-insensitive dwarfing genes is restricted to areas where heat and drought stress condition prevails during grain filling.

The *Rht-D1b* dwarf allele was found only in the cultivar 'Pandas' having the wild tall allele *Rht-B1a* (Supplementary Table S1, available online only at http://journals.cambridge.org). This cultivar originated from Italy, carried the 165 bp allele for *Xgwm261* locus, besides having Bezostaya as one of the parents in its pedigree. 'Pandas' is a semi-dwarf wheat cultivar with approximately 67–75 cm plant height, good yield potential, wide adaptation and is widely grown in the Mediterranean part of Turkey (Yücel *et al.*, 2009).

It has been suggested that the presence of the GA-insensitive dwarfing genes is associated with a reduction in coleoptiles length and hence a poorer rate of seedling emergence from impacted soils (Allan, 1989). In addition, they appear to exert a negative effect on spikelet fertility and grain yield in environments suffering from frequent episodes of heat stress (Worland and Law, 1985). Ellis *et al.* (2005) have suggested that both *Rht-1* dwarfing alleles also negatively affect the growth of young plants, but that this effect is not mirrored by *Rht8*. Therefore, *Rht8* might be more suitable in reducing final plant height, without compromising early plant growth (Ellis *et al.*, 2005). In this study, the *Xgwm261* locus is quite polymorphic, and seven alleles (165, 169, 174, 192, 196, 202 and 211 bp) were represented in the Turkish core collection. About 76% of the accessions carried either the 165 bp, the 174 bp or the 192 bp alleles, and the other four alleles were each rather rare.

The 211 bp allele was present in 'Melez-13', '4-22' and 'Kırik'. Cultivar Melez-13 came from a cross of Italian cultivar Mentana (Strampelli cultivar carrier of 165 bp allele) with unknown local landrace, and later on cultivar '4-22' was selected from Melez-13 population. This finding suggested that 211 bp allele was already present in old Turkish local cultivars. Worland *et al.* (2001) reported the presence of this same allele in a number of observed Turkish cultivars. Ganeva *et al.* (2005) also suggested that the 211 bp present in the Bulgarian cultivar 'Ivanov' may have originated from Turkish germplasm.

About 26% of the studied Turkish wheat cultivars and landraces carried the 192 bp allele at microsatellite *Xgwm261* locus. However, the frequency of the 192 bp allele in Turkish wheat is much lower than that in Italian (60%) and Yugoslavian (86%) wheat (Guedira *et al.*, 2010). Correlated selection for this allele may have been driven by its linkage with photoperiod-insensitive

