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REGULAR ARTICLE

Durum wheat with the introgressed *TaMATE1B* gene shows resistance to terminal drought by ensuring deep root growth in acidic and Al^{3+}-toxic subsoils

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Abstract

Background and aims High aluminum (Al^{3+}) concentrations associated with subsoil acidity is a major constraint to durum wheat (*Triticum turgidum*) production as it inhibits root growth affecting crop tolerance to drought. This study evaluated the introgressed *TaMATE1B* gene on drought resistance and Al^{3+} toxicity in durum wheat.

Methods Durum wheat lines Jandaroi–*TaMATE1B* (introgressed with the *TaMATE1B* gene) and Jandaroi–null (without *TaMATE1B* gene) were grown in 1-m deep columns filled with re-constructed field soil with Al^{3+}-rich acid subsoil in a glasshouse under well-watered conditions until the onset of ear emergence (Z_{51}), before imposing well-watered and terminal drought treatments.

Results Jandaroi–*TaMATE1B* produced 25.3 % higher grain yield than Jandaroi–null under well-watered conditions and 49.0 % higher grain yield under terminal drought. Terminal drought reduced grain yield by 47.7 % in Jandaroi–*TaMATE1B* and 72 % in Jandaroi–null, relative to well-watered conditions. The effects of *TaMATE1B* on grain yield can be attributed to increased root growth and proliferation below 0.4 m in Al^{3+}-toxic soil. Jandaroi–*TaMATE1B* had 34.5 and 32.0 % more total root biomass than Jandaroi–null in the well-watered and terminal drought treatments, respectively ($P \leq 0.05$). Jandaroi–*TaMATE1B* had a significantly higher root: shoot ratio than Jandaroi–

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null at Z_{51}. Introgression of the *TaMATE1B* gene did not affect grain-filling duration, but terminal drought reduced it by 24 days in both lines.
Conclusions Introgression of the Al^{3+}-tolerant *TaMATE1B* gene into durum wheat improved terminal drought resistance by enabling root growth and proliferation into deep layers of Al^{3+}-rich acidic soil.

Keywords Subsoil Al^{3+} toxicity · *Triticum turgidum* · *TaMATE1B* gene · Root system · Water stress · Acid soil

Introduction

Tetraploid durum wheat (AABB, *Triticum turgidum*) is well-known for its high grain protein content and market price, hardness, intense yellow color, nutty flavor and excellent milling properties, but its planting area only accounts for 8 % of the global area sown to bread wheat (Beres et al. 2020). One of the soil constraints limiting the durum wheat cropping area is soil acidity due to durum wheat's sensitivity to Al^{3+} toxicity (Foy and da Silva 1991; Bona et al. 1993, 1995). Subsoil acidity with high Al^{3+}concentration inhibits the growth, development and grain yield of durum wheat lines (e.g. genotypes) that lack Al^{3+} tolerance genes (Han et al. 2014; Pereira 2018) with root growth and proliferation hampered in strongly acidic and Al^{3+} toxic subsoil layers (Pooniya et al. 2019). Inhibition of root growth into subsoil reduces water and nutrient uptake from deep reservoir increasing the chance of severe water stress when topsoil drying in dry environments and dry seasons. In the past, selection of durum wheat germplasm for tolerance of acidic soils with high Al^{3+}, as a strategy for improving crop production on acid soils, has not been possible due to the lack of variation in Al^{3+} tolerance in this species (Ryan et al. 2010; Wayima et al. 2019). In contrast, hexaploid bread wheat (AABBDD, *Triticum aestivum*) has large variation in Al^{3+} tolerance (Camargo et al. 1992; Moustakas et al. 1992; Cosic et al. 1994), with many genotypes relying on the *TaALMT1* and *TaMATE1B* genes (Delhaize et al. 2012b). The *TaALMT1* gene located on chromosome 4D confers Al^{3+}-activated malate efflux from root tips while the *TaMATE1B* gene located on chromosome 4B is responsible for constitutive citrate efflux from root tips (Sasaki et al. 2004; Delhaize et al. 2012b; Tovkach et al. 2013). Both malate and citrate chelate Al^{3+} to reduce its toxicity allowing root growth (Delhaize et al. 2012a; Pereira 2018). As an alternative to screening natural durum wheat germplasm, the *TaALMT1* and *TaMATE1B* genes of hexaploid bread wheat were introgressed into a semi-dwarf Australian elite durum wheat cultivar 'Jandaroi' as described by Han et al. (2016).

The root system of the introgressed line, Jandaroi–*TaMATE1B* (with *TaMATE1B* gene), grew and proliferated to 1.0 m soil depth, with the soil pH decreasing from 4.81 to 3.55 and Al^{3+} concentration increasing from 1.25 to 28.3 mg kg^{-1} (Pooniya et al. 2019). Under these conditions where water was added to the top of pots, the surface soil with low concentrations of toxic Al^{3+} remained moist enabling roots to take up sufficient water resulting in no significant difference in shoot biomass and grain yield between Jandaroi–*TaMATE1B* and Jandaroi–null (without *TaMATE1B* gene). The lack of difference in shoot biomass and grain yield occurred despite Jandaroi–*TaMATE1B* having developed deeper roots down the profile.

Deep roots play a critical role in drought resistance as they can access water deeper in the soil profile when combined with other traits, such as root length density and root hair density (Chen et al. 2015; Fang et al. 2017; Palta and Turner 2019). We hypothesized that the introgressed line Jandaroi–*TaMATE1B*, would have better drought resistance than Jandaroi–null when grown in acidic soils with high Al^{3+} under drought conditions. End-of-season drought, or terminal drought, is a common feature of durum wheat grown under rainfed conditions in non-acidic, non-Al^{3+} toxic soils, as the crop progressively depletes available water in the soil profile during the reproductive stage, reducing grain yield (Habash et al. 2014; Boussakouran et al. 2019).

A plant's ability to survive or produce grain in water-deficit environments is termed drought resistance (Palta and Turner 2019). Here we related drought resistance to grain yield in durum wheat under terminal drought, rather than its survival, and investigated the connection between drought resistance and differences in root growth at depth. We investigated the effect of the *TaMATE1B* gene on improving drought resistance and adaptation to acid soil with high Al^{3+} concentration under terminal drought. We tested the hypothesis that introgression of the *TaMATE1B* gene into durum wheat promotes root growth and proliferation and increases its resistance to terminal drought and Al^{3+} toxicity in acidic soil.

