Anatolian Journal of Botany
5(1):65-77 (2021)
Research article *doi:10.30616/ajb.907233*

Root-based characterization of intergeneric hybrids with *Triticum* and *Aegilops* species in early vegetative and stem elongation growth stages

Hayati AKMAN
Selçuk University, Sarayönü Vacational School, Department of Plant and Animal Production, Konya, Turkey
hayatiakman@selcuk.edu.tr

Received : 31.03.2021
Accepted : 27.04.2021
Online : 12.05.2021

Erken vejetatif ve sapa kalkma gelişme dönemlerinde *Triticum* ve *Aegilops* türleriyle intergenerik hibritlerin kök bazlı karakterizayonu

Abstract: Cultivated and wild species of wheat are valuable breeding resources used for the development of new cultivars with superior root traits suited to drought and non-stressed conditions. The present study aimed to determine genotypes with superior root traits and phenotypic variability among intergeneric hybrids with *Triticum* and *Aegilops* species in the early vegetative (Z11) and stem elongation (Z31) growth stages. Results indicated that phenotypic variability in rooting depth was 3.2- and 3.4 fold among the genotypes in Z11 and Z31, and it was as great as 20- and 23.8 fold for root biomass, respectively. Hierarchical clustering among 35 genotypes for root traits in both growth stages identified four major clusters, grouping the six deep-rooted genotypes in cluster 2 and three genotypes with high root biomass in cluster 1. In both growth stages, significant associations were found among the root traits. Also, the relationship was stronger between the root and shoot biomass in Z11 (r^2=0.83) than in Z31 (r^2=0.44). As an overall assessment, the suggested genotypes with superior root characteristics such as deep roots and/or high root biomass sustained in both growth stages might be used for the development of new cultivars.

Key words: Intergeneric hybrids, phenotypic variability, root traits, *Triticum* species, wheat wild relatives

Özet: Buğdayın kültüre alınmış ve yabani türleri, kurak ve stres içermeyen şartlara uygun üstün kök özelliklerine sahip yeni çeşitlerin geliştirilmesi için kullanılabilecek değerli ıslah materyalleridir. Bu çalışma, erken vejetatif (Z11) ve sapa kalkma (Z31) gelişme dönemlerinde *Triticum* ve *Aegilops* türleriyle birlikte intergenerik hibritler arasındaki fenotipik farklılığı ve üstün kök özelliklerine sahip genotipleri belirlemeyi amaçlamaktadır. Araştırma sonuçları, genotipler arasında kök derinliği bakımından Z11 ve Z31 gelişme dönemlerinde sırasıyla 3.2 ve 3.4 kat, kök biyoması bakımından ise 20 ve 23.8 kat önemli bir fenotipik farklılığın olduğunu göstermiştir. Hiyerarşik kümelemede her iki gelişme döneminde kök özellikleri değerlendirildiğinde 35 genotip dört farklı gruba ayrılmıştır, gurup 1'de yüksek kök biyomasına sahip 3 genotip ve grup 2'de ise derin köklü altı genotip yer almıştır. Her iki gelişme döneminde de kök özellikleri arasında önemli ilişkiler tespit edilmiştir. Bununla birlikte, Z11'de (r^2=0.83) kök ve sürgün biyoması arasındaki ilişki, Z31'den (r^2=0.44) daha güçlü bulunmuştur. Genel bir değerlendirme olarak her iki gelişme döneminde de derin köklere ve/veya yüksek kök biyoması gibi üstün kök özelliklerine sahip genotipler yeni çeşitlerin geliştirilmesinde kullanılabilir.

Anahtar Kelimeler: İntergenerik hibritler, fenotipik çeşitlilik, kök özellikleri, *Triticum* türleri, yabani buğday akrabaları

Citation: Akman H (2021). Root-based characterization of intergeneric hybrids with Triticum and Aegilops species in early vegetative and stem elongation growth stages. Anatolian Journal of Botany 5(1): 65-77.

1. Introduction

Wheat is a staple crop of historical economic importance that is widely grown worldwide. It was first domesticated 10-12 thousand years ago in the Fertile Crescent, an area including Southeastern Turkey (Maron, 2019). With evolution over 300 thousand years, wild tetraploid wheat, *Triticum dicoccoides*, was derived from *T. urartu* (genome A) and most likely from *Aegilops speltoides* (genome B) (Dvorak and Akhunov, 2005; Nevo, 2011). Cultivated hulled emmer wheat was created by plant selection of wild emmer and then evolved into the free-threshing ears of *T. turgidum*, *T. polonicum*, *T. turanicum*, and *T. carthlicum* by natural mutation (Peng et al., 2011). Another wild diploid wheat used in this study, *T. boeoticum*, has been described as the wild progenitor of *T. monococcum* (Özkan et al., 2010). The D genome donor of the hexaploid wheat species *T. aestivum* and *T. spelta* has been regarded as *Ae. tauschii*. The oldest cultivated and hulled wheat genotypes, spelt wheat (*T. spelta*), einkorn wheat (*T. monococcum*), emmer wheat (*T. dicoccum*), and Vavilov wheat (*T. vavilovii*), are found among the wild and modern wheats (Adu et al., 2011). Different cultivated and wild species of wheat, landraces, and wheat hybrids offer biotic and abiotic stress tolerance, high biochemical contents, and quality in the improvement of new cultivars (Mathre et al., 1985; Arzani and Ashraf, 2017; Li et al., 2018; Ullah et al., 2018; Kishii, 2019).

Little is known about the root systems of wheat genetic resources, and root studies have not traditionally been a common objective of breeding programs (Friedli et al., 2019). Recently, however, the importance of root studies has been well understood. Selection of genotypes with superior roots through phenotyping of root traits may contribute to the improvement of promising cultivars with desirable root traits. Breeders have recently given priority to the improvement of higher adaptation capability and climate-resilient cultivars to avoid yield losses (Banga and Kang, 2014). For this purpose, cultivars with deep root systems may explore deep soil profile under water deficit, while a dense root system may improve nutrient uptake and support higher yield and above-ground biomass (Manschadi et al., 2006; Sayar et al., 2007; Prasad et al., 2008; Bengough et al., 2011; Heřmanská et al., 2015).

Considering the evaluation of root traits towards the use of genetic resources in breeding programs, the present study aimed to i) determine phenotypic variability for root and shoot features and their relationships, and ii) selection of genotypes with superior root traits for the rain-fed and irrigated conditions in a set of *Triticum* and *Aegilops* species together with their hybrids in early vegetative and stem elongation growth stages.

2. Materials and Method

This study was conducted to characterize root and shoot parameters and their relationships in early vegetative growth stage (Z11 on the Zadoks scale of cereal growth) for two weeks after germination in controlled conditions in first experiment and at stem elongation growth stage (Z31) during the nodal root growth stage in second experiment in a glasshouse.

Table 1. Taxa, accession number, country of origin, local/GRIN and common names of the studied material.

Taxa	Accession No.	PL	Local name or GRIN name	Common name/origin
		Triticum taxa and intergeneric hybrids		
Agrotriticum ssp.	PI 550715	8×	Agrotana	*Agropyron* × *Triticum,* USA
Elytritilops ssp.	PI 605347	-	Sando Selection 538	*Elymus* × *Triticum* x *Aegilops,* USA
T. aestivum L. ssp. *aestivum*	-	6×	5924[a]	Common wheat, line, Australia
T. aestivum L. ssp. *aestivum*	-	6×	Ahmetağa[b]	Common wheat, cultivar, Konya, Turkey
T. aestivum L. ssp. *aestivum*	-	6×	Ak 702[c]	Common wheat, old cultivar, Eskişehir, Turkey
T. aestivum L. ssp. *aestivum*	PI 660669	6×	Daws High PPO	Common wheat/NIL, USA
T. aestivum L. ssp. *aestivum*	-	6×	Tir [d]	Common wheat, landrace, Van, Turkey
T. aestivum L. ssp. *compactum* (Host) Mac Key	PI 159101	6×	Spitskop	South Africa
T. aestivum L. ssp. *spelta* (L.) Thell.	PI 295064	6×	Weisser Granenspeltz	Spelt wheat, Bulgaria
T. aestivum L. ssp. *sphaerococcum* (Percival) Mac Key	PI 277142	6×	Acarp	India
T. boeoticum Boiss.	PI 352270	2×	Baydaricum	Wild einkorn, Germany
T. ispahanicum Heslot	PI 330548	4×	184	England
T. monococcum L. ssp. *monococcum*	PI 192063	2×	Escanha Menor	Einkorn, Portugal
T. petropavlovskyi Udacz. et Migusch.	PI 585015	6×	Maik	*T. aestivum* × *T. polonicum,* China
T. soveticum ssp. *fungicidum* (Zhuk.)	PI 251015	8×	-	*T. carthlicum* × *T. timopheevii,* Russia
T. timopheevii (Zhuk.) Zhuk. ssp. *armeniacum* (Jakubz.) Slageren	PI 538522	4×	G3217	Wild form of *T. timopheevii*, Iraq
T. turgidum L. ssp. *carthlicum* (Nevski) Á. Löve & D. Löve	PI 70738	4×	22	Persian Wheat, Iraq
T. turgidum L. ssp. *dicoccoides* (Körn. ex Asch. & Graebn.) Thell.	PI 346783	4×	Nakhichevan	Wild wheat, Hungary
T. turgidum L. ssp. *dicoccum* (Schrank ex Schübl.) Thell.	-	4×	Kavılca[d]	Emmer, Kars, Turkey
T. turgidum L. ssp. *durum* (Desf.) van Slageren	-	4×	Altın 40/98[e]	Durum wheat, cultivar, Ankara, Turkey
T. turgidum L. ssp. *durum* (Desf.) van Slageren	-	4×	Berkmen 469[e]	Durum wheat, cultivar, Ankara, Turkey
T. turgidum L. ssp. *durum* (Desf.) van Slageren	-	4×	Gır[a]	Durum wheat, landrace, Turkey
T. turgidum L. ssp. *durum* (Desf.) van Slageren	-	4×	Meram 2002[b]	Durum wheat, cultivar, Konya, Turkey
T. turgidum L. ssp. *durum* (Desf.) van Slageren	-	4×	Yılmaz 98[e]	Durum wheat, cultivar, Ankara, Turkey
T. turgidum L. ssp. *polonicum* (L.) Thell.	PI 185309	4×	Polonicum	Polish wheat, Argentina
T. turgidum L. ssp. *turanicum* (Jakubz.) Á. Löve & D. Löve	PI 68293	4×	351	Khorasan wheat, Azerbaijan
T. turgidum L. ssp. *turgidum*	PI 134953	4×	Lusitanicum	Portugal
T. urartu Tumanian ex Gandilyan	PI 662281	2×	IG 117911	Wild einkorn, Syria
T. vavilovii Jakubz.	PI 428342	6×	-	Vavilov’s wheat, Sweeden
		Aegilops taxa		
Ae. biuncialis Vis.	Clae 67	4×	2215a	Turkey
Ae. caudata L.	PI 277000	2×	M10	Unknown
Ae. columnaris Zhuk.	Clea 34	4×	No. 1	Unknown
Ae. comosa Sm.	PI 542174	2×	84TK154-018	Turkey
Ae. crassa Boiss.	PI 219863	-	72	Iraq, Arbil
Ae. geniculata Roth	Clae 65	4×	Sando 253	Unknown
Ae. juvenalis (Thell.) Eig	PI 276693	6×	19	Unknown
Ae. kotschyii Boiss.	Clae 36	4×	No. 4	Unknown
Ae. neglecta Req. ex Bertol.	PI 170198	4×	2640	Turkey
Ae. peregrina (Hack.) Maire & Weiller var. *brachyathera* (Boiss.) Maire & Weiller	PI 542236	4×	84TK075-030	Turkey
Ae. speltodies Tausch var. *speltoides*	PI 542259	2×	84TK109-078	Turkey
Ae. tauschii Coss.	Clae 1	2×	2001	Pakistan

USDA, ARS, National Genetic Resources Program. Germplasm Resources Information Network (GRIN). (Online Database] National Germplasm Resources Laboratory, Beltsville, Maryland, USA. Available: http.//www.ars-grin.gov. Note: Accessions with PI and Clae numbers were supplied from the USDA ARS. PL indicates ploidy level of the studied material.