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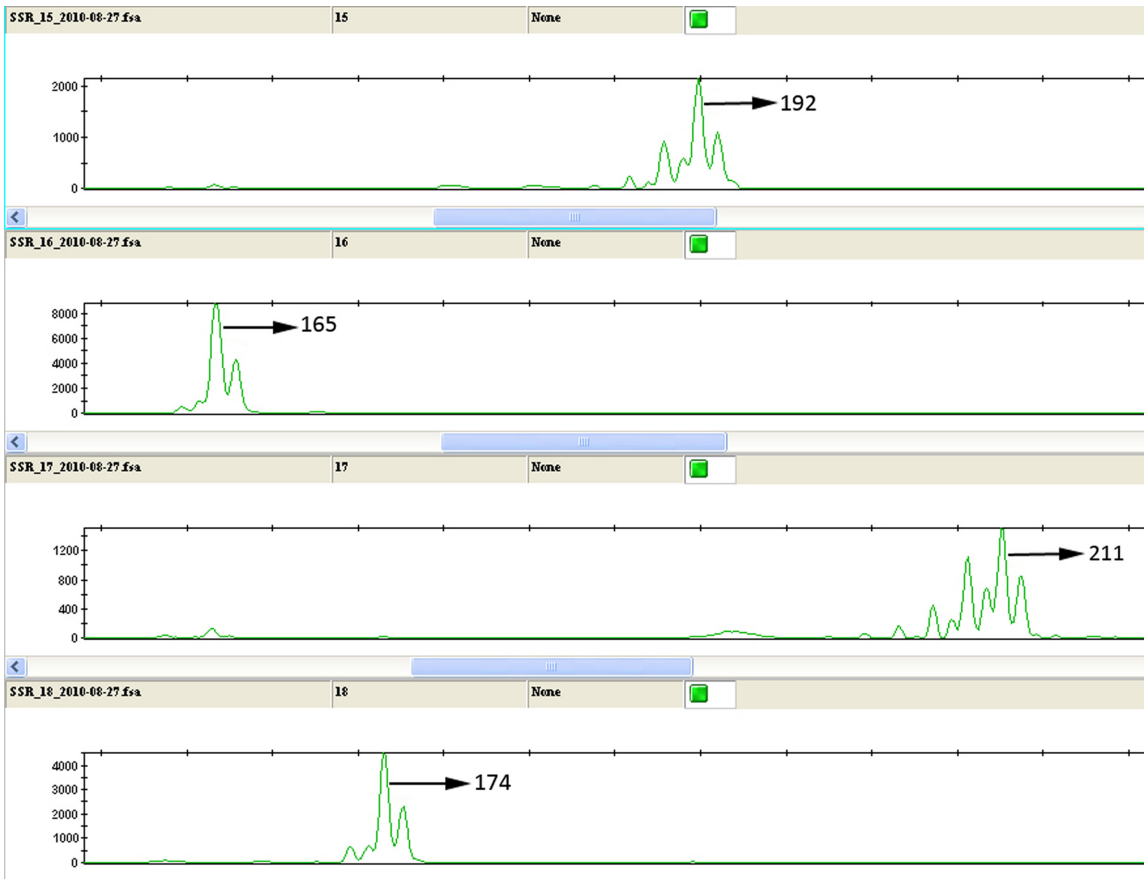

Fig. 2. Allelic variation at *Xgwm261*. The arrows show the calculated size of each DNA fragment. Saraybosna (192 bp), Pandas (165 bp), Kırik (211 bp) and Porsuk 2800 (174 bp) (A colour version of this figure can be found online at journals.cambridge.org/pgr).

allele at *Ppd-D1*, For example, the cultivar 'Çukurova86' and Doğankent1, Pehlivan, Golia having 192 bp allele at *Xgwm261* locus, also carried photoperiod-insensitive allele *Ppd-D1a* (Andeden *et al.*, 2011). However, we also observed that 192 bp allele is not always associated with *Ppd-D1a*. Some wheat cultivars having *Ppd-D1a* allele carried alleles other than 192 bp (Andeden *et al.*, 2011).

It is very interesting to note that *Xgwm261*-$_{192}$ allele was also present in Turkish wheat landraces (Koca Buğday, Kırmızı Başak and Arpatan), explaining the one of the probable source of 192 bp allele into Turkish wheat cultivars. In this case, one could expect that *Xgwm261*-$_{192}$ allele in Turkish wheat is not associated with height-reducing gene. It could be assumed that 192 bp allele might appear around 1965–1970. At that time Norin-10-derived CIMMYT material was heavily used in Turkish wheat programmes, which shows the second possibility of height neutral *Xgwm261*-$_{192}$ allele. Both of these possibilities have been described by Ellis *et al.* (2007); they stated that N Borlaug's semi-dwarf Mexican varieties have different haplotype in which *Xgwm261*-$_{192}$ allele is not associated with height-reducing gene. They proposed a hypothesis that *Xgwm261*-$_{192}$ arose prior to the evolution of *Rht8* and, in such case, it would be expected to persist in landraces as observed in Turkish landraces (Supplementary Table S1, available online only at http://journals.cambridge.org). Third possible pathway of 192 bp allele in the Turkish wheat-breeding programme is the use of Russian wheat cultivars 'Bezostaya and Kavkas'. Bezostaya, which is universally recognized photoperiod insensitive, semi-dwarf wheat cultivar carrying *Xgwm261*-$_{192}$, contained Strampelli variety 'Ardito' in its pedigree (Worland *et al.*, 1998; Borojevic and Borojevic, 2005). Bezostaya and Kavkas were among the key varieties used in Turkish wheat-breeding programme, thus providing an independent source of Akakomugi 192 bp allele in Turkish wheat gene pool. In such case, cultivars carrying Akakomugi *Xgwm261*-$_{192}$ allele should be associated with height-reducing genes. Turkish cultivars carrying photoperiod-insensitive allele (*Ppd-D1a*) should have Akakomugi *Xgwm261*-$_{192}$ haplotypes associated with reduced plant height. At the moment, it is difficult to distinguish the above-mentioned *Xgwm261*-$_{192}$ haplotypes in Turkish wheat without having phenotypic data for plant height,

