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Evaluation of barley semi-dwarf allele *sdw1.d* in a near isogenic line

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Abstract Semi-dwarf genes have been used to alleviate lodging and increase harvest index in barley. The present study was conducted to determine the effect of widely used *sdw1.d* allele on agronomic characters. The *sdw1.d* was transferred from cv. Triumph to cv. Tokak 157/37 using marker assisted backcross breeding, and a near-isogenic line was developed. Parents and Tokak + *sdw1.d* near isogenic line were evaluated in three rainfed, fall-planted and seven rainfed, spring-planted trials in Tokat province of Turkey. The *sdw1.d* allele in Tokak 157/37 background shortened plant height by 20–30 cm, decreased lodging by 40–60%, delayed heading time by 5–7 days, and produced 74–178 more spikes per square meter. On the other hand, *sdw1.d* reduced thousand-seed weights in most trials by about 3–5 g. However, *sdw1.d* produced greater seed weights in trials where precipitation was higher. Tokak + *sdw1.d* near isogenic line produced higher grain yields especially in fall planted trials with high rainfall. Due to its higher spike number per area and improved harvest index, Tokak + *sdw1.d* NIL merits further studies under different ecological and growing practices.

Keywords Grain yield · Harvest index · Lodging · Marker assisted backcross · Plant height · Semi dwarf

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Introduction

Plant stature is associated with lodging tolerance but it has conflicting effects on barley grain yields under different water availability conditions. Tall cultivars are preferred by farmers in low rainfall areas because they have higher grain yields. However, in regions where precipitation is abundant, taller barley plants generally lodge, resulting in serious yield and quality losses. Various semi-dwarf-genes have been employed to remedy the lodging problem in barley. The *sdw1* is a commonly used barley semi-dwarf gene and different alleles of this gene have varying effects on plant characteristics.

Lodging causes significant problems in grain production of barley. First, it limits the photosynthesis capacity and carbohydrate assimilation of the plant. Besides, lodging prevents water and nutrient intake, decreases light inception, creates a favorable environment for diseases, and causes losses in harvest (Dockter and Hansson 2015). Lodging at early grain filling period can cause grain yield losses between 50 and 80% (Jezowski et al. 2005; Berry et al. 2006). Due to fungus and mycotoxin development on lodged plants (Nakajima et al. 2008), lodging negatively affects the physical quality of the grain. In addition to stem fragility (Berry et al. 2006) and inadequate root development (Tams et al. 2004), lodging also occurs due to taller plant stature (Kuczyńska et al. 2013). Thus, lodging could become a performance limiting factor for barley crop especially in high yielding environments.

Barley has various short stature genes such as *sdw1, brachytic, erectoid and uzu.* Different alleles of *sdw1* gene have been created and are commonly used in Europe and America to shorten plant height in barley (Jia et al. 2009). It has turned out recently that the gibberellin *20-oxidase (HvGA20ox2)* is the functional gene of barley *sdw1* mutants (Xu et al. 2017). At least five alleles of this gene have been identified to date. These are *sdw1.a* in cv. Jotun, *sdw1.c* in cv. Abed Denso, *sdw1.d* in cvs. Triumph and Diamant, *sdw1.e* in mutant line 'Risø no. 9265 (Xu et al. 2017) and *sdw1.Lockyer* (Dang et al. 2020). The alleles *sdw1.a, sdw1.c* and *sdw1.d* were used for the development of modern barley cultivars. The *sdw1.Lockyer* allele was reported to have similar effects to *sdw1.d* (Dang et al. 2020). However, there are no reports for use of *sdw1.e* allele in a barley breeding program (Dockter and Hansson 2015). The *sdw1.d* allele is highly preferred in malt barley breeding programs in Europe, Canada and America while *sdw1.a* has been limited to feed barley cultivars due to its negative impact on malting quality (Xu et al. 2017). The *sdw1.d* allele confers 16–20 cm shorter stature and consistently late heading compared to the wild allele (Kuczyńska et al. 2013). The effect of *sdw1.d* on grain yields, on the other hand, is variable. Reduced grain yields due to *sdw1.d* were reported by Thomas et al. (1991) and Hellewell et al. (2000) while Thomas et al. (1995) and Kuczyńska et al. (2014) found positive effects of *sdw1.d* on grain yield. However, there has been no study yet evaluating the *sdw1.d* using near isogenic lines (NILs), an approach considered superior to other methods to study the effects of genes (Kaeppler et al. 1993).

Tokak 157/37 cultivar (cv. Tokak hereafter) is a two-row barley cultivar used for both malt and feed purposes in Turkey. It has been used in many regions of Anatolia due to its drought tolerance (Ozturk et al. 2002) and high adaptability (Akcura and Yuksel 2012). The seed size of cv. Tokak is quite high, and seeds contain a high amount of starch (Kandemir 2004). However, in regions with good level of precipitation, this cultivar cannot attain high yields due to serious lodging problem. Therefore, despite its superior adaptability, use of cv. Tokak in Turkey has been seriously declined. We transferred *sdw1.d* allele from cv. Triumph to cv. Tokak and developed BC_6F_2 near isogenic lines using marker-assisted backcross breeding. The objectives of the present study were to determine the effect of *sdw1.d* allele transferred to cv. Tokak on (a) plant height and lodging severity, and (b) on grain yield and its components in three rainfed fall-planted and seven rainfed spring-planted field trials.