Materials and methods

Plant materials, soil, and experimental design

Two durum wheat (tetraploid AABB, *Triticum turgidum*) lines (genotypes) — one with the *TaMATE1B* gene (Jandaroi–*TaMATE1B*) introgressed from bread wheat (hexaploid AABBDD, *Triticum aestivum*), and a parental line that lacked the *TaMATE1B* gene (Jandaroi–null) — were used as experimental germplasm. The procedure for introgressing the Al^{3+}-tolerant allele of *TaMATE1B* from bread wheat into durum wheat was described in Han et al. (2016). The *TaMATE1B* gene was originally crossed and then backcrossed into the Australian durum cultivar Jandaroi. For the current work, we used a *TaMATE1B* line that had been backcrossed three times to cultivar Jandaroi as summarized in Pooniya et al. (2019). For convenience, here we refer to line with the *TaMATE1B* locus introgressed as having the *TaMATE1B* gene bearing in mind that genes linked to *TaMATE1B* could also have been introgresssed. The durum lines differ in their tolerance to Al^{3+} and a study using similar Al^{3+}-toxic soils to this study reported that root growth below 0.25 m in the soil profile was inhibited in Jandaroi–null and unrestricted in Jandaroi–*TaMATE1B* (Pooniya et al. 2019). Here, the two lines were grown in 17.7 L polyvinyl chloride (PVC) columns (0.15 m diameter, 1.0 m deep) inserted with a long sleeve clear plastic bag (150 μm thick) to facilitate recovery of the root system at harvest. The plastic bag had small holes in the bottom to enable drainage. The PVC column had a fixed bottom lid and short plastic tubes connected to a bottle to collect any drainage. Each column was filled with soil to a depth of 1.0 m, with a 4-cm layer of gravel at the bottom to facilitate drainage. This technique does not restrict root development in bread wheat and durum wheat (Arduini et al. 2014; Aziz et al. 2016; Pampana et al. 2016; Saradadevi et al. 2017; Figueroa-Bustos et al. 2019; Tekin et al. 2020). Moreover, large, tall pots simulate water extraction and root development in the field more effectively than smaller pots (Turner 2019).

The soil used in this study was described in Pooniya et al. (2019); briefly, it was a brownish-yellow, well-drained sandy soil, Regolithic Chernic Tenosol (Isbell 1993), collected in 0.2 m sections from the 0–1.0 m profile of a field site at Merredin (31°64' S, 117°24' E), Western Australia. The soil comprised of 78.6 % brownish-yellow sand, 4.5 % silt, and 16.9 % clay. The pH, measured in a 1:5 suspension of soil in 0.01 M $CaCl_2$, was 4.81 in the top 0–0.1 m, decreasing progressively to 3.81 in the 0.2–0.3 m layer beyond which the changes were not significant (Fig. 1). The Al^{3+}concentration was 1.25 mg kg^{-1} in the top 0.1 m layer, increasing to 25.5 mg kg^{-1} in the 0.2–0.3 layer beyond which, the changes were not significant (Fig. 1). Colwell P was 81.3 mg kg^{-1} in the top 0.1 m layer, decreasing to 10.4 mg kg^{-1} in the 0.3–0.6 m layer beyond which, the changes were not significant (Fig. 1). The soil contained 4.8 μg g^{-1} of nitrate-N, 3.6 μg g^{-1} of ammonium-N, and 639 μg g^{-1} of Colwell K. To reconstitute the soil profile, each 0.2 m section of soil was air-dried and sieved to 2 mm before being packed in the columns, starting with the 0.8–1.0 m bottom layer, and ending with the top 0.2 m layer. Each 0.2 m soil layer was packed to a bulk density of approximately 1.51 g cm^{-3}. The soil in each column was watered slowly by hand to saturation to minimize drainage. Before sowing, the equivalent of 60 kg N ha^{-1} as urea, 45 kg P ha^{-1} as amended superphosphate (with Cu, Zn, Mo, S), and 55 kg K ha^{-1} as potash were mixed into the top 0.1 m of soil in each column. These rates corresponded with the optimal nutrient supply for durum wheat production on neutral–alkaline sandy soils in Australia (Anderson 2004; Kneipp 2008) and mimicked the application of fertilizers for field-grown wheat. The randomized complete block design comprised the two durum wheat lines (Jandaroi–*TaMATE1B* and Jandaroi–null), two watering treatments [well-watered (WW) and terminal drought (TD)], and three harvests [onset of ear emergence in the mainstem (Z_{51}, on the Zadoks scale of wheat growth; Zadoks et al. 1974; one day before inducing terminal drought), grain milk development (Z_{75}), and physiological maturity (Z_{91})], with eight replicates for a total of 96 columns. Half of the columns (48) was used for plant water status and gas exchange measurements during water stress development, and the other half was used to measure shoot and root system traits on three occasions during the experiment. The two watering treatments were imposed at the onset of ear emergence in the mainstem (Z_{51}). Terminal drought was induced by withholding water in half of the columns from Z_{51} to physiological maturity (Z_{91}). The other half of the columns were well-watered for the duration of the experiment.

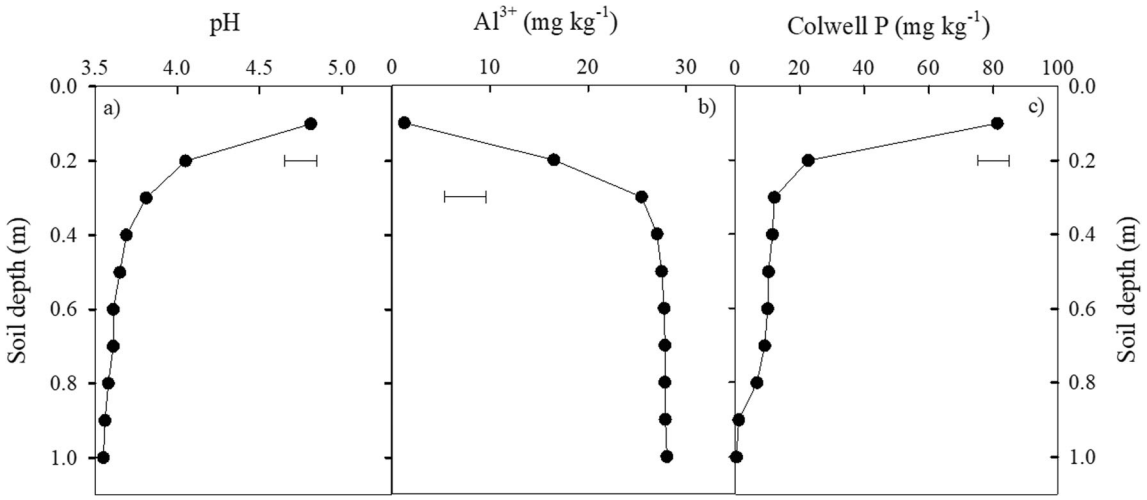

Fig. 1 Changes in **a** pH, **b** Al^{3+}concentration, and **c** Colwell P concentration with soil depth from 0 to 1.0 m in the soil collected from a field site at Merredin, Western Australia. The same soil was used to fill the columns where the introgressed durum wheat line Jandaroi–*TaMATE1B* and Jandaroi–null were grown. Values for each soil depth are the mean of nine holes

Planting and maintenance

Four seeds per column were sown on 14 May 2019 and thinned to two plants at the two-leaf stage (Z_{12}) for an approximated density of 114 plants m^{-2} for field-grown wheat (Lemerle et al. 2004). At the third-leaf stage (Z_{13}), a layer of plastic beads (~ 2.5 cm) was uniformly spread on the soil surface in each column to prevent loss of soil water by evaporation. A water-soluble fertilizer (Scott Peter excel) with 15 % N, 2.2 % P, and 12.4 % each of K, Mg, Cu, Zn, Mo and S was supplied during watering at the onset of tillering (Z_{23}).