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although it can be depicted from their pedigree. However, detailed field trial is also needed to elucidate the effect of different alleles on the plant height of Turkish wheat under different production environment.

The most frequent *Xgwm261* allele was the 165 bp amplicon in the Turkish wheat varieties, which was also common in a sample of CIMMYT-based Australian, Chinese, Greek, Portuguese, Spanish and Turkish cultivars (Zheleva *et al.*, 2006). Worland *et al.* (1998) reported that Strampelli cultivar Mentana carries $Xgwm261_{165}$ allele. This cultivar used as parental line in some crossing experiment in Turkish wheat programme as well. Mentana was also one of the important parents in the Mexican and CIMMYT wheat research and breeding programme and may be the source of 165 bp allele in the CIMMYT cultivars. It is also important to note that 165 bp allele started to be appeared in Turkish cultivars in 1970.

$Xgwm261_{174}$ allele was present only in eight genotypes. Interestingly, the 174 bp allele mostly exists in cultivars released until 1979 before introducing the CIMMYT material to Turkey. The two cultivars Sertak-52 and Sivas-111/33 carried the 174 bp allele, and these were directly selected from local landraces and subsequently registered as cultivars. Andeden *et al.* (2011) mentioned that these cultivars carry the photoperiod-sensitive allele (*Ppd-D1b*). Both of these cultivars were grown in the Central Anatolian region and Northern Turkey, where growing period of the wheat crop is longer due to cold temperature compared with the other parts of Turkey. Worland *et al.* (1998) reported that the 174 bp allele was common in Northern European wheat, where most of the wheat cultivars are photoperiod sensitive due to long life cycle of wheat-growing period. Ahmad and Sorrells (2002) also found that the 174 bp allele to be present in Great Britain, German and French wheat cultivar.

All the cultivars in the core set released prior to 1979 were *Rht-B1a* + *Rht-D1a*. This indicates the reality that selection for reduced plant height was not undertaken in Turkey until the CIMMYT germplasm had been introduced. The Turkish 'National Wheat Release and Training Project' was established in 1967 and was initiated with genetic input from CIMMYT and other international organizations. Since that time, the proportion of cultivars that were semi-dwarf (either *Rht-B1b* or *Rht8*) has increased rapidly. In the Mediterranean and South-east Anatolian regions of Turkey, where high temperatures are common place from anthesis onwards and especially during grain filling, since the GA-insensitive *Rht-1* dwarfing genes are not well adapted to these conditions, *Rht8* would be a valuable resource for Turkish wheat breeding.

In this study, we have provided information concerning the allelic state at the three major semi-dwarfing genes across a core collection of Turkish bread wheat. Together with matching data concerned with vernalization and photoperiod requirement genes (Andeden *et al.*, 2011) and the 1B/1R and 1A/1R wheat–rye translocations (Yediay *et al.*, 2010), this information should allow for a more rational use of this collection for the purpose of wheat improvement. We expect that this will facilitate advances in cultivar adaptation, raising grain productivity through the application of marker-assisted selection. To understand the history and origin of different alleles of dwarfing genes in Turkish wheat germplasm, further detailed study is needed over large collection of germplasm containing all old Turkish cultivars and local landraces.

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