Materials and methods

Near isogenic line development

Plants were grown in 4-L pots containing equal amounts of soil, peat, perlite and sand in a greenhouse or growth chamber. Plants of parents and crosses were grown under 16 h of light/8 h of dark conditions, and under temperatures not exceeding 22 ± 2 °C. Plants were fertilized with compound fertilizer (15–15–15).

For lodging tolerance, *the sdw1.d* allele was transferred from cv. Triumph to cv. Tokak with marker assisted backcross breeding. The F_1 plants obtained after the initial hybridization were backcrossed to cv. Tokak for six generations, and then a selfing was made. In backcross and selfing generations, *sdw1.d* allele was tracked by linked markers, and a BC_6F_2 NIL was produced. Embryo culture was used to accelerate the breeding generations (Yildirim et al. 2019), and BC_6F_2 NIL was developed in about two years.

DNA analyses were carried out in Molecular Biotechnology Laboratory of the Field Crops Department at Tokat Gaziosmanpasa University, Faculty of Agriculture. Genomic DNA was isolated according to Doyle and Doyle (1990) when plants reached to three to four-leaf stage. SSR markers Bmag0606, Bmag0013 and GBM1037 around *sdw1* locus were used for transferring the *sdw1.d* allele. Bmag0013 marker was reported to co-segregate with *sdw1* (Kuczyńska et al. 2014). Bmag606 and GBM1037, on the other hand, were reported to flank *sdw1* locus on both sides with distances of 11 and 9 cM, respectively (Varshney et al. 2007).

PCR reactions were carried out in 40 µl reaction volumes containing 50 ng genomic DNA, 2.0 mM $MgCl_2$, 0.2 mM dNTP, 0.25 mM each primer, 0.5 U Taq Polymerase (Promega) (Kandemir et al. 2010). PCR reactions were performed using 32 cycles of 45 s. at 94 °C, 45 s. at 55–58 °C depending upon the annealing temperature of the primers used and 45 s. at 72 °C. A hot start of five min. at 94 °C before the cycles and a final extension step of 5 min at 72 °C after the cycles were also used.

Amplified DNA fragments were run in 3% MetaPhor agarose gels (Lonza Cat. No: 50180) with 1 X TBE buffer. DNA fragments were visualized with ethidium bromide dye added to the gels using an imaging system (Vilber Lourmat CN-08). DNA bands were analyzed using Biocapt software (version: 11.02).

Field trials

The Tokak + *sdw1.d* NIL and parent cultivars were evaluated in field trials in experimental areas of Tokat Gaziosmanpasa University, Agricultural Application and Research Center in Kazova plain of Tokat Province in Turkey (Latitude: 40° 19′ 56.0″ N, Longitude: 36° 28′ 23.0″ E, and Altitude: 623 m). The experimental design was randomized complete blocks with four replications.

The monthly total precipitation and average temperature values for the experimental years are given in Figs. 1 and 2, respectively. The planting dates, soil analysis results of the experimental land and amount of total precipitation from planting to the maturity are given as a Supplement file (Table S1). The plots consisted of five rows of 3 m with 20 cm row spacing. The seeding rate was 200 kg/ha, and hand planting was made. Two rows of wheat were planted between the plots and at the ends of blocks using a lodging resistant wheat, cv. Kızıltan-91, to prevent lodging of one plot from intervening that of another plot.

The plots were fertilized with 80 kg/ha of nitrogen and 80 kg/ha of P_2O_5 using ammonium nitrate and triple super phosphate fertilizers. All of the phosphorus and half of the nitrogen fertilizers were applied in planting while the other half of the nitrogen was given before the stem elongation. Weed control was performed whenever necessary using 800 g/ha 2,4-D.

In field trials, heading time, maturity, plant height, lodging ratio and grain yield were evaluated according to Kandemir et al. (2000). Briefly, heading time was number of days from planting to awn emergence for 50% of the plants in a plot. Plant height was the distance from the ground to the tip of the spike excluding awns. Maturity period was number of days from planting to the time when 50% of spikes in