[a] Department of Field Crops, Selçuk University, [b] Bahri Dağdaş International Agricultural Research Institute, [c]Transitional Zone Agricultural Research Institute, [d] Local farmer, [e] Field Crops Central Research Institute

Germplasm samples of 10 *Triticum* species or 19 taxa and 12 *Aegilops* species with 2 intergeneric hybrids were selected to represent a wide range of diversity in the two separate experiments (Table 1). Genotypes of non-Turkish and Turkish origin were obtained from the US Department of Agriculture's National Plant Germplasm System (https://www.ars-grin.gov). Also, materials of Turkish origin, including landrace, old, and modern cultivars were supplied from institutes and local farmers in different regions of the country (Table 1).

2.1. Controlled condition experiment

The first experiment was carried out under controlled conditions to evaluate coleoptile length with root and shoot traits. Three seeds of each genotype as three replications were placed in the middle of a wet germination towel 5 cm apart. The samples were rolled loosely and secured with a rubber band. They were then placed vertically in plastic bags in a dark room at 15-16 °C for 15 days. The room humidity was between 50-60%. Coleoptile length was determined with a ruler as the distance from the scutellum to the tip of the coleoptile. The seminal root depth was measured, and the number of seminal roots was manually counted. Root and shoot biomasses were recorded after dehydrated thoroughly with an absorbent towel. Root proportion of total biomass and root biomass-to-shoot biomass ratio were calculated as root-to-total biomass ratio and root-to-shoot ratio, respectively.

2.2. Glasshouse experiment

The second experiment was conducted under glasshouse conditions from April 11 to May 18. Seeds were sown into long columns (100 cm in depth and 12 cm in diameter), which were filled with field soil. The climate of the glasshouse was measured with a data logger (T & D Corporation/TR-74Ui) recording data in five-minute intervals. The glasshouse temperature in April and May was 22.2 °C day / 10 °C night and 24.0 °C day / 13.4 °C night, respectively. The mean relative humidity in April and May was respectively approximately 39.7% day / 73.4% night and 37.8% day / 66.5% night with photosynthetic photon flux densities of 249.9 µmol m^{-2} s^{-1} and 216.7 µmol m^{-2} s^{-1} during the day. The soil used in the experiment, taken from the field (0-40 cm), was clay-loam with low organic matter (1.7%) and a high level of $CaCO_3$ (23.7%) and Ca (5491 mg/kg). EC was 0.6 mmhos/cm. Soil pH was 7.7 and no salinity problems were observed. Levels of P_2O_5 (4.58 mg/kg), Zn (0.67 mg/kg), and Mn (8.13 mg/kg) were low, while K_2O (1265 kg/ha), Mg (464.4 mg/kg), Fe (5.1 mg/kg), and Cu (3.1 mg/kg) were found to be adequate.

All measurements were conducted for a single plant grown individually in a column (Fig. 1). Leaf chlorophyll content was measured with a Minolta SPAD-502. As morphological characteristics shoot height was measured and number of tillers was counted. Washed and cleaned roots were measured for the longest rooting depth. The number of nodal roots was counted manually. Root and shoot biomasses were recorded after drying at 80 °C for three days.

Figure 1. *Triticum* and *Aegilops* species with hybrids grown in 100 cm columns (12 cm in diameter) under glasshouse conditions.

2.3. Statistical analysis

The experiments were arranged in a completely randomized design with three replications. Analysis of variance was performed with the MSTAT-C statistical package and significant differences between means were tested by the Least Significant Difference (LSD) test. Regression analysis was performed in a Microsoft Excel (Excel version in Microsoft Office 2016 for Windows) for significantly correlated traits. The root morphological data (root biomass, rooting depth, root-to-shoot ratio, root-to total biomass ratio, numbers of seminal and nodal roots) for both growth stages were converted to text format and imported to DARwin 6 software (Perrier and Jacquemoud-Collet, 2006). The groups were determined by hierarchical clustering for root data. A dendrogram was constructed using the Euclidean distance and unweighted pair group linkage methods (UPGMA).

3. Results

Significant differences were found among the genotypes in terms of investigated traits and their relationships in two experiments (Tables 2 and 3).

3.1. Phenotypic variability in root system

Results indicated significant variations among the genotypes in terms of rooting depth, root biomass, root-to-shoot ratio, root-to-total biomass ratio, and numbers of seminal and nodal roots in the early vegetative and at stem elongation growth stages ($P<0.01$; Tables 2 and 3).

The lowest and highest rooting depths among *Aegilops* species were obtained from *Ae. caudata* (6.6 cm) and *Ae. geniculata* (13 cm) in the early growth stage (Z11) and from *Ae. crassa* (35.7 cm) and *Ae. neglecta* (88.3) in the stem elongation stage (Z31). Shallow- and deep-rooted genotypes among the wheat species and wheat hybrids were respectively observed in *T. urartu* (9 cm) and *T. turanicum* (21.2 cm) in Z11 and in *T. urartu* (34.8 cm) and *T. aestivum* 'Ak 702' (116.7 cm) in Z31. The rooting depth

Table 2. Shoot height (SH), coleoptile length (CL) shoot biomass (SB), number of seminal roots (SRN), rooting depth (RD), root biomass (RB), root-to-shoot ratio (R/S), and root-to-total biomass ratio (R/TB) of *Triticum* species, *Aegilops* species and hybrids in the Z11 growth stage.