Plants were grown from May to November 2019 in an evaporatively-cooled glasshouse at The University of Western Australia, Perth, Australia (31°93' S, 115°83' E) with an average maximum air temperature of 24 °C, minimum temperature of 10 °C, and mean relative humidity of 60 %. During the experiment, the glasshouse received 11 to 12 h of natural day light (photoperiod), with an average maximum photosynthetic photon flux density of 941 ± 20 μmol m^{-2} s^{-1} measured at plant level at 13:00 h. The positions of the columns were rotated weekly to minimize spatial variability. From sowing to ear emergence, before inducing terminal drought, all plants were watered twice a week to maintain the column soil water capacity close to 80 ± 5 % of field capacity. Columns were watered to weight, and the amount of water supplied was based on the amount of water transpired.

Sampling and measurements

Phenology was regularly monitored, and developmental stages recorded when 50 % of the plants in each genotype had reached a particular stage (Zadoks et al. 1974). The grain-filling duration was calculated as the difference between days to physiological maturity and anthesis.

Shoot and root system traits were measured at the day before terminal drought was applied (Z_{51}), at grain milk development (Z_{75}) and at final harvest (Z_{91}). On each occasion, four columns (8 plants) per line per treatment were harvested and the shoots were separated from the roots by cutting at the crown. The number of tillers was recorded before separating stems and leaves. Leaf area was measured using a portable leaf area meter (LI-3000, Li-COR Bioscience, Lincoln, NE, USA) and specific leaf area (SLA) was calculated as leaf area per unit leaf dry weight. Stems and leaves were oven-dried separately at 60 °C for 48 h to estimate shoot biomass. At final harvest, the number of tillers and spikes per plant was counted. Spikes were separated from shoots, oven-dried at 60 °C for 48 h before being threshed by hand, re-dried, and the grain weighed. Grain number per plant was recorded. Harvest index (HI) was calculated as the ratio of grain yield to shoot biomass.

Immediately after harvesting the shoots, the plastic bag in each column was removed from the column and cut to open. The soil profile was sampled in 0.2 m sections from the top by cutting the soil with a carbon steel blade. The roots in each 0.2 m section were

recovered from the soil by washing through a 1.4 mm sieve to produce a clean sample (Palta and Fillery 1993). The recovered roots from each 0.2 m soil section were placed in plastic bags at 4 °C before scanning at 400 dpi (Epson Perfection V800, Long Beach, CA, USA) to quantify root morphological traits. The root samples were dried and weighed after scanning as per the shoot samples. Scanned images of root sections from the first two harvests were analyzed using WinRHIZO Pro Software (v2009, Regent Instrument, Quebec, QC, Canada) to generate root length, root surface area, root volume, and average root diameter (Chen et al. 2011). Specific root length (SRL), an indirect measure of root system thickness, was estimated as total root length divided by total root biomass (Aziz et al. 2016; Benlloch-Gonzalez et al. 2014; Liao et al. 2004, 2006).

Leaf net photosynthesis rate (Pn) and stomatal conductance (*gs*) were measured on day 0, 12, 24, 36, 40, and 48 after inducing terminal drought at ear emergence. Five measurements were made on the top fully expanded leaves from mainstem and tillers on four replicate plants from 10:30 to 13:30 h on days with clear sky using a LI-COR gas-exchanged system (LI-6400, LI-COR Bioscience, Lincoln, NE, USA) and LED light source in the leaf chamber. In the LI-COR cuvette, CO_2 concentration was set to 380 μmol mol^{-1} and LED light intensity to 900 μmol m^{-2} s^{-1}, being the average saturation intensity for photosynthesis in wheat. Immediately after these measurements were made, leaf water potential (ψ_{leaf}) was measured using a Scholander pressure chamber (model 1000, PMS Instrument Co., Oregon, USA). The leaf was loosely covered with a plastic sheath before excision and during the measurement to avoid evaporation (Turner 1988).

The amount of water applied to each column at watering was recorded, and total water use calculated as the sum of water applied after planting to ear emergence (Z_{51}), plus the water used after inducing terminal drought to physiological maturity (Z_{91}). During this period, all columns were weighed twice a week. Water use after inducing terminal drought was calculated as the difference in weight of individual columns at ear emergence (Z_{51}) and at maturity (Z_{91}) plus the water applied in-between. Water use efficiency (WUE_{grain}) was calculated as grain yield per unit of total water used. Soil water content (SWC) was calculated as:

$$SWC = [1 - (Wc - Wn)/(Wc - Wd))] \times 100$$

where Wc is initial column weight at saturation, Wn is column weight on the measurement day, and Wd is column weight with dry soil.

Statistical analysis

A one-way analysis of variance (ANOVA) was used to determine genotype effects at the first harvest, and two-way ANOVA was used to determine genotype and drought effects for the second and final harvests, using SPSS statistical software package (Version 19.0, SPSS Institute Inc., USA). Statistical variations of the data were expressed as standard deviations, with the significance of the data calculated at $P \leq 0.05$. Graphical presentations were made in Sigmaplot software 10.0.

Results

Phenology

The two lines produced the first visible spikelets on the main stem ear (Z_{51}) at similar times, but Jandaroi–*TaMATE1B* reached 50 % anthesis four days later than Jandaroi–null under well-watered conditions and two days later under terminal drought ($P \leq 0.05$; Fig. 2a; Table 1). Jandaroi–*TaMATE1B* reached physiological maturity (Z_{91}) five days later than Jandaroi–null under well-watered conditions and three days later under terminal drought (Table 1) [Fig. 2b photographed at soft drought stage (Z_{81})]. Terminal drought did not significantly affect time to 50 % anthesis in either line, but reduced time to physiological maturity by 24 days in Jandaroi–*TaMATE1B* and 22 days in Jandaroi–null. Both lines had similar grain-filling durations under well-watered and terminal drought conditions, respectively, but terminal drought shortened the grain-filling duration by 24 days in both lines (Table 1).