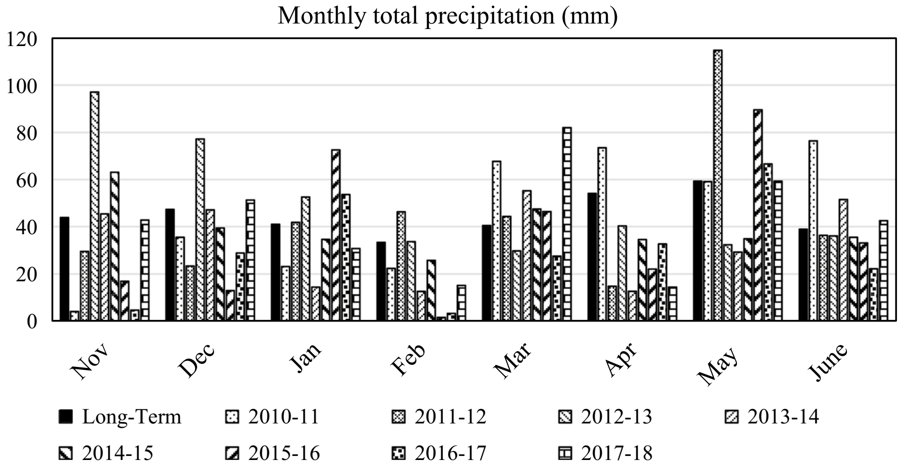

Fig. 1 Precipitation values for the region in long term and experimental years

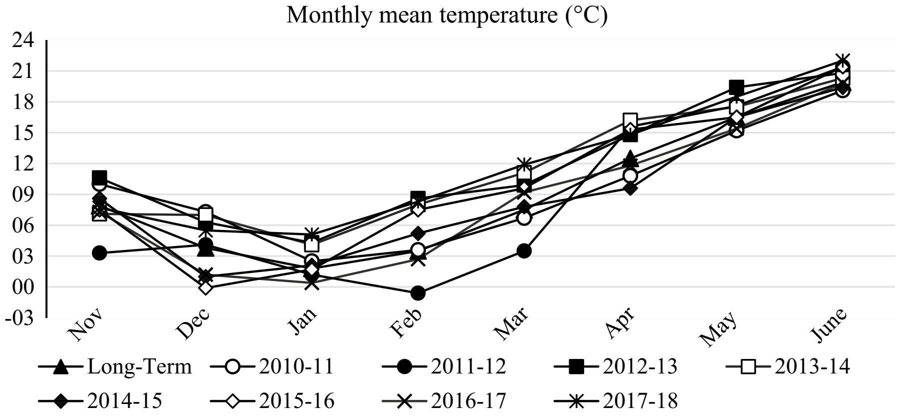

Fig. 2 Temperature values for the region in long term and experimental years

a plot lost green color. Number of grains per spike, number of spikes per square meter, thousand-seed weight, biological yield and harvest index were evaluated according to Aisawi et al. (2015). Plant height and spike traits were measured on 20 plants or spikes in a plot. Thousand-seed weight, grain yield and biological yield were calculated based on 12% moisture content.

Tokak + *sdw1.d* NIL and parents were evaluated in three fall-planted and seven spring-planted trials under field conditions. There were considerable differences between the trials for precipitation during vegetation periods (Table S1). Therefore, fall- and spring-planted trials were classified within themselves as low- and high-rainfall trials according to the amount of precipitation for the simplicity of discussions. Spring trials of 2013S (138.4 mm), 2014S (161.2 mm), 2015S (152.3 mm) and 2017S (148.9 mm) were relatively low-rainfall while 2011S (299.1 mm), 2012S (210.0 mm) and 2018S (198.9 mm) were high-rainfall trials. Similarly, of fall-planted trials, 2017F (239.3 mm) was relatively low rainfall whereas 2016F (295 mm) and 2018F (338.3 mm) were high rainfall trials.

Statistical analyses

The data were subjected to analysis of variance using MSTAT software (Freed et al. 1988). $p<0.05$ was considered statistically significant. The differences among the means were compared using the Duncan's multiple range test. Genotype main effect, genotype × environment interaction (GGE) biplot analysis and the "comparing two genotypes" view of the GGE biplot were determined using GEA-R software (genotype x environment analysis with R for Windows) (Pacheco et al. 2015). The "comparing two genotypes" view of the GGE biplot was used to visualize the comparison of two genotypes for all trials (Frutos et al. 2014).

Results and discussion

The results of the field trials are shown in Table 1, and the mean values of the experiments are illustrated in Fig. 3. In all trials, significant differences in heading dates were observed between Tokak + *sdw1.d* NIL and parents ($p<0.01$). In fall-planted trials, *sdw1.d* delayed heading by six to seven days ($p<0.01$) with Tokak + *sdw1.d* NIL heading significantly later than either parent. In spring-planted trials, *Tokak + sdw1.d* NIL reached heading four to five days later than cv. Tokak ($p<0.01$). With one exception, in all spring-planted trials, heading date of Tokak + *sdw1.d* NIL was not significantly different from donor parent cv. Triumph. The *sdw1* gene is characterized by late heading time (Kuczyńska et al. 2013). Previous studies reported three to seven days of delaying due to *sdw1.d* (Teplyakova et al. 2017; Dang et al. 2020). More pronounced delaying due to *sdw1.d* in fall trials compared to spring trials was also reported by Laurie et al. (1995).