Taxa	SH (cm)	CL (cm)	SB (g)	SRN plant^{-1}	RD (cm)	RB (g)	R/S plant^{-1}	R/TB (%)
Ae. biuncialis	$15.3^{\text{e-l}}$	$5.5^{\text{k-n}}$	$0.13^{\text{k-o}}$	$2.5^{\text{j–n}}$	8.3^{lm}	0.02^{kl}	0.16^{ij}	14.0^{mn}
Ae. brachyathera	$17.3^{\text{b-g}}$	$6.6^{\text{g-k}}$	0.06^{opq}	$2.7^{\text{i-m}}$	10.8^{kl}	0.03^{jkl}	$0.46^{\text{a-f}}$	$31.4^{\text{a-g}}$
Ae. caudata	$10.3^{\text{n-q}}$	4.6^{nop}	$0.14^{\text{k-n}}$	$2.4^{\text{k-n}}$	6.6^{m}	0.03^{jkl}	$0.26^{\text{f-j}}$	$20.6^{\text{i-n}}$
Ae. columnaris	$13.1^{\text{h-o}}$	$5.2^{\text{l-o}}$	$0.08^{\text{m-q}}$	$2.9^{\text{h-l}}$	9.7^{l}	0.02^{kl}	$0.26^{\text{f-j}}$	$20.6^{\text{i-n}}$
Ae. comosa	$11.6^{\text{l-p}}$	$5.5^{\text{k-n}}$	0.05^{pq}	2.2^{mn}	9.2^{lm}	0.01^{l}	$0.33^{\text{c-j}}$	$24.5^{\text{d-l}}$
Ae. geniculata	$16.7^{\text{c-i}}$	$6.3^{\text{h-l}}$	$0.07^{\text{n-q}}$	$3.0^{\text{h-k}}$	13.0^{jk}	0.02^{kl}	$0.25^{\text{g-j}}$	$20.1^{\text{i-n}}$
Ae. juvenalis	$14.7^{\text{f-m}}$	$6.0^{\text{i-m}}$	$0.07^{\text{n-q}}$	$2.7^{\text{i-m}}$	11.3^{kl}	0.02^{kl}	$0.24^{\text{g-j}}$	$19.2^{\text{j-n}}$
Ae. kotschyi	$13.9^{\text{g-n}}$	$5.6^{\text{j-n}}$	$0.20^{\text{f-k}}$	2.3^{lmn}	10.8^{kl}	$0.05^{\text{h-k}}$	$0.28^{\text{d-j}}$	$21.7^{\text{h-m}}$
Ae. neglecta	6.9^{q}	3.2^{qr}	0.05^{pq}	1.9^{n}	8.8^{lm}	0.01^{l}	0.21^{hij}	17.2^{lmn}
Ae. tauschii	$12.7^{\text{i-p}}$	$6.8^{\text{f-j}}$	0.06^{opq}	$3.0^{\text{h-k}}$	10.7^{kl}	0.01^{l}	0.14^{j}	11.8^{n}
'Agrotriticum'	8.8^{pq}	3.7^{pqr}	0.05^{pq}	2.3^{lmn}	$16.5^{\text{b-h}}$	0.03^{jkl}	0.54^{ab}	$34.1^{\text{a-d}}$
'Elytritilops'	$17.3^{\text{b-g}}$	8.3^{bcd}	0.27^{def}	$3.0^{\text{h-k}}$	$14.7^{\text{g-j}}$	0.10^{def}	$0.37^{\text{b-h}}$	$26.9^{\text{b-k}}$
T. aestivum '5924'	$11.3^{\text{l-p}}$	$5.2^{\text{l-o}}$	0.28^{cde}	$3.5^{\text{e-h}}$	$18.2^{\text{a-d}}$	$0.07^{\text{f-i}}$	$0.30^{\text{d-j}}$	$22.5^{\text{f-m}}$
T. aestivum 'Ahmetağa'	$10.8^{\text{m-q}}$	$4.4^{\text{n-q}}$	$0.26^{\text{d-g}}$	$3.0^{\text{h-k}}$	$18.2^{\text{a-d}}$	0.12^{de}	$0.48^{\text{a-d}}$	$32.1^{\text{a-f}}$
T. aestivum 'Ak 702'	$17.0^{\text{b-h}}$	$5.3^{\text{l-o}}$	0.36^{ab}	$2.9^{\text{h-l}}$	$15.8^{\text{c-j}}$	0.18^{ab}	0.52^{abc}	$33.5^{\text{a-d}}$
T. aestivum 'Daws High PPO'	9.7^{opq}	3.1^{r}	0.32^{bcd}	$3.0^{\text{h-k}}$	$14.9^{\text{f-j}}$	0.19^{ab}	0.64^{a}	37.7^{a}
T. aestivum 'Tir'	$19.3^{\text{a-e}}$	9.3^{b}	$0.23^{\text{e-i}}$	4.7^{ab}	18.6^{abc}	0.10^{def}	$0.42^{\text{b-g}}$	$29.2^{\text{a-I}}$
T. armeniacum	$16.7^{\text{c-i}}$	$7.0^{\text{e-i}}$	$0.12^{\text{l-p}}$	$3.0^{\text{h-k}}$	$13.5^{\text{h-k}}$	$0.04^{\text{i-l}}$	$0.31^{\text{d-j}}$	$23.3^{\text{e-m}}$
T. boeoticum	$11.3^{\text{l-p}}$	3.8^{pqr}	0.06^{opq}	$3.0^{\text{h-k}}$	10.9^{kl}	0.03^{jkl}	$0.40^{\text{b-h}}$	$28.4^{\text{a-k}}$
T. carthlicum	$14.3^{\text{f-n}}$	$7.0^{\text{e-i}}$	$0.19^{\text{g-l}}$	4.0^{cde}	19.5^{ab}	0.08^{fgh}	$0.42^{\text{b-g}}$	$29.5^{\text{a-i}}$
T. compactum	$19.6^{\text{a-d}}$	$7.1^{\text{d-i}}$	$0.14^{\text{k-n}}$	3.8^{def}	$16.4^{\text{c-h}}$	$0.07^{\text{f-i}}$	$0.48^{\text{a-d}}$	$32.2^{\text{a-e}}$
T. dicoccoides	$16.3^{\text{d-i}}$	$8.0^{\text{c-f}}$	$0.09^{\text{m-q}}$	$3.0^{\text{h-k}}$	$15.2^{\text{d-j}}$	0.03^{jkl}	$0.30^{\text{d-j}}$	$23.3^{\text{e-m}}$
T. dicoccum	20.5^{abc}	$6.6^{\text{g-k}}$	$0.13^{\text{k-o}}$	4.5^{abc}	$17.9^{\text{b-f}}$	$0.06^{\text{g-j}}$	$0.47^{\text{a-e}}$	$31.8^{\text{a-g}}$
T. durum 'Altın 40/98'	$11.7^{\text{k-p}}$	$4.8^{\text{m-p}}$	$0.18^{\text{h-l}}$	5.0^{a}	$18.0^{\text{b-e}}$	$0.05^{\text{h-k}}$	$0.26^{\text{f-j}}$	$20.8^{\text{i-n}}$
T. durum 'Berkmen 469'	$15.9^{\text{d-j}}$	$6.6^{\text{g-k}}$	0.42^{a}	$3.0^{\text{h-k}}$	$16.4^{\text{c-h}}$	0.16^{bc}	$0.38^{\text{b-h}}$	$27.3^{\text{b-k}}$
T. durum 'Gır'	$15.3^{\text{e-l}}$	$7.2^{\text{d-i}}$	$0.22^{\text{e-j}}$	$3.5^{\text{e-h}}$	18.8^{abc}	$0.05^{\text{h-k}}$	$0.23^{\text{g-j}}$	$18.8^{\text{k-n}}$
T. durum 'Meram 2002'	$12.8^{\text{i-p}}$	$4.8^{\text{m-p}}$	0.35^{abc}	$3.2^{\text{f-i}}$	$16.3^{\text{c-i}}$	0.13^{cd}	$0.36^{\text{b-i}}$	$26.4^{\text{b-l}}$
T. durum 'Yılmaz 98'	$11.3^{\text{l-p}}$	$4.1^{\text{o-r}}$	0.39^{ab}	4.2^{bcd}	$15.3^{\text{d-j}}$	0.20^{a}	0.52^{abc}	34.3^{abc}
T. fungicidum	20.7^{abc}	9.0^{bc}	$0.24^{\text{e-i}}$	4.7^{ab}	$15.0^{\text{e-j}}$	$0.07^{\text{f-i}}$	$0.29^{\text{d-j}}$	$22.3^{\text{g-m}}$
T. ispahanicum	21.7^{a}	11.3^{a}	$0.17^{\text{i-l}}$	5.0^{a}	$15.3^{\text{d-j}}$	0.08^{fgh}	$0.46^{\text{a-f}}$	$31.3^{\text{a-h}}$
T. monococum	$12.0^{\text{j-p}}$	4.7^{nop}	$0.07^{\text{n-q}}$	$3.0^{\text{h-k}}$	13.3^{ijk}	$0.04^{\text{i-l}}$	0.55^{ab}	35.0^{ab}
T. petropavlovskyi	$19.7^{\text{a-d}}$	$7.4^{\text{d-h}}$	$0.25^{\text{d-h}}$	$3.1^{\text{g-j}}$	$17.9^{\text{b-f}}$	0.08^{fgl}	$0.33^{\text{c-j}}$	$25.1^{\text{c-l}}$
T. polonicum	$16.3^{\text{d-i}}$	$7.5^{\text{d-h}}$	$0.14^{\text{k-n}}$	$3.0^{\text{h-k}}$	$13.7^{\text{h-k}}$	$0.06^{\text{g-j}}$	$0.41^{\text{b-h}}$	$28.7^{\text{a-j}}$
T. spelta	$15.8^{\text{d-k}}$	$5.6^{\text{j-m}}$	$0.09^{\text{m-q}}$	$2.7^{\text{i-m}}$	12.9^{jk}	0.03^{jkl}	$0.39^{\text{b-h}}$	$28.0^{\text{b-k}}$
T. sphaerococcum	$16.0^{\text{d-j}}$	$6.1^{\text{l-k}}$	$0.15^{\text{j-m}}$	$3.0^{\text{h-k}}$	$15.0^{\text{e-j}}$	$0.06^{\text{g-j}}$	$0.41^{\text{b-h}}$	$28.8^{\text{a-j}}$
T. turanicum	21.0^{ab}	$8.2^{\text{c-e}}$	$0.24^{\text{e-i}}$	$3.0^{\text{h-k}}$	21.2^{a}	0.09^{efg}	$0.35^{\text{b-i}}$	$25.9^{\text{b-l}}$
T. turgidum	$19.0^{\text{a-e}}$	$7.5^{\text{d-h}}$	$0.19^{\text{g-l}}$	4.0^{cde}	$17.8^{\text{b-f}}$	0.08^{fgl}	$0.40^{\text{b-h}}$	$28.4^{\text{a-k}}$
T. urartu	$11.7^{\text{k-p}}$	$5.2^{\text{l-o}}$	0.04^{q}	$3.0^{\text{h-k}}$	9.0^{lm}	0.01^{l}	$0.27^{\text{e-j}}$	$21.4^{\text{i-n}}$
T. vavilovii	$18.3^{\text{a-f}}$	$7.7^{\text{d-g}}$	$0.25^{\text{d-h}}$	$3.7^{\text{d-g}}$	$17.7^{\text{b-g}}$	$0.07^{\text{f-i}}$	$0.30^{\text{d-j}}$	$23.1^{\text{e-m}}$
Mean	15.0	6.2	0.17	3.2	14.4	0.07	0.36	25.9
LSD (0.01)	4.19	1.27	0.075	0.69	3.1	0.034	0.21	9.64
CV (%)	13.0	9.5	19.9	9.8	9.8	23.7	26.4	17.3

in the great majority of genotypes was 12.8-18.9 cm in Z11, while in Z31 the rooting depth of genotypes was almost equally distributed across a range of 34.8-116.7 cm (Fig. 3). In Z11 and Z31, the phenotypic variability in rooting depth was 3.2- fold and 3.4-fold, respectively.

According to the mean values, the rooting depth of *Aegilops* species was shallower than that of *Triticum* species and the hybrids in both Z11 and Z31 (Fig. 4). Furthermore, rooting depth was linked with number of seminal roots, number of nodal roots, and root biomass in both Z11 and Z31 (Fig. 5).

High variation of root biomass was observed as a 20-fold difference in a range between 0.01 g and 0.20 g in Z11 and a 23.8-fold difference ranging between 0.11 g and 2.62 g in Z31 among the genotypes (Tables 2 and 3). Most of the genotypes possessed values between 0.01 g and 0.11 g in Z11 and 0.1 g and 1.5 g in Z31 (Fig. 3). The mean root biomasses of *Triticum* species and hybrids were higher in Z11 (4-fold) and Z31 (3.1-fold) than that of the *Aegilops* species (Fig. 4). In Z11, D genome progenitor *Ae. tauschii* (0.01 g), *Ae. comosa* (0.01 g), and *Ae. neglecta* (0.01 g) had the lowest root biomass and *Ae. kotschyi* (0.05 g) had the highest value among the *Aegilops* species. *T. durum* 'Yılmaz 98' (0.20 g) and *T. urartu* (0.01 g) showed the highest and lowest values, respectively, among the *Triticum* species and hybrids. The lowest and highest root biomass values in Z31 were obtained from *Ae. crassa* (0.15 g) and a wheat ancestor, *Ae. speltoides* (0.77 g), among the *Aegilops* species and from *T. boeoticum* (0.11 g) and *T. dicoccum* (2.62 g) among the *Triticum* species and hybrids (Tables 2 and 3).

Significant variation was observed in the seminal root number of genotypes, ranging from 1.9 to 5 in Z11, and in number of nodal roots, ranging from 4 to 21 in Z31

Table 3. SPAD chlorophyll (CHL), number of tillers (TN), shoot height, (SH), shoot biomass (SB), number of nodal roots (NRN), rooting depth (RD), root biomass (RB), root-to-shoot ratio (R/S), and root-to-total biomass ratio (R/TB) of *Triticum* species, *Aegilops* species and wheat hybrids in the Z31 growth stage.