Soil drying, leaf water potential, stomatal conductance and leaf photosynthesis

During the first 14 days of withholding water, soil water content (SWC) decreased rapidly from 80 to 57 % in both lines (Fig. 3a). Over the next 20 days, SWC decreased to 22.0 % in Jandaroi–*TaMATE1B* and 46.0 % in Jandaroi–null (Fig. 3a). Well-watered plants of both lines maintained leaf water potential (ψ_{leaf}) between −

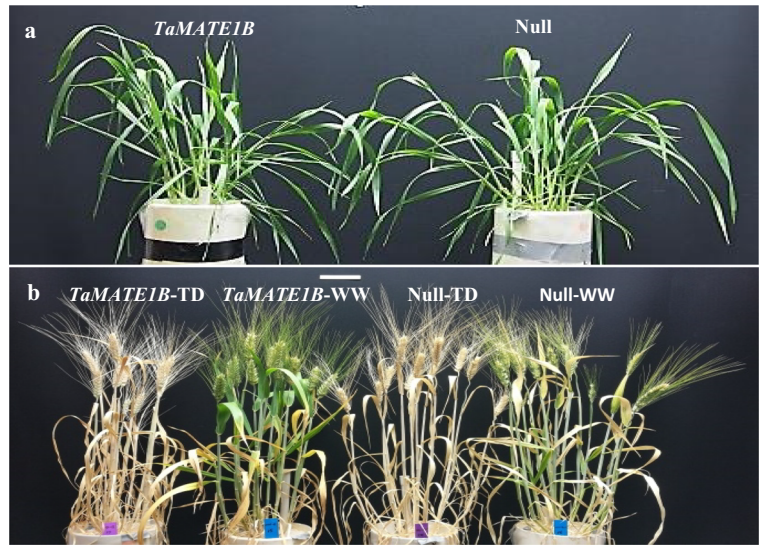

Fig. 2 **a** Durum wheat plants of genotypes Jandaroi–*TaMATE1B* and Jandaroi–null after first awn emergence (Z_{51}) before imposing drought, and at **b** the soft dough stage (Z_{81}) under well-watered (WW) and terminal drought (TD) conditions

0.85 and − 1.1 MPa (Fig. 3b). Terminal drought decreased ψ_{leaf} rapidly, declining to − 1.9 MPa in Jandaroi–*TaMATE1B* and − 2.1 MPa in Jandaroi–null after 27 days of terminal drought. Over the next 17 days, ψ_{leaf} decreased to − 2.7 MPa in Jandaroi–*TaMATE1B* and − 3.1 MPa in Jandaroi–null. Well-watered plants maintained stomatal conductance (g_s) between 470 and 352 mmol m^{-2} s^{-1} in Jandaroi–*TaMATE1B*, and 470 and 290 mmol m^{-2} s^{-1} in Jandaroi–null (Fig. 3c). During the first 14 days of terminal drought, g_s decreased rapidly from 470 to 157 mmol m^{-2} s^{-1} in both lines. Over the next 21 days, Jandaroi–*TaMATE1B* maintained g_s at about 157 mmol m^{-2} s^{-1} whereas Jandaroi–null decreased to 19.5 mmol m^{-2} s^{-1}. Over the next 5 days, g_s decreased slowly in Jandaroi–*TaMATE1B* to 91.5 mmol m^{-2} s^{-1} while Jandaroi–null maintained g_s at about 19.5 mmol m^{-2} s^{-1}. The leaf photosynthesis rate (P_n) of well-watered plants ranged from 12.8 to 20 µmol m^{-2} s^{-1} in Jandaroi–*TaMATE1B* and 11 to 20 µmol m^{-2} s^{-1} in Jandaroi–null (Fig. 1d). During the first 14 days of terminal drought, P_n decreased rapidly from 20 to 14 µmol m^{-2} s^{-1} in both lines (Fig. 3d). Over the next 21 days, Jandaroi–*TaMATE1B* maintained P_n at about 14 µmol m^{-2} s^{-1} while Jandaroi–null decreased to 3.5 µmol m^{-2} s^{-1}. Over the next 5 days, P_n decreased to 6.5 µmol m^{-2} s^{-1} in Jandaroi–*TaMATE1B* and 2.0 µmol m^{-2} s^{-1} in Jandaroi–null (Fig. 3d).

Table 1 Days to first visible awn on the mainstem (Z_{51}), anthesis (Z_{61}), physiological maturity (Z_{91}), and grain-filling duration of the introgressed durum wheat line Jandaroi–TaMATE1B and Jandaroi–null

Genotype	First visible awn	Days to anthesis		Days to physiological maturity		Grain-filling duration	
		WW	TD	WW	TD	WW	TD
TaMATE1B	67a	76a	76a	119a	95c	43a	19b
Null	65a	72b	74b	114b	92d	42a	18b

Terminal drought (TD) was induced from the first visible awn on the main stem (Z_{51}) by withholding watering

For each trait, mean values (n = 4) followed by different letters differ significantly at $P \leq 0.05$

Shoot traits before and during terminal drought

The day before inducing terminal drought, at the onset of awn emergence (Z_{51}), Jandaroi–*TaMATE1B* had 28.6 % more leaf area than Jandaroi–null but both lines had similar specific leaf areas ($P \leq 0.05$; Fig. 4), indicating no differences in leaf thickness between Jandaroi–*TaMATE1B* and Jandaroi–null before inducing drought stress. Both lines had similar shoot biomass before inducing terminal drought (Z_{51}) (Fig. 5a). At grain milk development (Z_{75}), both lines had similar shoot biomass in the well-watered and terminal drought treatments, respectively, but terminal drought reduced shoot biomass in both lines by 33.5 % ($P \leq 0.05$; Fig. 5b). At final harvest, well-watered Jandaroi–*TaMATE1B* had 12.5 % more shoot biomass than well-watered Jandaroi–null ($P \leq 0.05$; Fig. 5c), but terminal drought reduced shoot