Significant differences were also found between Tokak + *sdw1.d* NIL and parent cultivars in terms of time to maturity in all trials ($p<0.01$). The *sdw1.d* allele delayed the maturity of cv. Tokak by three to six days in fall-planted trials and by two to six days in

Table 1 Agronomic traits of Tokak + *sdw1.d* NIL and parent cultivars

Genotype/Trials	2011S		2012S		2013S		2014S		2015S		2017S		2018S		2016F		2017F		2018F	
Heading time (day)																				
Tokak	80.5	b	65.5	b	79.8	b	79.7	c	77.8	b	84.3	b	92.3	b	179.3	b	162.8	b	157.0	b
Triumph	85.0	a	69.0	a	85.3	a	83.7	b	81.3	a	88.0	a	97.0	a	181.0	b	160.3	b	157.3	b
Tokak + *sdw1.d* NIL	85.6	a	69.5	a	84.8	a	85.6	a	83.0	a	88.0	a	97.3	a	185.3	a	170.0	a	163.0	a
Maturity (day)																				
Tokak	120.5	c	137.3	c	121.0	c	121.7	c	119.3	c	110.3	c	111.7	c	225.5	c	201.3	c	190.0	b
Triumph	125.0	a	144.3	a	130.0	a	128.0	a	128.3	a	119.0	a	121.0	a	232.8	a	212.3	a	193.3	a
Tokak + *sdw1.d* NIL	123.0	b	142.3	b	125.3	b	124.7	b	124.3	b	113.0	b	115.7	b	228.8	b	207.8	b	191.7	ab
Plant height (cm)																				
Tokak	115.3	a	93.0	a	72.9	a	77.6	a	101.2	a	95.6	a	84.3	a	93.8	a	113.2	a	103.3	a
Triumph	96.2	b	79.9	b	58.3	b	61.0	b	78.0	b	75.0	b	66.0	b	70.9	b	81.9	b	81.7	b
Tokak + *sdw1.d* NIL	92.6	b	73.2	b	53.3	c	52.8	c	70.7	c	72.5	b	64.8	b	72.3	b	73.7	c	77.3	b
Lodging (%)																				
Tokak	92.5	a	95.0	a	37.5	a	33.3	a	50.0	a	35.0	a	83.3	a	98.7	a	100.0	a	93.3	a
Triumph	42.5	b	12.5	c	0.0	b	0.0	b	0.0	b	5.0	b	0.0	b	0.0	c	20.0	b	1.7	b
Tokak + *sdw1.d* NIL	60.0	b	37.5	b	17.5	a	0.0	b	0.0	b	2.5	b	11.7	b	37.5	b	35.0	b	11.7	b
Number of grains per spike																				
Tokak	22.0	b	21.9	b	21.7	b	23.0	b	21.0	b	22.4	b	19.4	b	21.8	b	23.7	b	21.3	b
Triumph	28.3	a	30.9	a	26.9	a	27.0	a	23.0	a	26.8	a	24.1	a	29.1	a	26.5	a	23.6	a
Tokak + *sdw1.d* NIL	22.2	b	21.8	b	21.2	b	22.7	b	19.6	b	22.6	b	20.4	b	22.1	b	25.1	ab	20.8	b
Thousand-seed weight (g)																				
Tokak	55.3	a	58.5	a	60.3	a	53.0	a	58.6	a	50.4	a	46.4	b	59.3	a	37.3	a	49.0	b
Triumph	40.8	b	41.9	b	43.8	c	44.9	b	44.7	b	38.8	c	40.7	c	41.9	c	34.5	b	34.4	c
Tokak + *sdw1.d* NIL	56.1	a	55.0	a	48.8	b	44.8	b	47.7	b	44.1	b	52.5	a	54.8	b	32.7	ab	50.4	a
Number of spikes per square meter																				
Tokak	353.1	^{ns}	356.8	c	246.2	b	276.7	b	257.0	b	291.0	b	427.2	c	366.2	c	402.8	c	400.0	c
Triumph	473.0		476.6	a	281.9	ab	393.2	a	339.2	a	407.1	a	546.6	a	437.5	b	503.1	b	709.0	a
Tokak + *sdw1.d* NIL	407.0		394.6	b	337.2	a	361.4	a	385.6	a	373.8	a	466.6	b	560.0	a	584.7	a	560.4	b

Table 1 (continued)