Taxa	CHL (μmol m^{-2})	TN plant^{-1}	SH (cm)	SB (g)	NRN plant^{-1}	RD (cm)	RB (g)	R/S plant^{-1}	R/TB (%)
Ae. biuncialis	43.0$^{\text{e-i}}$	7.3$^{\text{cd}}$	21.3$^{\text{nop}}$	0.48$^{\text{q-r}}$	9.3$^{\text{c-h}}$	68.8$^{\text{h-m}}$	0.52$^{\text{j-m}}$	1.08$^{\text{d-k}}$	51.9$^{\text{g-l}}$
Ae. brachyathera	43.3$^{\text{e-i}}$	6.0$^{\text{cde}}$	24.0$^{\text{m-p}}$	0.28$^{\text{qr}}$	6.7$^{\text{h-k}}$	76.2$^{\text{g-k}}$	0.42$^{\text{j-n}}$	1.53$^{\text{d-g}}$	60.1$^{\text{cd}}$
Ae. caudata	37.7$^{\text{i}}$	12.0$^{\text{b}}$	21.7$^{\text{nop}}$	0.61$^{\text{nop}}$	8.0$^{\text{f-j}}$	46.3$^{\text{n-q}}$	0.51$^{\text{j-m}}$	0.88$^{\text{g-p}}$	46.1$^{\text{m-p}}$
Ae. comosa	49.9$^{\text{b-g}}$	8.3$^{\text{c}}$	22.3$^{\text{nop}}$	0.42$^{\text{q-r}}$	8.0$^{\text{f-j}}$	57.7$^{\text{j-p}}$	0.31$^{\text{lmn}}$	0.75$^{\text{j-q}}$	42.1$^{\text{pq}}$
Ae. crassa	41.0$^{\text{hi}}$	8.0$^{\text{c}}$	21.7$^{\text{nop}}$	0.86$^{\text{i-n}}$	7.0$^{\text{h-k}}$	35.7$^{\text{pq}}$	0.15$^{\text{lmn}}$	0.18$^{\text{q}}$	15.4$^{\text{t}}$
Ae. geniculata	53.5$^{\text{bcd}}$	11.0$^{\text{b}}$	18.3$^{\text{p}}$	0.46$^{\text{q-r}}$	12.0$^{\text{bcd}}$	51.3$^{\text{l-q}}$	0.53$^{\text{jkl}}$	1.18$^{\text{d-l}}$	53.1$^{\text{g-k}}$
Ae. juvenalis	-	14.7$^{\text{a}}$	21.0$^{\text{nop}}$	0.66$^{\text{mno}}$	5.3$^{\text{ijk}}$	68.0$^{\text{h-n}}$	0.16$^{\text{lmn}}$	0.25$^{\text{pq}}$	19.4$^{\text{t}}$
Ae. kotschyii	41.2$^{\text{ghi}}$	7.0$^{\text{cd}}$	19.7$^{\text{op}}$	0.34$^{\text{a}}$	9.0$^{\text{d-h}}$	71.0$^{\text{h-l}}$	0.37$^{\text{k-n}}$	1.11$^{\text{d-k}}$	52.5$^{\text{g-l}}$
Ae. neglecta	48.7$^{\text{b-h}}$	13.0$^{\text{ab}}$	19.0$^{\text{op}}$	0.69$^{\text{l-o}}$	7.3$^{\text{g-k}}$	88.3$^{\text{b-h}}$	0.42$^{\text{j-n}}$	0.63$^{\text{k-q}}$	38.0$^{\text{qr}}$
Ae. speltoides	83.7$^{\text{a}}$	7.0$^{\text{cd}}$	22.0$^{\text{nop}}$	0.46$^{\text{q-r}}$	9.7$^{\text{c-h}}$	60.0$^{\text{i-o}}$	0.77$^{\text{ij}}$	1.69$^{\text{cde}}$	62.6$^{\text{c}}$
Ae. tauschii	40.8$^{\text{hi}}$	4.3$^{\text{efg}}$	26.3$^{\text{k-n}}$	0.34$^{\text{pqr}}$	7.3$^{\text{g-k}}$	85.3$^{\text{d-h}}$	0.21$^{\text{lmn}}$	0.62$^{\text{k-q}}$	38.1$^{\text{qr}}$
'Agrotriticum'	41.6$^{\text{f-i}}$	3.3$^{\text{fg}}$	19.0$^{\text{op}}$	0.20$^{\text{r}}$	4.7$^{\text{jk}}$	38.2$^{\text{opq}}$	0.23$^{\text{lmn}}$	1.16$^{\text{d-l}}$	53.3$^{\text{f-j}}$
'Elytritilops'	44.3$^{\text{e-i}}$	4.3$^{\text{efg}}$	59.0$^{\text{a}}$	1.46$^{\text{cde}}$	9.3$^{\text{c-h}}$	75.7$^{\text{g-k}}$	0.53$^{\text{jkl}}$	0.36$^{\text{n-q}}$	26.6$^{\text{s}}$
T. aestivum '5924'	46.1$^{\text{b-f}}$	2.7$^{\text{g}}$	49.7$^{\text{cd}}$	1.37$^{\text{d-g}}$	9.0$^{\text{d-h}}$	73.7$^{\text{h-k}}$	0.44$^{\text{j-n}}$	0.34$^{\text{opq}}$	24.8$^{\text{s}}$
T. aestivum 'Ahmetağa'	50.8$^{\text{b-e}}$	4.3$^{\text{efg}}$	37.3$^{\text{ij}}$	1.14$^{\text{f-i}}$	12.3$^{\text{bcd}}$	86.0$^{\text{c-h}}$	1.89$^{\text{c}}$	1.66$^{\text{c-f}}$	62.2$^{\text{c}}$
T. aestivum 'Ak 702'	49.3$^{\text{b-h}}$	8.0$^{\text{c}}$	43.3$^{\text{e-h}}$	2.02$^{\text{b}}$	18.7$^{\text{a}}$	116.7$^{\text{a}}$	1.92$^{\text{c}}$	0.96$^{\text{g-o}}$	48.7$^{\text{j-o}}$
T. aestivum 'Daws High PPO'	50.8$^{\text{b-e}}$	7.0$^{\text{cd}}$	24.5$^{\text{l-o}}$	0.56$^{\text{n-q}}$	11.7$^{\text{b-e}}$	73.7$^{\text{h-k}}$	0.73$^{\text{ijk}}$	1.31$^{\text{d-j}}$	56.6$^{\text{d-g}}$
T. aestivum 'Tir'	50.3$^{\text{bc}}$	7.7$^{\text{cd}}$	44.7$^{\text{d-g}}$	1.38$^{\text{d-g}}$	11.7$^{\text{b-e}}$	106.8$^{\text{a-d}}$	1.27$^{\text{fgh}}$	0.93$^{\text{g-o}}$	48.0$^{\text{k-o}}$
T. armeniacum	44.4$^{\text{e-i}}$	5.3$^{\text{def}}$	20.3$^{\text{op}}$	0.54$^{\text{opq}}$	7.0$^{\text{h-k}}$	88.0$^{\text{b-h}}$	1.24$^{\text{fgh}}$	2.32$^{\text{bc}}$	69.3$^{\text{b}}$
T. boeoticum	43.6$^{\text{e-i}}$	6.0$^{\text{cde}}$	21.0$^{\text{nop}}$	0.28$^{\text{qr}}$	4.0$^{\text{k}}$	49.7$^{\text{l-q}}$	0.11$^{\text{n}}$	0.40$^{\text{m-q}}$	28.4$^{\text{s}}$
T. compactum	43.7$^{\text{e-i}}$	3.3$^{\text{fg}}$	40.7$^{\text{f-i}}$	0.70$^{\text{k-o}}$	6.7$^{\text{h-k}}$	100.7$^{\text{a-e}}$	1.02$^{\text{ghi}}$	1.46$^{\text{d-h}}$	59.2$^{\text{cde}}$
T. dicoccoides	44.7$^{\text{e-i}}$	6.0$^{\text{cde}}$	41.0$^{\text{f-i}}$	1.52$^{\text{cd}}$	11.7$^{\text{b-e}}$	108.0$^{\text{abc}}$	1.37$^{\text{d-g}}$	0.93$^{\text{g-o}}$	47.8$^{\text{l-o}}$
T. dicoccum	43.8$^{\text{e-i}}$	8.3$^{\text{c}}$	55.0$^{\text{bc}}$	2.16$^{\text{b}}$	19.0$^{\text{a}}$	109.5$^{\text{ab}}$	2.62$^{\text{a}}$	1.21$^{\text{d-l}}$	54.8$^{\text{e-I}}$
T. durum 'Altın 40/98'	55.8$^{\text{b}}$	8.0$^{\text{c}}$	30.0$^{\text{kl}}$	1.00$^{\text{h-l}}$	9.0$^{\text{d-h}}$	96.3$^{\text{a-g}}$	2.35$^{\text{ab}}$	2.49$^{\text{b}}$	70.0$^{\text{b}}$
T. durum 'Berkmen 469'	50.6$^{\text{b-e}}$	8.3$^{\text{c}}$	38.3$^{\text{hi}}$	1.61$^{\text{cd}}$	10.0$^{\text{c-h}}$	101.7$^{\text{a-e}}$	1.70$^{\text{cde}}$	1.05$^{\text{e-m}}$	51.2$^{\text{h-m}}$
T. durum 'Yılmaz 98'	54.8$^{\text{bcd}}$	7.0$^{\text{cd}}$	29.7$^{\text{klm}}$	0.42$^{\text{o-r}}$	11.0$^{\text{b-f}}$	80.7$^{\text{e-I}}$	1.98$^{\text{bc}}$	4.75$^{\text{a}}$	82.3$^{\text{a}}$
T. fungicidum	40.6$^{\text{hi}}$	2.0$^{\text{g}}$	43.3$^{\text{e-h}}$	0.73$^{\text{j-o}}$	9.0$^{\text{d-h}}$	86.3$^{\text{c-h}}$	1.02$^{\text{ghi}}$	1.43$^{\text{d-i}}$	58.3$^{\text{c-f}}$
T. ispahanicum	44.0$^{\text{e-i}}$	4.0$^{\text{efg}}$	44.7$^{\text{d-g}}$	0.95$^{\text{h-m}}$	6.7$^{\text{h-k}}$	55.3$^{\text{k-q}}$	0.54$^{\text{jkl}}$	0.57$^{\text{l-q}}$	36.4$^{\text{r}}$
T. monococcum	43.6$^{\text{e-i}}$	7.0$^{\text{cd}}$	39.0$^{\text{ghi}}$	1.04$^{\text{hij}}$	14.0$^{\text{b}}$	78.0$^{\text{f-j}}$	1.32$^{\text{e-h}}$	1.25$^{\text{d-k}}$	55.4$^{\text{d-h}}$
T. petropavlovskyi	54.8$^{\text{bc}}$	3.3$^{\text{fg}}$	48.0$^{\text{b}}$	1.46$^{\text{cde}}$	12.7$^{\text{bc}}$	101.3$^{\text{a-e}}$	1.37$^{\text{d-g}}$	0.95$^{\text{g-o}}$	48.0$^{\text{k-o}}$
T. polonicum	49.2$^{\text{b-h}}$	2.0$^{\text{g}}$	65.0$^{\text{a}}$	1.45$^{\text{c-f}}$	12.0$^{\text{bcd}}$	103.8$^{\text{a-d}}$	1.43$^{\text{def}}$	0.99$^{\text{f-o}}$	49.7$^{\text{i-n}}$
T. spelta	42.4$^{\text{e-i}}$	7.0$^{\text{cd}}$	32.0$^{\text{jk}}$	1.13$^{\text{ghi}}$	21.0$^{\text{a}}$	60.8$^{\text{i-n}}$	0.94$^{\text{hi}}$	0.85$^{\text{h-q}}$	45.6$^{\text{nop}}$
T. sphaerococcum	41.5$^{\text{ghi}}$	3.0$^{\text{fg}}$	39.3$^{\text{f-i}}$	1.11$^{\text{ghi}}$	8.3$^{\text{e-i}}$	85.3$^{\text{d-h}}$	1.20$^{\text{fgh}}$	1.10$^{\text{d-k}}$	51.5$^{\text{g-l}}$
T. turanicum	49.0$^{\text{b-h}}$	3.0$^{\text{fg}}$	58.7$^{\text{b}}$	1.70$^{\text{c}}$	10.7$^{\text{b-g}}$	99.7$^{\text{a-f}}$	1.37$^{\text{d-g}}$	0.83$^{\text{h-q}}$	44.5$^{\text{op}}$
T. turgidum	45.4$^{\text{d-i}}$	2.7$^{\text{g}}$	45.0$^{\text{def}}$	1.01$^{\text{h-k}}$	7.3$^{\text{g-k}}$	47.7$^{\text{m-q}}$	1.75$^{\text{cd}}$	1.75$^{\text{cd}}$	63.3$^{\text{c}}$
T. urartu	44.7$^{\text{e-i}}$	4.3$^{\text{efg}}$	18.7$^{\text{p}}$	0.17$^{\text{r}}$	4.3$^{\text{k}}$	34.8$^{\text{q}}$	0.13$^{\text{mn}}$	0.78$^{\text{i-q}}$	41.3$^{\text{pqr}}$
T. vavilovii	53.9$^{\text{e-i}}$	4.0$^{\text{efg}}$	42.0$^{\text{f-i}}$	1.18$^{\text{e-h}}$	10.7$^{\text{b-g}}$	50.0$^{\text{l-q}}$	1.18$^{\text{fgh}}$	1.02$^{\text{e-n}}$	49.9$^{\text{i-n}}$
Mean	47.4	6.2	34.2	0.92	9.8	76.1	0.97	1.16	48.8
LSD (0.01)	8.78	2.47	5.72	0.31	3.44	22.33	0.40	0.68	5.14
CV (%)	8.60	18.3	7.70	15.7	16.3	13.6	18.8	27.1	11.6

(Tables 2 and 3). *Triticum* species and hybrids had more seminal and nodal roots than *Aegilops* species (Fig. 4). Most genotypes exhibited 2.5-3.0 seminal roots/plant in Z11 and 6.6-11.7 nodal roots/plant in Z31 (Fig. 4). This study further revealed that the number of nodal roots in Z31 was linked to rooting depth (r^2=0.22) and root biomass (r^2=0.36) (Fig. 5).