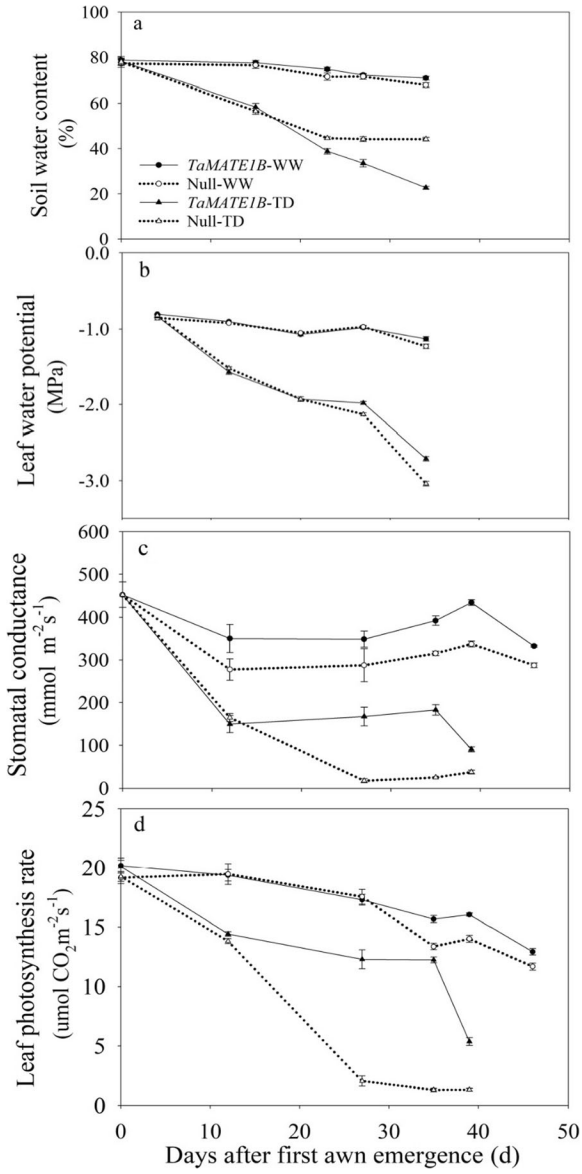

Fig. 3 **a** Changes in soil water content (% of column water capacity), **b** leaf water potential, **c** stomatal conductance and **d** leaf photosynthesis rate in the introgressed durum wheat line Jandaroi–*TaMATE1B* (filled symbols) and Jandaroi–null (open symbols) under well-watered (WW, solid lines) and terminal drought (TD, dashed lines) conditions. Terminal drought was induced by withholding watering from the first visible awn on the main stem (Z_{51}). Vertical bars are s.e.m (n = 4)

biomass in both lines by about 40.2 %. Tiller numbers did not differ between Jandaroi–*TaMATE1B* and Jandaroi–null at the onset of awn emergence (Z_{51}) (Fig. 5d) and at the grain milk development stage (Fig. 5e).

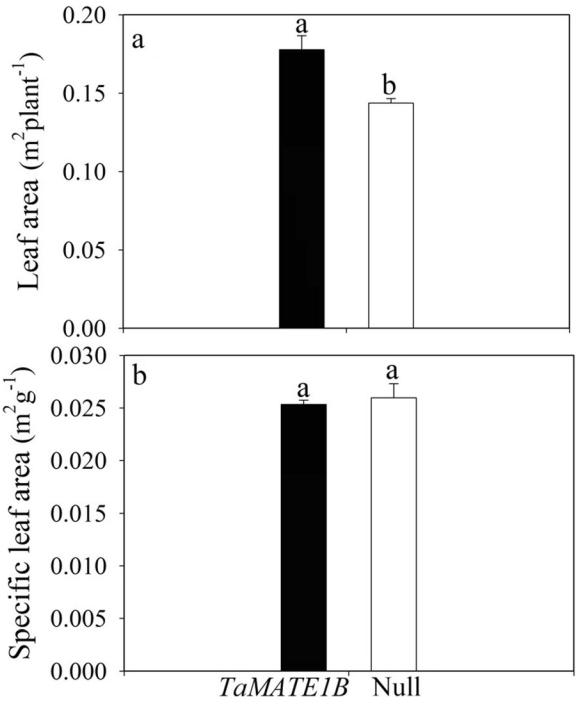

Fig. 4 **a** Leaf area and **b** specific leaf area in the introgressed durum wheat line Jandaroi–*TaMATE1B* (filled symbols) and Jandaroi–null (open symbols), at the first visible awn on the main stem (Z_{51}), just before inducing terminal drought. Means followed by different letters differ significantly ($P \leq 0.05$). Vertical error bars are s.e.m (n = 4)

Root traits before and during terminal drought

At the onset of awn emergence (Z_{51}), just before inducing terminal drought, Jandaroi–*TaMATE1B* had 33.5 % more total root length and root biomass than Jandaroi–null (Fig. 6a, b). Jandaroi–*TaMATE1B* had a 26.8 % higher root: shoot ratio ($P \leq 0.05$) than Jandaroi–null (Fig. 6d), but there was no significant difference in specific root length (SRL) between the two lines (Fig. 6c). Jandaroi–null had 44 and 39 % more root length and root biomass, respectively, than Jandaroi–*TaMATE1B* in the top 0.2 m of the soil profile; however, Jandaroi–null had no vertical root growth below 0.4 m such that Jandaroi–*TaMATE1B* had more total root length and root biomass in the 1.0 m soil profile than Jandaroi–null (Figs. 6a and b and 7).

At the grain milk development stage (Z_{75}), Jandaroi–*TaMATE1B* had 32.5 and 18.0 % more total root length than Jandaroi–null in the well-watered and terminal drought treatments, respectively (Fig. 8a). Under terminal drought, total root length decreased more in Jandaroi–*TaMATE1B* (23.7 %) than Jandaroi–null

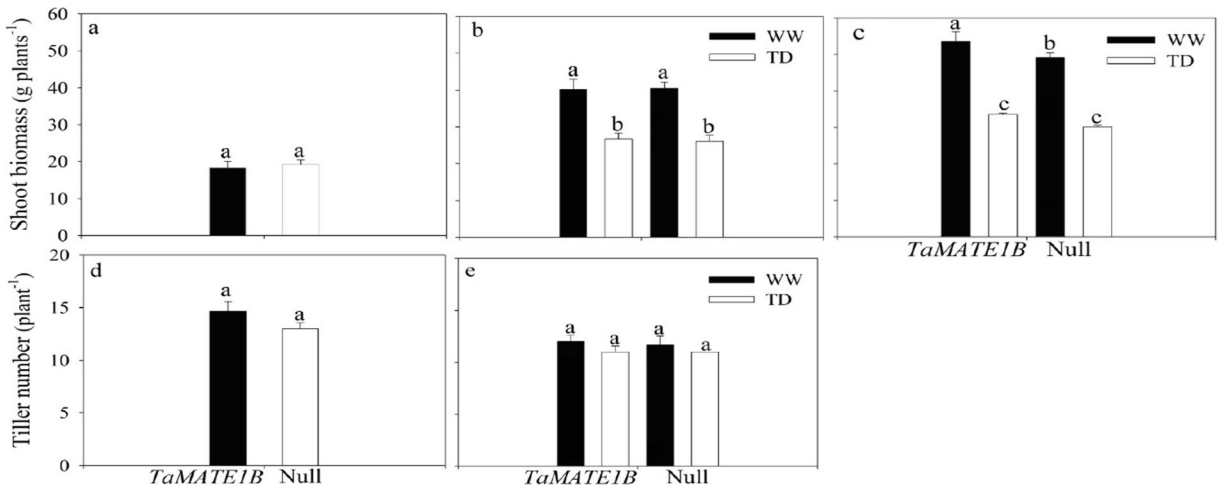

Fig. 5 **a** Shoot biomass at the first visible awn on the main stem (Z_{51}), just before inducing terminal drought, **b** shoot biomass at grain milk development (Z_{75}), **c** shoot biomass at final harvest, **d** tiller number just before terminal drought was induced (Z_{51}), and **e** tiller number at grain milk development (Z_{75}) in the introgressed durum wheat line Jandaroi–*TaMATE1B* and Jandaroi–null under well-watered (WW) and terminal drought (TD) conditions. Means followed by different letters differ significantly ($P \leq 0.05$). Vertical error bars are s.e.m (n = 4)