Genotype/Trials	2011S	2012S	2013S	2014S	2015S	2017S	2018S	2016F	2017F	2018F
Grain yield (t/ha)										
Tokak	4.30 b	4.57 b	3.22 b	3.37 b	3.16 b	3.29 b	4.45 b	4.73 b	3.56 b	4.18 b
Triumph	5.46 a	6.17 a	3.32 ab	4.77 a	3.49 a	4.23 a	5.37 a	5.34 b	4.60 a	5.76 a
Tokak + *sdw1.d* NIL	5.07 a	4.73 b	3.49 a	3.68 b	3.61 a	3.73 ab	4.99 a	6.94 a	4.78 a	5.88 a
Biological yield (t/ha)										
Tokak	13.25 b	10.43 b	6.79 ns	8.34 b	7.55 b	8.36 b	8.47 b	11.83 b	8.97 b	9.54 b
Triumph	14.71 a	13.29 a	7.09	10.91 a	8.03 a	10.48 a	9.56 a	10.91 b	9.91 a	11.87 a
Tokak + *sdw1.d* NIL	13.69 ab	10.17 b	7.07	8.22 b	8.01 a	8.94 ab	8.99 ab	14.23 a	10.34 a	12.28 a
Harvest index (%)										
Tokak	32.3 b	43.8 b	47.4 b	40.5 c	41.9 b	39.3 ns	52.5 b	40.0 b	39.7 b	43.7 b
Triumph	37.0 a	46.5 a	46.8 b	43.7 b	43.3 ab	40.4	55.6 a	48.9 a	46.2 a	48.5 a
Tokak + *sdw1.d* NIL	37.0 a	46.5 a	49.3 a	44.7 a	45.0 a	41.7	55.5 a	48.7 a	46.4 a	47.8 a

Differences between the means with the same letter are not significant at p < 0:05. ns not-significant

S spring planting, *F* fall planting, *NIL* near isogenic line

spring-planted trials. In all trials, cv. Tokak reached maturity first while cv. Triumph matured a few days later and Tokak + *sdw1.d* NIL matured the latest. The *sdw1* gene was previously mentioned to be associated with late maturity (Dockter and Hansson 2015; Maurer et al. 2016). Hellewel et al. (2000) observed three days of delaying in maturity due to *sdw1.d*. Since late maturity is associated with lower drought tolerance (Shavrukov et al. 2017), this delaying could interfere with superior drought tolerance character of cv. Tokak, which is the main reason for the superior adaptability of the cultivar (Akcura and Yuksel 2012).

The plant height of the two parents and Tokak + *sdw1.d* NIL showed significant differences ($p < 0.01$). In fall-planted trials, plant height of cv. Tokak ranged from 93.8 to 113.2 cm while height of Tokak + *sdw1.d* NIL varied from 72.3 to 77.3 cm. In other words, *sdw1.d* reduced the height of cv. Tokak by about 20–40 cm. In spring trials, on the other hand, plant height of cv. Tokak ranged from 72.9 to 115.3 cm, and that of Tokak + *sdw1.d* NIL

varied between 52.8 cm and 92.6 cm. Thus, the height decrease due to *sdw1.d* in spring-planted trials was about 20–30 cm. The height of the NIL was generally similar to cv. Triumph except for summer trials of 2013S, 2014S, 2015S and 2017S, where precipitation was relatively low. Developing shorter plants is an effective way to improve lodging tolerance. The *sdw1.d* is a short stature allele of barley *sdw1* gene that has been accepted in many parts of the world (Xu et al. 2017). The *sdw1.d* allele was reported to shorten the plant height between 10 and 30 cm in previous studies (Hellewel et al. 2000; Dockter and Hansson 2015). Teplyakova et al. (2017) observed that the doubled haploid lines carrying *sdw1.d* had plant heights of 50–87 cm. Dang et al. (2020) reported that the lines carrying *sdw1.d* allele had taller plants in areas where the precipitation was moderate compared to the high-rainfall areas.

Significant differences were observed for lodging percentage among the genotypes studied ($p < 0.01$). In fall-planted trials, cv. Tokak suffered from 93.3 to 100.0% lodging, while lodging of Tokak + *sdw1.d* NIL varied from 11.7 to 37.5%. Thus, about 60–80% less lodging was observed due to *sdw1.d* in fall-planted trials. In spring trials, lodging of cv. Tokak varied between 33.3 and 95.0% whereas Tokak + *sdw1.d* NIL did not lodge in some trials and had 60% or less lodging in others. Thus, reduction of