With respect to the root-to-shoot and root-to-total biomass ratios, significant differences were observed in Z11, ranging from 0.14 to 0.64% and from 11.8 to 37.7%, respectively (Table 2). They also varied from 0.18 to 4.75 for the root-to-shoot ratio and 15.4 to 82.3% for root-to-total biomass ratio in Z31 (Table 3). The mean values in *Aegilops* species were lower than those of the *Triticum* species and hybrids in both Z11 and Z31 (Fig. 4). The genotypes mostly had root-to-shoot ratios of 0.25-0.50 in Z11 and there were three genotypes with values above 1.81 for the root-to-shoot ratio in Z31 (Fig. 3). The lowest and highest values for root-to-shoot and root-to-total biomass ratios were obtained from *Ae. tauschii* and *Ae. brachyathera* among *Aegilops* species and *T. durum* 'Gır' and *T. aestivum* 'Daws High PPO' among *Triticum* species and hybrids in Z11, respectively. The lowest and highest values were obtained from *Ae. crassa* and *Ae. speltoides* among *Aegilops* species and *T. aestivum* '5924' and *T. durum* 'Yılmaz 98' among wheat species and hybrids in Z31.

3.2. Phenotypic variability in shoot traits

This study proved that significant variations exist among the genotypes in terms of coleoptile length, shoot height, number of tillers, shoot biomass, and SPAD chlorophyll in the early vegetative and stem elongation growth stages (P<0.01; Tables 2 and 3). Coleoptile length varied from 3.1 to 11.3 cm in studied genotypes (Table 2). The lowest coleoptile length was obtained from the 'Daws High PPO' line, while *T. ispahanicum* had the highest coleoptile length among genotypes. The mean coleoptile length of *Aegilops* species (5.5 cm) was lower than that of *Triticum* species and hybrids (6.4 cm) (Table 2). Moreover, the progenitor of the wheat D genome, *A. tauschii*, had the highest coleoptile length compared to other *Aegilops* species. Shoot height in the early growth and stem elongation stages of the genotypes ranged from 6.9 to

Table 4. *Triticum* species and hybrids paired in 10 genotypes for the lowest and the highest rooting depth and root biomass in both Z11 and Z31 growth stages.

High rooting depth (cm)				High root biomass (g)			
Genotypes	Z11	Genotypes	Z31	Genotypes	Z11	Genotypes	Z31
T. turanicum	21.2	Ak 702	116.7	Yılmaz 98	0.20	T. *dicoccum*	2.62
*T. carthlicum**	19.5	*T. dicoccum*	109.5	Daws High PPO	0.19	Altın 40/98	2.35
Gır	18.8	*T. dicoccoides*	108.0	Ak 702	0.18	Yılmaz 98	1.98
Tir	18.6	Tir	106.8	Berkmen 469	0.16	Ak 702	1.92
Altın 40/98	18.0	*T. petropavlovskyi*	101.3	Ahmetağa	0.12	Ahmetağa	1.89
T. dicoccum	17.9	*T. turanicum*	99.7	*T. turanicum*	0.09	*T. turgidum*	1.75
T. petropavlovskyi	17.9	Altın 40/98	96.3	*T. turgidum*	0.08	Berkmen 469	1.70
						T. turanicum	1.37
Low rooting depth (cm)				Low root biomass (g)			
Genotypes	Z11	Genotypes	Z31	Genotypes	Z11	Genotypes	Z31
T. urartu	9.0	*T. urartu*	34.8	*T. urartu*	0.01	*T. boeoticum*	0.11
T. boeoticum	10.9	*T. boeoticum*	49.7	*T. dicoccoides**	0.03	*T. urartu*	0.13
T. spelta	12.9	*T. spelta*	60.8	*T. boeoticum*	0.03	Agrotriticum	0.23
Elytritilops	14.7	Daws High PPO	73.7	Agrotriticum	0.03	*T. spelta*	0.94
Daws High PPO	14.9	Elytritilops	75.7	*T. spelta*	0.03		

21.7 cm and 18.3 to 65.0 cm, respectively. The mean shoot height of *Triticum* species and hybrids was higher than that of *Aegilops* species in both growth stages and the mean shoot biomass was approximately 2-fold higher in both growth stages compared to *Aegilops* species. Minimum and maximum shoot biomass values were obtained in a range from 0.04 to 0.42 g and from 0.17 to 2.16 g in the Z11 and Z31 growth stages, respectively, among the genotypes (Tables 2 and 3). The shoot biomass was highest for *Ae. kotschyi* in Z11 and *Ae. crassa* in Z31 among the *Aegilops* species. Among the *Triticum* species and hybrids, *T. aestivum* 'Ak 702' and *T. durum* 'Berkmen 469' had higher shoot biomass in both growth stages while *T. urartu*, 'Agrotriticum', and *T. boeoticum* possessed the lowest shoot biomasses. Table 3 shows significant variations among the genotypes regarding number of tillers, ranging from 2 to 14.7. The mean number of tillers in the *Aegilops* species (9) was higher than that of *Triticum* species and hybrids (5.1). SPAD chlorophyll ranged from 37.7 to 83.7 µmol m^{-2} among the genotypes in Z31. According to the results, *Ae. speltoides* had the highest mean SPAD chlorophyll values among the mean values of genotypes (47.4 µmol m^{-2}).

3.3. Hierarchical clustering

Hierarchical cluster analysis revealed the relationship among the genotypes using a dendrogram constructed from the dissimilarity matrix. The results proved that all 35 genotypes were grouped into four main clusters in terms of rooting depth, number of seminal roots, number of nodal roots, root biomass, root-to-shoot ratio, and root-to-total biomass ratio in both Z11 and Z31. Groups were formed in clusters 1, 2, 3, and 4, including 9 genotypes in cluster 1, 9 genotypes in cluster 2, 5 genotypes in cluster 3, and 12 genotypes in cluster 4 (Fig. 2). *Aegilops* species were grouped in clusters 3 and 4 with the except for *Ae. brachyathera.* The two wheat progenitors *T. urartu* and *T. boeoticum*, with low root biomass, as well as the hulled genotypes *T. spelta*, *T. vavilovii*, *T. ispahanicum*, and Agrotriticum were grouped in cluster 1. Cluster 3 contained D genome progenitor *Ae. tauschii* together with *Ae. neglecta*. The genotypes with shallow rooting and low biomass in both the Z11 and Z31 growth stages were included in clusters 3 and 4 (Fig. 2). The deep-rooted genotypes for both growth stages, *T. dicoccum*, *T. dicoccoides*, *T. petropavlovskyi*, *T. turanicum*, and *T. aestivum* 'Ak 702' and 'Tir' were placed in cluster 2. Furthermore, the cultivars with high root biomass for both growth stages ('Altın 40/98', 'Yılmaz 98', and 'Ahmetağa') constituted cluster 1 (Fig. 2). The wild form of *T. timopheevii*, *T. armeniacum*, was in the same cluster as *T. fungicidum* (*T. carthlicum* × *T. timopheevii*). Moreover, a wild form of *T. dicoccum*, *T. dicoccoides*, was in the same cluster as *T. dicoccum*. This study further indicated that wheat hybrids with genotypes of different genera such as 'Elytritilops' (*Elymus* × *Triticum* × *Aegilops*) and 'Agrotriticum' (*Agropyron* × *Triticum*) had low root biomass and shallow rooting depth, appearing in clusters 3 and 4.

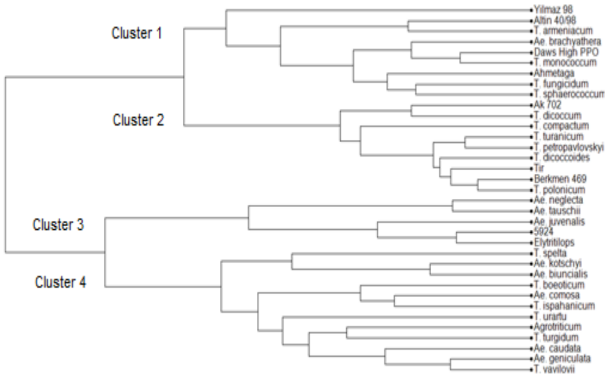

Figure 2. Hierarchical clustering of *Triticum* and *Aegilops* taxa, and hybrids for root traits such as rooting depth, number of seminal roots, number of nodal roots, root biomass, root-to-shoot ratio, and root-to-total biomass ratio in both Z11 and Z31 growth stages.

4. Discussions

4.1. Root traits of genotypes

4.1.1. Deep-rooted genotypes in drought conditions

This study showed that in the Z11 growth stage, genotypes including *T. turanicum*, *T. carthlicum*, *T. durum* genotypes 'Gır' and 'Altın 40/98', *T. aestivum* genotypes 'Tir', line '5924', 'Ahmetağa', *T. dicoccum*, and *T. petropavlovskyi* had deep roots, while *T. aestivum* genotypes 'Ak 702', 'Tir', *T. durum* 'Berkmen 469', *T. dicoccum*, *T. dicoccoides*, *T. polonicum*, *T. petropavlovskyi*, and *T. compactum* were found to have rooting depths of more than 100 cm among the *Triticum* species in Z31. Root traits in the early growth stage can be used as a secondary selection criterion in breeding programs (Manschadi et al., 2006). In this context, *T. boeoticum* and *T. urartu* with 14 chromosomes as diploid wild forms of wheat possessed shallow rooting patterns in both growth stages. In Z11 and Z31, *Triticum* species and wheat hybrids had deeper rooting than *Aegilops* species (Fig. 4). The rooting pattern in wheat species and in hybrids was affected by high shoot biomass, which was remobilized from higher leaf photosynthesis reserves to roots, important for meeting carbon requirements. A previous study of wheat cultivars grown in a mixture of peat and perlite found greater rooting depths in Z31, ranging from 189 to 216.6 cm (mean of two years), in comparison to values of 34.8-116.7 cm in the present study (Akman et al., 2017b). However, the present study used field soil in the rooting zone, which was reported to pose mechanical impedance to root growth, determining the root elongation and proliferation within a soil profile (Bengough and Mullins, 1990). The selected deep-rooted genotypes could be utilized in breeding programs to access the water from deep soil in water-limited conditions (Sayar et al., 2007).