(7.4 %) ($P \leq 0.05$; Fig. 8a). Jandaroi–*TaMATE1B* had 34.5 and 32.0 % more total root biomass than Jandaroi–null in the well-watered and terminal drought treatments, respectively ($P \leq 0.05$; Fig. 8b). Terminal drought reduced total root biomass in Jandaroi–*TaMATE1B* by 13.8 % and Jandaroi–null by 10.6 % (Fig. 8b). Well-watered Jandaroi–*TaMATE1B* had 44.6 % greater SRL than Jandaroi–null ($P \leq 0.05$; Fig. 8c), indicating that Jandaroi–*TaMATE1B* had a thinner root system than Jandaroi–null. Well-watered

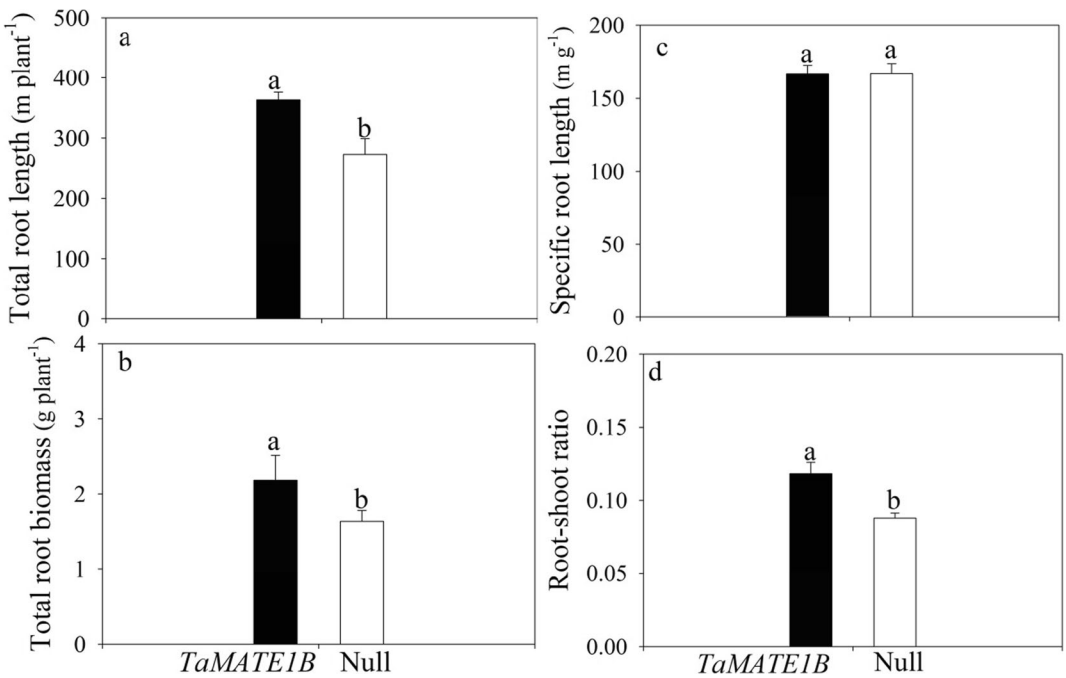

Fig. 6 **a** Total root length, **b** root biomass **c**, specific root length and **d** root-shoot ratio in the introgressed durum wheat line Jandaroi–*TaMATE1B* and Jandaroi–null at the first visible awn on the main stem (Z_{51}), just before inducing terminal drought. Vertical bars are s.e.m (N = 4)

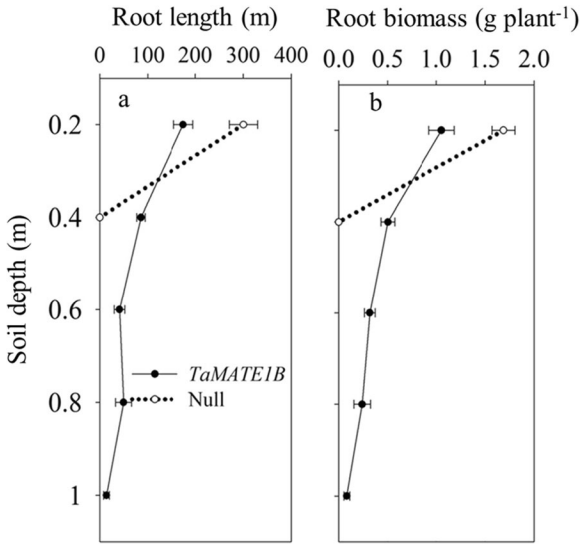

Fig. 7 **a** Root length and **b** root biomass distribution in the soil profile in the introgressed durum wheat line Jandaroi–*TaMATE1B* and Jandaroi–null at the first visible awn on the main stem (Z_{51}), just before inducing terminal drought. Horizontal bars are s.e.m ($n = 4$)

Jandaroi–*TaMATE1B* had an 18.2 % higher root: shoot ratio than Jandaroi–null. Terminal drought increased the root:shoot ratio in Jandaroi–*TaMATE1B* but did not affect the root:shoot ratio in Jandaroi–null ($P \leq 0.05$; Fig. 8d).

Under well-watered conditions, root length and root biomass of Jandaroi –null in the top 0.2 m of the soil profile was 43 and 40 % greater than those of Jandaroi–*TaMATE1B*, respectively ($P \leq 0.05$; Fig. 9a). Terminal drought reduced root length and root biomass in the top 0.2 m of the soil profile more in Jandaroi–null (35 and 34 %, respectively) than Jandaroi–*TaMATE1B* (30 and 26 %, respectively) compared to their counterparties under well-watered conditions (Fig. 9).

Water use and water use efficiency

Well-watered Jandaroi–*TaMATE1B* and Jandaroi–null used similar amounts of water pre- and post-anthesis, and during the whole experiment (Table 2). Terminal drought reduced pre-anthesis water use by about 20 % in both lines and post-anthesis water use to nil. Terminal drought reduced total water use by about 43 % in both lines ($P \leq 0.05$; Table 2). Jandaroi–*TaMATE1B* had 23.5 and 48.0 % higher water use efficiency than Jandaroi–null under well-watered and terminal drought conditions, respectively ($P \leq 0.05$; Table 2). Terminal drought reduced water use efficiency in Jandaroi–*TaMATE1B* by18.4 % and Jandaroi–null by 16.7 % (Table 2).