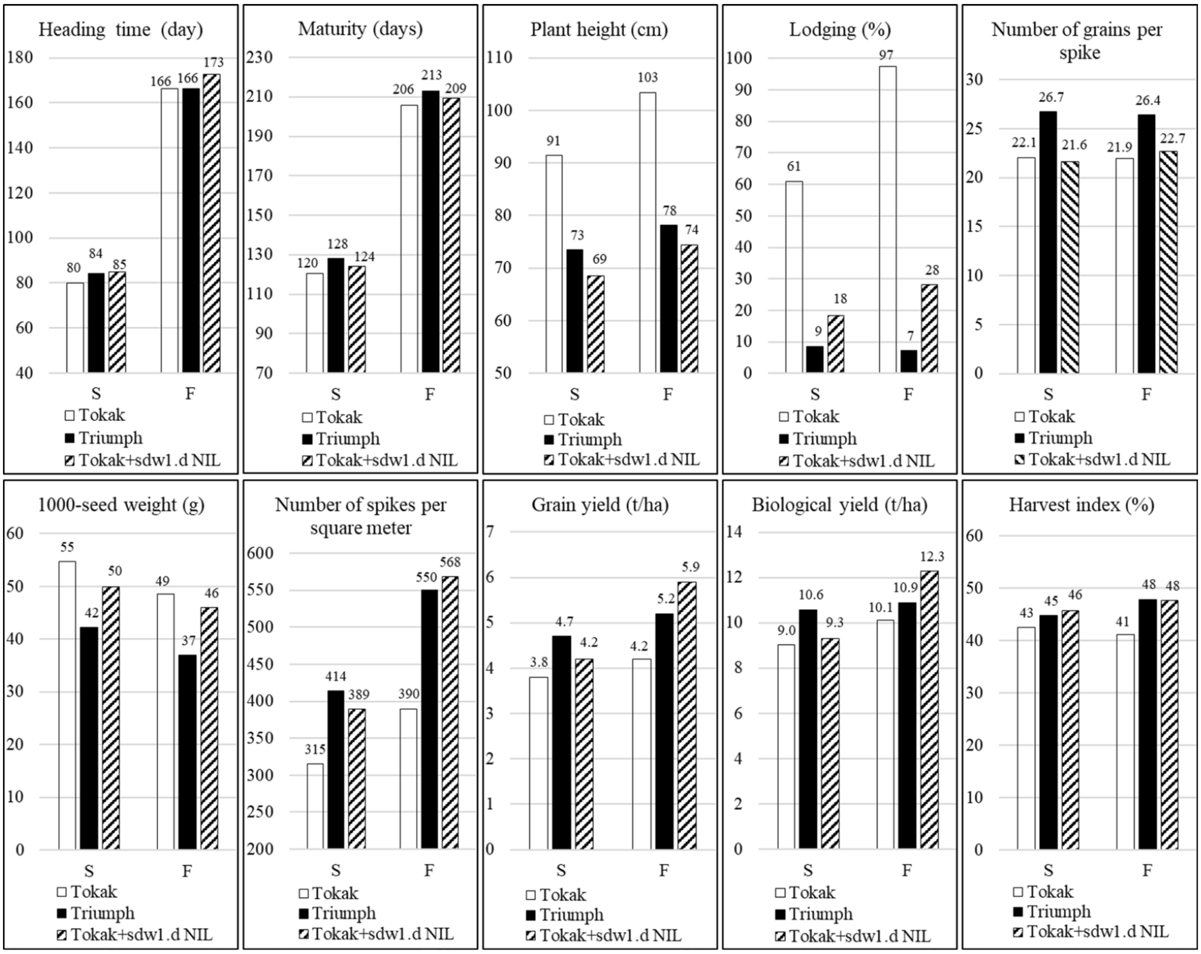

Fig. 3 Agronomic trait means of Tokak + *sdw1.d* NIL and parent cultivars across the fall- and spring-planted trials. F: fall-planted. S: spring-planted

lodging by *sdw1.d* in spring-planted trials was about 20–70%. The lodging percentages of Tokak + *sdw1.d* NIL were similar to those of cv. Triumph in all trials except for 2012S and 2016F. Lodging severity is a character highly affected by rainfall in addition to winds (Nakajima et al. 2008). Previously, *sdw1.d* allele was reported to decrease lodging severity by about 65% (Dockter and Hansson 2015). Thus, the findings of the present study confirmed the effectiveness of *sdw1.d* in reducing the severity of lodging in barley.

Number of seeds per spike was similar in cv. Tokak (range: 19.4–23.7) and Tokak + *sdw1.d* NIL (range: 19.6–25.1) while cv. Triumph (range: 23.0–30.9) had significantly higher number of seeds per spike ($p < 0.01$). Our findings confirmed the lack of an association between the *sdw1* gene and number of seeds per spike trait as reviewed by Kuczyńska et al. (2013).

The genotypes studied had significant differences for thousand-seed weight in all locations ($p < 0.01$). In fall-planted trials, thousand-seed weight of cv. Tokak varied from 37.3 to 59.3 g and that of Tokak + *sdw1.d* NIL varied from 32.7 to 54.8 g. Thus, *sdw1.d* allele resulted in a 4.5 g reduction in 2016F trial, a 1 g increase in 2018F trial while no change was observed in 2017F trial. In spring-planted trials, on the other hand, *sdw1.d* did not affect thousand-seed weight in Tokak + *sdw1.d* NIL compared to recurrent parent cv. Tokak at 2011S and 2012S trials while a 6.1 g increase was observed in 2018S trial and 6.1–11.5 g reductions took place in other spring trials. Thousand-seed weight of cv. Triumph was lower than those of cv. Tokak and Tokak + *sdw1.d*, and these differences were significant in most trials. Thousand-seed weight is an important yield component. Cv. Tokak can attain very high seed weights under favorable conditions (Kandemir 2004). However, the high lodging character of the cultivar during the grain filling period prevents high seed weights. Although the *sdw1.d* allele generally reduced thousand-seed weights by around 3–5 g (Fig. 3), considering that Tokak + *sdw1.d* NIL had seed sizes similar to cv. Tokak in 2011S and 2012S trials, and higher in 2018S trial, it would not be wrong to conclude that *sdw1.d* produced higher seed weights in trials where precipitation was higher. On the other hand, Teplyakova et al. (2017) reported that *sdw1.d* did not affect seed size while Laurie et al. (1993) mentioned that it reduced seed size. Based on the results of previous studies, it could be stated that the effect of *sdw1.d* on seed size varies by environmental conditions.