4.1.2. Genotypes with high root biomass may be evaluated as breeding materials under non-stressed conditions

As a significant feature of plants, root biomass is an indicator of the size of a root system (Ehdaie et al., 2010). Large and shallow root systems can take up water from the upper layers of the soil during vegetative growth when rainfall is abundant in the winter (Manschadi et al., 2006). A small root system can be useful in rain-fed field areas with water-use efficiency (Passioura, 1983). In contrast, cultivars with large root systems had greater grain yields than cultivars with small root systems in rain-fed experiments in Central Europe (Středa et al., 2012). Contrasting results are due to the variable rainfall in dryland farming systems in various growth stages (Palta et al., 2011). Our results in Z31 agreed with those obtained in our previous study of field-grown wheat, suggesting that *T. aestivum* 'Ahmetağa', 'Ak 702', *T. durum* 'Berkmen 469', and *T. turgidum* had greater root biomass, while *T. aestivum* '5924' (line), *T. boeoticum*, and *Ae. biuncialis* possessed lower root biomass among genotypes (Akman et al., 2017a). A greater root system contributes to yield stability because during drought periods the root system can access water in deeper soil layers (Středa et al., 2012). The present study also revealed that *T. aestivum* 'Ak 702', 'Ahmetağa', 'Yılmaz 98', *T. durum* 'Berkmen 469', *T. turgidum*, and *T. turanicum* had the highest root biomass in both Z11 and Z31 while *T. urartu*, *T. boeoticum*, 'Agrotriticum', and *T. spelta* constituted the group of genotypes with the lowest root biomass. Moreover, among the genotypes studied, *T. dicoccum* and *T. durum* 'Altın 40/98' had higher root biomass in only Z31. Small amounts of shoot biomass contributing to low assimilate allocation in the *Aegilops* species led to smaller root biomass than in the *Triticum* species and hybrids.

4.1.3. Number of seminal and nodal roots

Two types of roots occur in wheat: seminal roots emerge directly from the embryo, while the later nodal roots come from the lower tiller nodes (Manske and Vlek, 2002). A higher number of seminal roots in wheat has been associated with more intensive root branching with at greater depths (Manschadi et al., 2008). Previous studies found that number of seminal roots varied from 3.2 to 5 in bread wheat genotypes, which falls between range of the number of seminal roots (2.7-5) in this study for wheat species and hybrids (Manschadi et al., 2008; Richard et al., 2015; Bektaş and Waines, 2020). In this study, the numbers of seminal root were not more than three per plant among *Aegilops* species. However, tetraploid wheat species *T. dicoccum* (4.5), *T. fungicidum* (4.7), *T. durum* 'Altın 40/98' (5), and *T. ispahanicum* (5) and the hexaploid landrace 'Tir' (4.7) possessed higher numbers of seminal roots than the other genotypes studied. In Z31, *T. aestivum* 'Ak 702' (18.7), *T. dicoccum* (19), and *T. spelta* (21) had the highest nodal root numbers among the studied genotypes. Thus, this study has further indicated that *T. dicoccum* has the highest numbers of seminal and nodal roots among other genotypes.

4.1.4. Root-to-shoot and root-to-total biomass ratios

The root-to-shoot ratio has been used to describe assimilate allocation to roots (Nakhforoosh et al., 2014). The root-to-total biomass ratio represents the assimilate proportion to roots into total biomass. Root-to-shoot and root-to-total biomass ratios were higher in Z31 than in Z11 as the growth stage. The results reported by Siddique et al. (1990) of a root-to-shoot ratio of 1.1 to 1.8 and a root-to-total biomass ratio of 52.1% to 64.4% in the 62 days after sowing were within the ranges of values found in the present study in Z31. This study indicated that an increase in root biomass generally enhanced the root-to-shoot and root-to-total biomass ratios; however, this was not always observed. This can be expressed as better representing assimilate accumulation into root growth up to the Z31 growth stage rather than that into shoot growth. The wild wheat ancestors *T. urartu* and *T. dicoccoides* and line 5924 were found to have low root-to-shoot and root-to-total biomass ratios in both Z11 and Z31 among the studied wheat species and hybrids, while *T. aestivum* 'Daws High PPO', 'Ahmetağa', *T. durum* 'Yılmaz 98', and *T. monococcum* had high ratios. Evaluating the *Aegilops* species, *Ae. brachyathera* had high root-to-shoot and root-to-total biomass ratios in both growth stages; however, *A. tauschii* had low values. *Ae. brachyathera* was a located *Aegilops* species in cluster 1 of the dendrogram with *Triticum* species and hybrids because it had relatively high rooting depth, root biomass, and root-to-shoot and root-to-total biomass ratios among the *Aegilops* species in both growth stages (Fig. 4). Although *T. aestivum* 'Ak 702' was among the genotypes with high root biomass in both growth stages, it was not included in the group with high root-to-shoot and root-to-total biomass ratios in Z31. This can be explained by the fact that the assimilating allocation into root biomass was lower than that into shoot biomass up to Z31.

4.2. Variability in shoot traits of genotypes

4.2.1. Shoot biomass

Plant breeders have primarily concentrated on grain yield rather than root growth; however, there is a critical

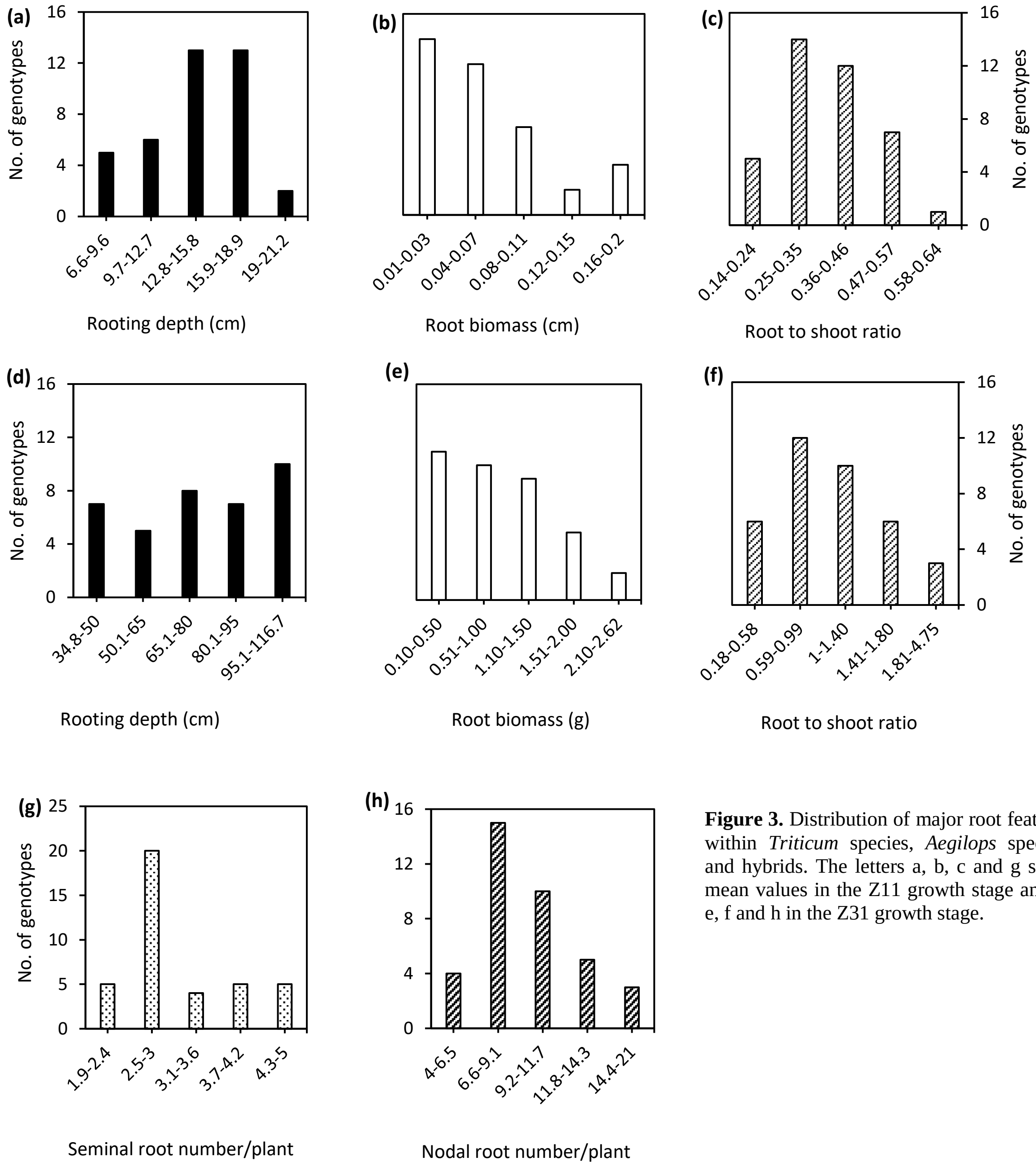

Figure 3. Distribution of major root features within *Triticum* species, *Aegilops* species, and hybrids. The letters a, b, c and g show mean values in the Z11 growth stage and d, e, f and h in the Z31 growth stage.

association between the root and shoot growth for high yield. In this study, shoot biomass was linked to root biomass more strongly in Z11 (r^2=0.83) than Z31 (r^2=0.44) (Fig. 5). The results were consistent with the findings of previous studies indicating a significant association between the root and shoot biomass (Sharma, 1993; Atta et al., 2013; Akman et al., 2017a). There was also a link between shoot biomass and rooting depth (r^2=0.41). Significant differences in shoot biomass were found among the genotypes. Compared to other wheat species and hybrids, *T. durum* 'Berkmen 469', and *T. aestivum* '5924' (line), 'Ak 702' maintained higher shoot biomass in both growth stages, while *T. urartu*, *T. boeoticum*, and 'Agrotriticum' had the lowest shoot biomass in both growth stages. Among the *Aegilops* species, *Ae. brachyathera* and *Ae. tauschii* had lower shoot biomass in both growth stages. *T. durum* 'Yılmaz 98', *T. aestivum* 'Daws High PPO', and *Ae. kotschyi* were ranked as genotypes with higher shoot biomass in Z11; however, they were among the bottom of genotypes with low shoot biomass in Z31. *T. durum* 'Yılmaz 98' had higher root biomass in Z31, when assimilates may be transported more into the roots. *T. aestivum* 'Daws High PPO' and *Ae. kotschyi* simultaneously had reduced root biomass and shoot biomass as their genotypic characteristics.