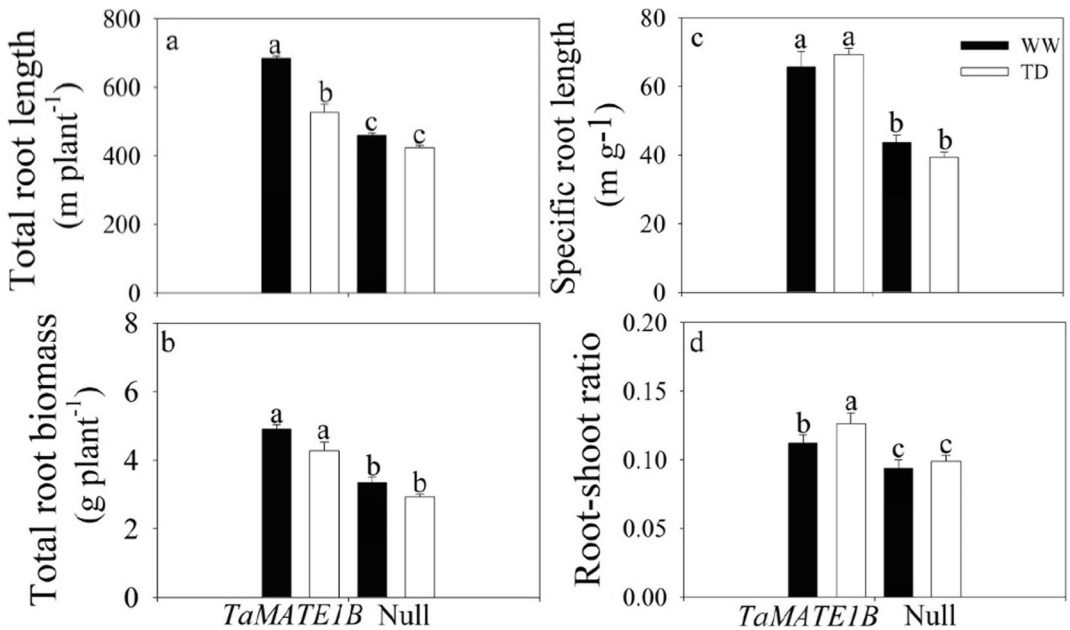

Fig. 8 **a** Total root length, **b** root biomass, **c** specific root length and **d** root: shoot ratio in the introgressed durum wheat line Jandaroi–*TaMATE1B* and Jandaroi–null under well-watered (WW) and terminal drought (TD) conditions. Measurements were taken at the grain milk development stage (Z_{75}). Vertical bars are s.e.m (n = 4)

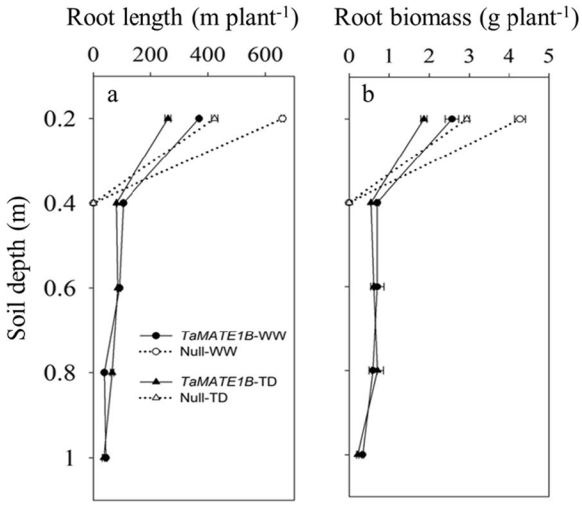

Fig. 9 **a** Root length and **b** root biomass distribution down the soil profile in the introgressed durum wheat line Jandaroi–*TaMATE1B* and Jandaroi–null under well-watered (WW) and terminal drought (TD) conditions. Measurements were taken at the grain milk development stage (Z_{75}). Horizontal bars represent s.e.m (n = 4)

Grain yield and yield components

Jandaroi–*TaMATE1B* yielded 25.4 and 48.8 % more grain than Jandaroi–null under well-watered and terminal drought conditions, respectively ($P \leq 0.05$; Table 3). Terminal drought reduced grain yield more in Jandaroi–null (53.0 %) than Jandaroi–*TaMATE1B* (31.0 %). Both lines produced similar spike numbers per plant regardless of the treatment. Well-watered Jandaroi–*TaMATE1B* produced 25.4 and 19.0 % more grain per plant and grains per spike, respectively, than well-watered Jandaroi–null, but the numbers did not differ between the two lines under terminal drought (Table 3). Both lines had similar 1000-grain weights under well-watered conditions; under terminal drought, Jandaroi–*TaMATE1B* had 46.8 % higher 1000-grain weight than Jandaroi–null (Table 3). Terminal drought reduced 1000-grain weight more in Jandaroi–null (49.3 %) than Jandaroi–*TaMATE1B* (15.5 %). Jandaroi–*TaMATE1B* had higher harvest index than Jandaroi–null under well-watered and terminal drought conditions (Table 3).

Discussion

Drought resistance is the ability of crops to produce grain yield when grown in water-limited environments (Palta and Turner 2019). Introgression of the Al^{3+}-tolerance *TaMATE1B* gene into durum wheat cultivar Jandaroi improved drought resistance, producing 48.8 % more grain yield than Jandaroi–null under terminal drought conditions ($P \leq 0.05$; Table 3). Terminal drought decreased leaf water potential from − 0.85 MPa to − 2.7 MPa in Jandaroi–*TaMATE1B* and − 3.1 MPa in Jandaroi–null (Fig. 3c); both values were below the − 2.2 MPa that is characteristic of wheat under severe water stress (Henson et al. 1989; Jensen et al. 1989). The increased grain yield of

Table 2 Pre- and post-anthesis water use, total water used, and water use efficiency (WUE) in the introgressed durum wheat line Jandaroi–*TaMATE1B* and Jandaroi–null

Genotypes	Water use (L plant^{-1})			WUE (g grain L^{-1})
	Pre-anthesis	Post-anthesis	Total	
Well-watered				
Jandaroi–*TaMATE1B*	8.35a	3.45a	11.8a	2.04b
Jandaroi–null	8.10a	3.40a	11.5a	1.56c
Terminal drought				
Jandaroi–*TaMATE1B*	6.65b	0.39b	7.04b	2.36a
Jandaroi–null	6.55b	0.00c	6.55b	1.30d
P values from ANOVA				
Genotype	0.002	0.008	0.008	0.095
Drought	0.000	0.000	0.000	0.000
Genotype × Drought	0.085	0.004	0.262	0.102

Terminal drought was induced from the first visible awns on the main stem (Z_{51}) by withholding watering

Mean values in each column followed by different letters differ significantly at $P \leq 0.05$

Table 3 Grain yield and yield components in the introgressed durum wheat line Jandaroi–*TaMATE1B* and Jandaroi–null