Number of spikes per square meter trait showed significant differences among the genotypes studied in all locations except for 2011S. In fall-planted trials, the number of spikes per square meter ranged from 366.2 to 402.8 in cv. Tokak, and from 560 to 584.7 in Tokak + *sdw1.d* NIL. In other words, when introgressed into cv. Tokak, the *sdw1.d* resulted in 160.4–193.8 more spikes per square meter. Jia et al. (2011) and Kuczyńska et al. (2014) also reported that *sdw1.d* increased number of spikes per square meter. The presence of *sdw1.d* in a barley cultivar could mean higher production potential under desirable conditions. Besides, since higher number of tillers per area is associated with improved drought tolerance (Al-Ajlouni et al. 2016), the Tokak + *sdw1.d* NIL could have better drought tolerance characteristics.

Grain yield of cv. Triumph was consistently higher than that of cv. Tokak, and the difference was significant in 8 of the 10 trials. In fall-planted trials, the grain yield of cv. Tokak ranged from 3.56 to 4.73 t/ha, while Tokak + *sdw1.d* NIL had grain yields of 4.78–6.94 t/ha in these trials. Similarly, in four of the seven spring-planted trials, grain yields of Tokak + *sdw1.d* NIL (3.49–5.07 t/ha) were significantly higher than those of cv. Tokak (3.16–4.57 t/ha). Thus, *sdw1.d* resulted in significant yield increases of 0.26–0.77 t/ha in spring-planted trials, and 1.23–2.21 t/ha in fall-planted ones. Introduction of semi-dwarf genes into cultivars are known to increase the yield potential (Kuczyńska et al. 2014). In previous studies, however, conflicting results were obtained regarding the effect of *sdw1.d* on grain yields. Thomas et al. (1995) observed that *sdw1.d* increased grain yields in different locations by about 0.50 t/ha. Similarly, Kuczyńska et al. (2014) reported grain yield increases of 10% due to *sdw1.d*. Dang et al. (2020), on the other hand, found that *sdw1* did not affect grain yield in low rainfall conditions but resulted in 20% increases in moderate rainfall areas. In contrast, Hellewel et al. (2000) observed grain yield losses associated with *sdw1.d*. In these studies, semi-dwarf genes were evaluated based on a limited number of randomly selected segregating lines with no fixed genetic backgrounds. Therefore, the yield increases observed in the present study in relation to semi-dwarf character, which were generally consistent but only partially varied by the environmental conditions (Fig. 4), seemed more reliable.

Biomass yields of the genotypes studied were significantly different in all trials except for 2013S ($p < 0.05$). In all fall-planted trials, biological yield of Tokak + *sdw1.d* was about 1.37–2.73 t/ha higher

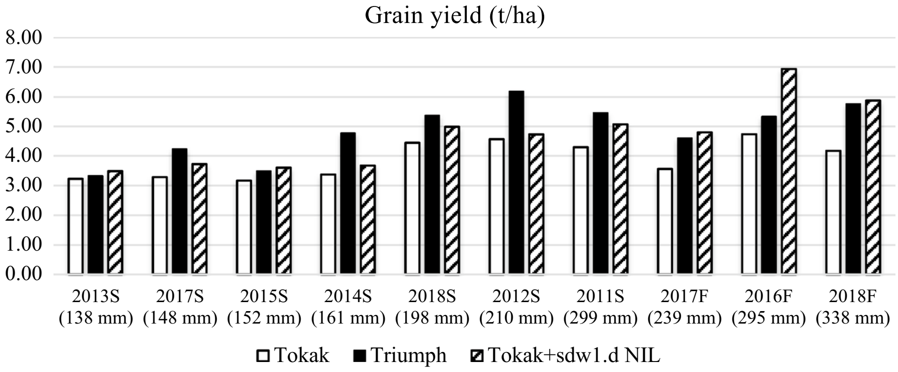

Fig. 4 Grain yields of Tokak + *sdw1.d* NIL and parent cultivars across trials. *F* fall-planted. *S* spring-planted. Values in parentheses are the amount of precipitation during the vegetation period. The field trials were ordered in the horizontal axis first based on planting season (fall or spring planting) and then based on amount of precipitation

than that of cv. Tokak. However, the positive effect of *sdw1.d* on biomass yields was less pronounced in spring-planted trials, and only in one of the seven trials, *sdw1.d* significantly increased biomass yield of Tokak + *sdw1.d* (by about 0.45 t/ha) compared to its recurrent parent cv. Tokak. Similarly, Teplyakova et al. (2017) pointed out that *sdw1.d* could be useful to attain higher biological yields in the environments with longer vegetative growing periods.