4.2.2. Coleoptile length

Selecting wheat cultivars with long coleoptiles is a significant target for sustaining emergence, weed competition, and grain yield in water-deficient regions of the world (Singh and Khanna-Chopra, 2010). Coleoptile length was reported to be affected by both genetic background and environmental factors (Allan et al., 1962;

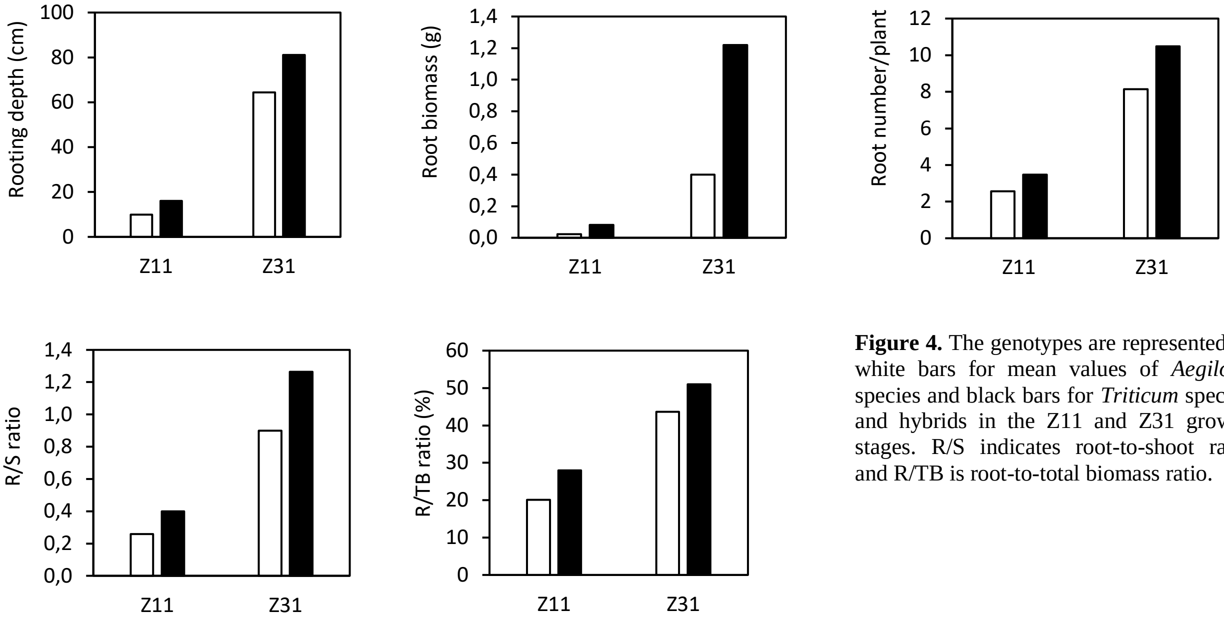

Figure 4. The genotypes are represented in white bars for mean values of *Aegilops* species and black bars for *Triticum* species and hybrids in the Z11 and Z31 growth stages. R/S indicates root-to-shoot ratio and R/TB is root-to-total biomass ratio.

Murray and Kuiper, 1988; Botwright et al., 2001). Wheat with long coleoptiles has greater emergence in deep planting than wheat with short coleoptiles (Rebetzke et al., 2007). However, Mohan et al. (2013) showed that coleoptiles longer than 9 cm had no advantage for emergence in deep planting. They also indicated that coleoptile length ranged from 3.4 to 11.4 cm in 662 studied wheat cultivars. Liatukas and Ruzgas (2011) showed that none of 564 winter wheat cultivars possessed a coleoptile length longer than 10 cm. In the present study, *T. ispahanicum* (11.3 cm), *T. aestivum* 'Tir' (9.3 cm), *T. fungicidum (*9 cm), *T. turanicum* (8.3 cm), and *T. dicoccoides* (8 cm) had the longest coleoptiles among the *Triticum* genotypes and wheat hybrids. *T. monococcum* (4.7 cm) and its wild form, *T. boeoticum* (3.8 cm), had shorter coleoptiles. Wheat progenitors *T. dicoccoides* and *T. urartu* had lengths of 8 cm and 5.2 cm, respectively. The D genome progenitor of bread wheat, *Ae. tauschii* (6.8 cm), possessed the longest coleoptile length among the *Aegilops* species.

4.2.3. Shoot height

Wheat grain yield was increased due to reduced height by controlled *Rht* alleles to improve semi-dwarf cultivars (Chapman et al., 2007). The present study revealed that modern wheat cultivars had lower shoot heights in both Z11 and Z31. However, different wheat species, landraces, and wheat hybrids were tall shoot height in both Z11 and Z31 (Tables 2 and 3). This is most likely due to the presence and/or absence of *Rht* alleles in the genotypes. An earlier study showed that semi-dwarf wheat cultivars had shorter root systems than tall cultivars in field experiments (Subbiah et al., 1968). Figure 4 indicates a relationship between shoot height and rooting depth ($r^2=0.30$). As for the *Aegilops* species, in both growth stages, *Ae. brachyathera* and *Ae. neglecta* exhibited taller and shorter shoot heights, respectively.

4.2.4. Number of Tillers

The set of genotypes used in this study exhibited significant variation for number of tillers. High tillering genotypes may compensate for lower numbers of plants caused by late drought or early frost (Acevedo et al., 2002; Elhani et al., 2007). In this study, both maximum and minimum number of tillers were observed in tetraploid wheat genotypes among the wheat species and hybrids in Z31. *T. durum* 'Berkmen 469', 'Altın 40/98', *T. dicoccum* (landrace), *T. aestivum* 'Ak 702' (old cultivar), 'Tir' (landrace) were found to be high tillering genotypes and are grown with superiority in regions of Turkey prone to early frost damage and late drought stress. The genotype with the lowest tillering, *T. polonicum*, was reported to have a high grain weight by Bienkowska et al. (2020) (57.9 mg) and Wang et al. (2002) (80 mg). This result was confirmed by Dreccer et al. (2013), who indicated that low tillering wheat lines accumulated more water-soluble carbohydrates in the stems, which supplied a higher grain number per spike and heavier kernels with minimal yield increase.

4.3. SPAD chlorophyll readings

SPAD chlorophyll meter readings allow for rapid assessment of chlorophyll density in plants (Puangbut et al., 2017). The chlorophyll content is a good indicator of the “stay-green” trait of photosynthetic tissue (Fotovat et al., 2007). It has been recommended that high chlorophyll content be used to represent a low degree of photoinhibition (Farquhar and Richards, 1984). Chlorophyll readings of the genotypes were similar among the *Aegilops* species, wheat species, and hybrids with one exception. An ancestor of wheat, *Ae. speltoides*, had exceptionally high chlorophyll (83.7 μmol m^{-2}) compared to the mean values of the other studied genotypes.

4.4. Selection of genotypes with superior root features for the target environment

Root traits have been neglected in the development of new cultivars, and more efforts are being taken in the measurement and explanation of below-ground traits (Richards, 2006; Bektaş et al., 2020). The root biomass and depth are valuable selection criteria in breeding programs. Also, measurements of these traits are

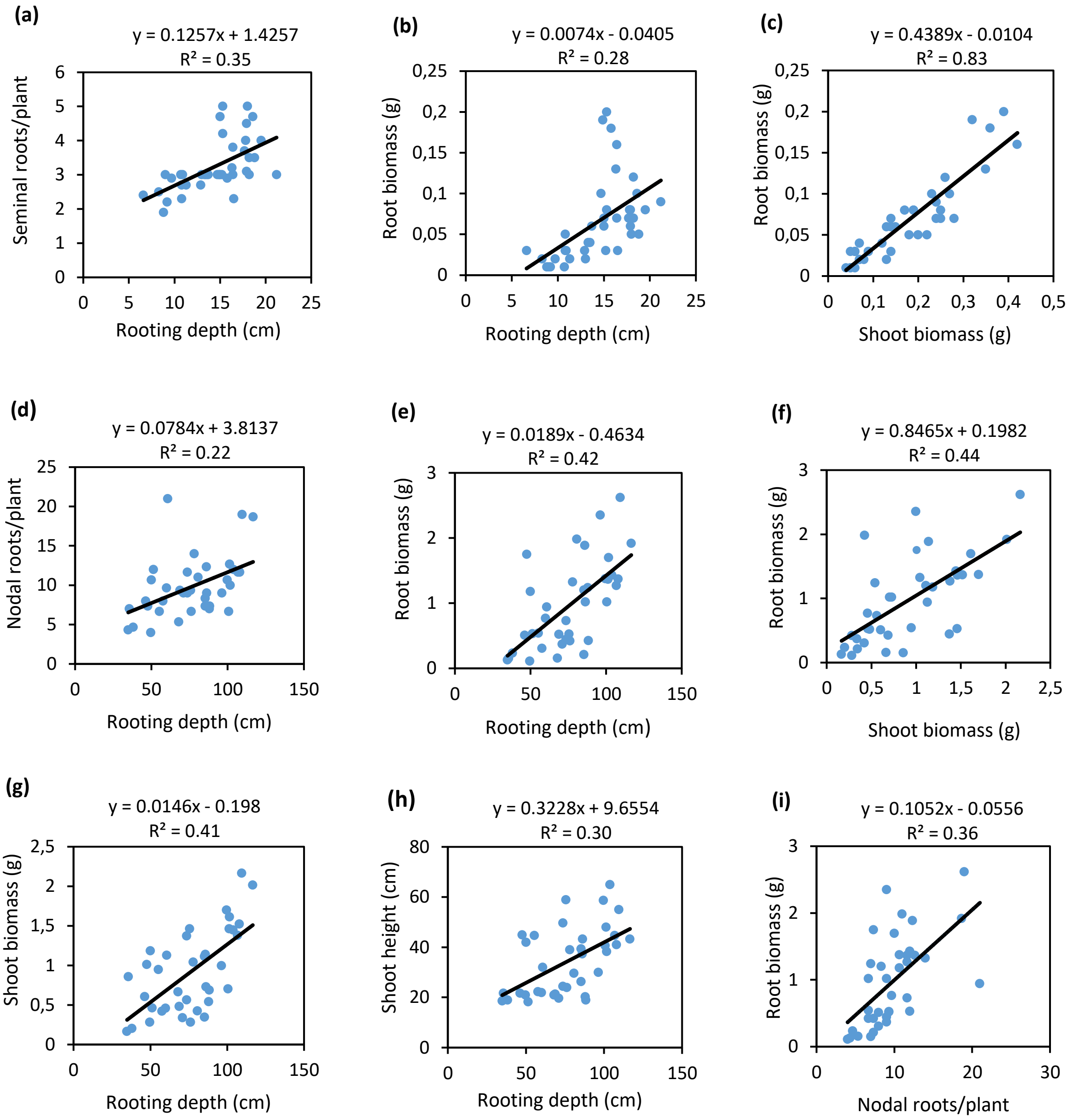

Figure 5. Relationships between/within root and shoot traits in the Z11 (a, b, and c) and Z31 (d, e, f, g, h, and i).

simple and inexpensive. The root traits should be phenotypically screened in both early vegetative and later growth stages for variability in drought-adaptive and non-stressed traits. The rooting depth and root biomass seem to be the primary selection features, substantially affecting the root system's architecture and therefore providing more water and nutrient uptake in the soil profile. In the present study, both deep-rooted and shallow-rooted genotypes were selected, as were genotypes with both low and high root biomass in the early vegetative and stem elongation stages. Deep rooting has been reported to increase wheat yield considerably by extracting more water from the deep soil profile under water deficit (Fang et al., 2017; El Hassouni et al., 2018). The genotypes *T. turanicum*, *T. aestivum* 'Tir', *T. durum* 'Altın 40/98', *T. dicoccum*, and *T. petropavlovskyi* were identified as having the deepest rooting in both Z11 and Z31 (Table 4).