Genotypes	Grain yield (g plant^{-1})	Shoot biomass (g plant^{-1})	Spikes plant^{-1}	Grains plant^{-1}	Grains spike^{-1}	1000-grain weight (g)	Harvest index
Well-watered							
TaMATE1B	24.1a	56.0a	12.0a	423.3a	35.4a	57.0a	0.43a
Null	18.0b	49.1b	11.0a	315.8b	28.7b	56.9a	0.37b
Terminal drought							
TaMATE1B	16.6c	33.5c	12.0a	336.0b	28.0b	49.5b	0.37b
Null	8.5d	30.1c	11.0a	307.5b	28.1b	27.7c	0.29c
P values from ANOVA							
Genotype	0.001	0.001	0.574	0.150	0.160	0.000	0.001
Drought	0.000	0.000	0.014	0.001	0.106	0.000	0.002
Genotype × Drought	0.290	0.165	0.014	0.030	0.166	0.000	0.560

Terminal drought was induced from the first visible awn on the main stem (Z_{51}) by withholding watering

Mean values of each trait (n = 4) followed by different letters differ significantly at $P \leq 0.05$

Jandaroi–*TaMATE1B* under terminal drought resulted from its ability to grow and proliferate roots in the Al^{3+}-rich acidic soil. The 12.9 cm increase in root length in Jandaroi–*TaMATE1B* under terminal drought conditions produced 1 g of grain yield per plant than Jandaroi–null (Table 3; Fig. 6). In contrast, root growth and proliferation of Jandaroi–null remained in the top 0.4 m, where the low Al^{3+} concentration did not significantly inhibit root growth (Fig. 7). The absence of severe Al^{3+} toxicity in the top layer of the soil profile enabled Jandaroi–null to grow an adequate root system to produce viable plants. Indeed, by final harvest, Jandaroi–null produced more roots in the top 20 cm of soil than Jandaroi–TaMATE1B. In the well-watered treatment, despite Jandaroi–null having sufficient water to maturity, there was still a yield penalty compared to Jandaroi–*TaMATE1B*, which may have been due to slight differences in their genetic background (about 6 % variation) (Han et al. 2016), and shorter time to anthesis (four days) and time to maturity (three days). The larger pot size and lower plant density than the early study of Pooniya et al. (2019) may explain the variations in shoot biomass and grain yields between the two lines under well-watered conditions when compared the two studies.

The root growth differences between Jandaroi–*TaMATE1B* and Jandaroi–null generated differences in soil water depletion under terminal drought conditions with SWC declining more in Jandaroi–*TaMATE1B* (from 80 to 22 %) than Jandaroi–null (from 80 to 46 %) (Fig. 3a). This reflects differences in root systems' ability to use available soil water below the top 0.4 m layer of the soil profile in the Al^{3+}-rich acidic soil; that is, Jandaroi–*TaMATE1B* has greater total and post-anthesis water use (7.04 and 0.39 L plant^{-1}, respectively) than Jandaroi–null (0 and 6.55 L plant^{-1}, respectively) (Table 2). The improved water use efficiency of Jandaroi–*TaMATE1B* resulted in higher grain yields than Jandaroi–null under terminal drought. The benefit of the *TaMATE1B* gene in improving durum grain yield on acid soil in the field has also been observed in trials on similar soils to those used in this glasshouse study (Anton Wasson and Emmanuel Delhaize, pers. comm.).

Since both lines have similar genetic backgrounds (Han et al. 2016; Pooniya et al. 2019), the greater grain yields of Jandaroi–*TaMATE1B* than Jandaroi–null under well-watered and terminal drought conditions in the glasshouse can be attributed to enhanced Al^{3+} tolerance conferred by *TaMATE1B*. The *TaMATE1B* gene confers Al^{3+} tolerance through citrate efflux (Sasaki et al. 2004; Delhaize et al. 2012b; Tovkach et al. 2013), detoxifying Al^{3+}outside the root tips enabling their growth (Zheng 2010; Brunner and Sperisen 2013). Nutrient uptake, particularly nitrogen (N) and phosphorous (P) was not measured in this study. The deeper root system of Jandaroi–*TaMATE1B* likely captured more N and P than Jandaroi–null to improve grain yield. Under well-watered condition, the improved grain yield in Jandaroi–*TaMATE1B* resulted from an increase in grain number, grain number per spike and HI due to its higher leaf area at the onset of awn emergence (Z_{51}) and total biomass at final harvest (Whan et al. 1991; Turner and

Nicolas 1998; Botwright et al. 2002). In wheat, leaf area and total biomass positively correlated with root length and root biomass (Watt et al. 2005; Palta et al. 2011; Pang et al. 2014). Under terminal drought conditions, the improved grain yield in Jandaroi–*TaMATE1B* mainly resulted from a smaller reduction in 1000-grain weight because the root system grew deeper into the soil profile of the Al^{3+}-rich acidic soil than Jandaroi–null, gaining access to additional available soil water, and offering more favorable conditions for grain filling. Jandaroi–*TaMATE1B* had a significantly higher root: shoot ratio than Jandaroi–null under well-watered conditions ($P \leq 0.05$; Fig. 8d). In another study, increased root to shoot biomass ratio during vegetative growth improved resistance of durum wheat to Cd stress and enhanced Cd accumulation (Arduini et al. 2014).

The delayed phenological development of Jandaroi–*TaMATE1B* under well-watered and terminal drought conditions was unexpected as the lines would share over 90 % of their genetic makeup from three backcrosses (Han et al. 2016; Pooniya et al. 2019). The phenological differences might have resulted from the restricted vertical root growth below the 0.4 m soil layer in Jandaroi–null. Differences in the time to anthesis and physiological maturity are more likely to be associated with differences in root system growth as delayed anthesis is associated with large root systems (Siddique et al. 1990; Aziz et al. 2016; Figueroa-Bustos et al. 2018). Indeed, the unrestricted vertical root growth and proliferation in Jandaroi–*TaMATE1B* in the Al^{3+} rich acidic soil resulted in longer roots and more root biomass than Jandaroi–null at the onset of awn emergence (Z_{51}), when terminal drought was induced. A deeper root system is important for improving drought resistance (Palta and Turner 2019) and adapting to soil Al^{3+} toxicity (Sponchiado et al. 1989), particularly in environments where terminal drought exacerbates the effects of soil Al^{3+} toxicity on wheat.

Conclusions

Unrestricted growth and proliferation of the root system in an introgressed durum wheat line Jandaroi–*TaMATE1B* grown in an Al^{3+} rich acidic subsoil improved tolerance to subsoil Al^{3+}, and improved drought resistance when terminal drought was induced at the onset of awn emergence (Z_{51}). The ability of Jandaroi–*TaMATE1B* to grow and proliferate roots below 0.4 m in an Al^{3+}-rich acidic subsoil enabled the capture and use of available water in deep soil. The better access to deep water by Jandaroi–*TaMATE1B*, particularly post-anthesis, resulted in more grain yield and water use efficiency than Jandaroi–null.

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Declarations

Conflict of interest The authors declare that there is no conflict of interest.

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