The genotypes studied had significant differences for harvest index in all trials except for 2017S ($p<0.05$). The *sdw1.d* allele increased harvest index of Tokak + *sdw1.d* NIL by 4.1–8.7% compared to cv. Tokak in fall-planted trials. In spring-planted trials, on the other hand, this increase varied between 1.9 and 4.7%. It is known that shorter-stature genotypes have higher harvest index (Peltonen-Sainio et al. 2008). Therefore, increased harvest index by *sdw1.d* was something expected. Indeed, higher harvest index due to *sdw.1d* was also reported by Jia et al. (2009).

GGE biplot analysis was performed in order to better show the effect of *sdw1.d* allele introgressed into cv. Tokak genetic background on grain yield under different environments. According to the results of the analysis, the first principal component was 66.33%, while the second was 33.67% (Fig. 5). GGE biplot had three sectors. Tokak + *sdw1.d* NIL was in the same sector as 2013S, 2015S, 2016F, 2017F and 2018F trials (Fig. 5a), which indicated that Tokak + *sdw1.d* NIL had superior performance in those trials (Frutos et al. 2014). On the other hand, a comparison of Tokak and Tokak + *sdw1.d* NIL revealed that Tokak + *sdw1.d* NIL also had better performance than Tokak in all trials (Fig. 5b).

The green revolution was mainly the result of employing short stature genes in crop cultivars. Various alleles of *sdw1* gene are among the most widely used short stature genes in barley. More than 160 modern barley cultivars carrying the *sdw1.d* short stature allele were developed in the world (Dang et al. 2020). In the present study, the effects of *sdw1.d* on grain yield and related traits were analyzed using a near isogenic line developed by marker-assisted transfer of *sdw1.d* to Turkish barley cv. Tokak. The transfer of *sdw1.d* into cv. Tokak genomic background shortened the plant height by 20–30 cm, improved its lodging tolerance by 40–60%, delayed heading time by 5–7 days, and produced 74–178 more spikes per square meter. Higher yields were achieved with NIL carrying *sdw1.d* compared to its recurrent parent cv. Tokak. Evaluating this NIL with contrasting traits for drought tolerance such as more tillers per area and higher harvest index on one hand and late heading on the other under drought conditions would be interesting.

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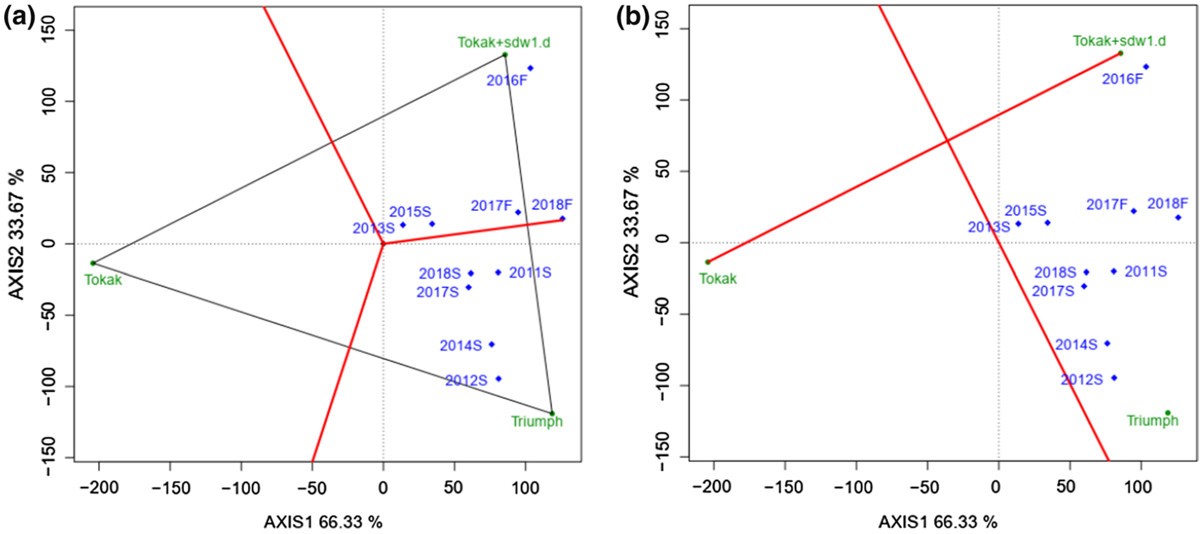

Fig. 5 The which-won-where view of the GGE biplot **a**, and comparing Tokak and Tokak + *sdw1.d* NIL **b**

Authors contributions NK and AY designed the research. IS and OAS carried out backcrosses, DNA analyses and field trials. IS and NK analyzed the data. IS, NK and AY wrote the manuscript.

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Code availability Not applicable.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

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