Our previous findings demonstrated that root biomass was positively and significantly correlated with grain yield in field-grown genotypes under well-watered conditions (Akman et al., 2017a). Qi et al. (2019) showed positive and significant relations between grain yield and root weight density of maize in topsoil (0-40 cm) in which a significant rate of root biomass accumulated. Kanbar et al. (2009) revealed that root biomass in rice had a significant effect on grain yield in well-watered conditions, but rooting depth was important for improving the grain yield in low-moisture conditions. There is no consensus on whether the improvement of wheat with a large root system for rain-fed conditions is the best scheme in breeding programs (Palta et al., 2011), and Passioura (1983) proved that a smaller root system may be beneficial in water-insufficient conditions. Our earlier findings in mature field-grown plants also identified the same genotypes as having high biomass, such as *T. aestivum* 'Ahmetağa', 'Ak 702', and *T. durum* 'Berkmen 469' (Akman et al., 2017a). As a result, the genotypes *T. durum* 'Yılmaz 98', 'Berkmen 469', *T. aestivum* 'Ak 702', 'Ahmetağa', *T. turgidum*, and *T. turanicum*, which maintained high root biomass consistently in both Z11 and Z31, can be evaluated for the cultivar improvement with desirable roots in both target environments. Moreover, the *T. turanicum*, *T. dicoccum*, *T. durum* 'Altın 40/98', and *T. aestivum* 'Ak 702' genotypes not only had high root biomass values but also deep-rooting features in both growth stages among the genotypes studied (Table 4). This study further supports that these genotypes should be evaluated for both water-deficit and non-stressed conditions with a view to using them in breeding programs to develop promising cultivars with desirable root systems.

References

Acevedo E, Silva P, Silva H (2002). Wheat growth and physiology. Bread Wheat, Improvement and Production 30: 39-70.

Adu MO, Sparkes DL, Parmar A, Yawson DO (2011). Stay green in wheat: Comparative study of modern bread wheat and ancient wheat cultivars. Journal of Agricultural and Biological Science 6: 16-24.

Akman H, Akgun N, Tamkoc A (2017a). Comparison of root and shoot traits of different wheat species and wild wheat relatives: Does feature of shoot biomass have positive and significant relationships with grain yield and root traits?. Revista de la Facultad de Agronomia de la Universidad del Zulia 34: 428-447.

Akman H, Akgun N, Tamkoc A (2017b). Screening for root and shoot traits in different wheat species and wild wheat relatives. Botanical Sciences 95: 147-154.

Allan R, Vogel O, Burleigh J (1962). Length and estimated number of coleoptile parenchyma cells of six wheat selections grown at two temperatues 1. Crop Science 2: 522-524.

Arzani A, Ashraf M (2017). Cultivated ancient wheats (*Triticum* spp.): A potential source of health-beneficial food products. Comprehensive Reviews in Food Science and Food Safety 16: 477-488.

Atta BM, Mahmood T, Trethowan TM (2013). Relationship between root morphology and grain yield of wheat in North-Western NSW, Australia. Australian Journal of Crop Science 7: 2108-2115.

Banga SS, Kang MS (2014). Developing climate-resilient crops. Journal of Crop Improvement 28: 57-87.

Bektaş H, Waines JG (2020). Effect of grain size on the root system architecture of bread wheat (*Triticum aestivum* L.). Turkish Journal of Agricultural Research 7: 78-84.

Bektaş H, Hohn CE, Waines JG (2020). Dissection of quantitative trait loci for root characters and day length sensitivity in SynOpDH wheat (*Triticum aestivum* L.) bi-parental mapping population. Plant Genetic Resources, 18(3): 130-142.

Bengough AG, McKenzie B, Hallett P, Valentine T (2011). Root elongation, water stress, and mechanical impedance: A review of limiting stresses and beneficial root tip traits. Journal of Experimental Botany 62: 59-68.

Bengough AG, Mullins CE (1990). Mechanical impedance to root growth: A review of experimental techniques and root growth responses. Journal of Soil Science 41: 341-358.

Bienkowska T, Suchowilska E, Wiwart M (2020). *Triticum polonicum* L. As promising source material for breeding new wheat cultivars. Journal of Elementology 25: 237-248.

Botwright T, Rebetzke G, Condon A, Richards R (2001). Influence of variety, seed position and seed source on screening for coleoptile length in bread wheat (T*riticum aestivum* L.). Euphytica 119: 349-356.

Chapman S, Mathews K, Trethowan R, Singh R (2007). Relationships between height and yield in near-isogenic spring wheats that contrast for major reduced height genes. Euphytica 157: 391-397.

Dreccer MF, Chapman SC, Rattey AR, Neal J, Song Y, Christopher JT, Reynolds M (2013). Developmental and growth controls of tillering and water-soluble carbohydrate accumulation in contrasting wheat (*Triticum aestivum* L.) genotypes: Can we dissect them?. Journal of Experimental Botany 64: 143-160.

Dvorak J, Akhunov ED (2005). Tempos of gene locus deletions and duplications and their relationship to recombination rate during diploid and polyploid evolution in the *Aegilops-Triticum* alliance. Genetics 171: 323-332.

Ehdaie B, Merhaut D, Ahmadian S, Hoops A, Khuong T, Layne A, Waines J (2010). Root system size influences water-nutrient uptake and nitrate leaching potential in wheat. Journal of Agronomy and Crop Science 196: 455-466.

El Hassouni K, Alahmad S, Belkadi B, Filali-Maltouf A, Hickey L, Bassi F (2018). Root system architecture and its association with yield under different water regimes in durum wheat. Crop Science 58: 2331-2346.

Elhani S, Martos V, Rharrabti Y, Royo C, del Moral LG (2007). Contribution of main stem and tillers to durum wheat (*Triticum turgidum* L. var. *durum*) grain yield and its components grown in mediterranean environments. Field Crops Research 103: 25-35.

Fang Y, Du Y, Wang J, Wu A, Qiao S, Xu B, Zhang S, Siddique KH, Chen Y (2017). Moderate drought stress affected root growth and grain yield in old, modern and newly released cultivars of winter wheat. Frontiers in Plant Science 8: 1-14.

Farquhar G, Richards R (1984). Isotopic composition of plant carbon correlates with water-use efficiency of wheat genotypes. Functional Plant Biology 11: 539-552.

Fotovat R, Valizadeh M, Toorchi M (2007). Association between water-use efficiency components and total chlorophyll content (spad) in wheat (*Triticum aestivum* L.) under well-watered and drought stress conditions. Journal of Food Agriculture & Environment 5: 225-227.

Friedli CN, Abiven S, Fossati D, Hund A (2019). Modern wheat semi-dwarfs root deep on demand: Response of rooting depth to drought in a set of Swiss era wheats covering 100 years of breeding. Euphytica 215: 85.

Heřmanská A, Středa T, Chloupek O (2015). Improved wheat grain yield by a new method of root selection. Agronomy for Sustainable Development 35: 195-202.

Kanbar A, Toorchi M, Shashidhar H (2009). Relationship between root and yield morphological characters in rainfed low land rice (*Oryza sativa* L.). Cereal Research Communications 37: 261-268.

Kishii M (2019). An update of recent use of *Aegilops* species in wheat breeding. Frontiers in Plant Science 10: 585.

Li D, Long D, Li T, Wu Y, Wang Y, Zeng J, Xu L, Fan X, Sha L, Zhang H (2018). Cytogenetics and stripe rust resistance of wheat–*Thinopyrum elongatum* hybrid derivatives. Molecular Cytogenetics 11: 1-16.

Liatukas Z, Ruzgas V (2011). Relationship of coleoptile length and plant height in winter wheat accessions. Pakistan Journal of Botany 43: 1535-1540.

Manschadi AM, Christopher J, deVoil P, Hammer GL (2006). The role of root architectural traits in adaptation of wheat to water-limited environments. Functional Plant Biology 33: 823-837.

Manschadi AM, Hammer GL, Christopher JT, Devoil P (2008). Genotypic variation in seedling root architectural traits and implications for drought adaptation in wheat (*Triticum aestivum* L.). Plant and Soil 303: 115-129.

Manske GG, Vlek PL (2002). Root architecture–wheat as a model plant. Plant Roots: The Hidden Half 3: 249-259.

Maron L (2019). Sequencing of ancient wheat genomes opens a window into the past. The Plant Journal 99: 199-200.

Mathre D, Johnston R, Martin J (1985). Sources of resistance to *Cephalosporium gramineum* in *Triticum* and *Agropyron* species. Euphytica 34: 419-424.

Mohan A, Schillinger WF, Gill KS (2013). Wheat seedling emergence from deep planting depths and its relationship with coleoptile length. PLoS One 8: 1-9.

Murray G, Kuiper J (1988). Emergence of wheat may be reduced by seed weather damage and azole fungicides and is related to coleoptile length. Australian Journal of Experimental Agriculture 28: 253-261.

Nakhforoosh A, Grausgruber H, Kaul H-P, Bodner G (2014). Wheat root diversity and root functional characterization. Plant and Soil 380: 211-229.

Nevo E (2011). Cereals. Wild Crop Relatives: Genomic and Breeding Resources. Springer.

Özkan H, Tuna M, Kilian B, Mori N, Ohta S (2010). Genome size variation in diploid and tetraploid wild wheats. AoB Plants 2010: 1-11.

Palta JA, Chen X, Milroy SP, Rebetzke GJ, Dreccer MF, Watt M (2011). Large root systems: Are they useful in adapting wheat to dry environments? Functional Plant Biology 38: 347-354.

Passioura J (1983). Roots and drought resistance. Agricultural Water Management 7: 265-280.

Peng J, Sun D, Nevo E (2011). Wild emmer wheat,'*Triticum dicoccoides*', occupies a pivotal position in wheat domestication process. Australian Journal of Crop Science 5: 1127-1143.

Perrier X, Jacquemoud-Collet JP (2006). DARwin software. Available from http://www.darwin.cirad.fr/darwin/Home.php / [accessed 25 December 2020].

Prasad P, Staggenborg S, Ristic Z (2008). Impacts of drought and/or heat stress on physiological, developmental, growth, and yield processes of crop plants. Response of crops to limited water: Understanding and modeling water stress effects on plant growth processes 1: 301-355.

Puangbut D, Jogloy S, Vorasoot N (2017). Association of photosynthetic traits with water use efficiency and spad chlorophyll meter reading of *Jerusalem artichoke* under drought conditions. Agricultural Water Management 188: 29-35.

Richards RA (2006). Physiological traits used in the breeding of new cultivars for water-scarce environments. Agricultural Water Management 80: 197-211.

Qi D, Hu T, Song X, Zhang M (2019). Effect of nitrogen supply method on root growth and grain yield of maize under alternate partial root-zone irrigation. Scientific Reports 9: 1-10.

Rebetzke G, Ellis M, Bonnett D, Richards R (2007). Molecular mapping of genes for coleoptile growth in bread wheat (T*riticum aestivum* L.). Theoretical and Applied Genetics 114: 1173-1183.

Richard CA, Hickey LT, Fletcher S, Jennings R, Chenu K, Christopher JT (2015). High-throughput phenotyping of seminal root traits in wheat. Plant Methods 11: 1-11.

Sayar R, Khemira H, Kharrat M (2007). Inheritance of deeper root length and grain yield in half-diallel durum wheat (*Triticum durum*) crosses. Annals of Applied Biology 151: 213-220.

Sharma R (1993). Selection for biomass yield in wheat. Euphytica 70: 35-42.

Siddique K, Belford R, Tennant D (1990). Root: Shoot ratios of old and modern, tall and semi-dwarf wheats in a mediterranean environment. Plant and Soil 121: 89-98.

Singh K, Khanna-Chopra R (2010). Physiology and QTL analysis of coleoptile length, a trait for drought tolerance in wheat. Journal of Plant Biology 37: 1-9.

Středa T, Dostál V, Horáková V, Chloupek O (2012). Effective use of water by wheat varieties with different root system sizes in rain-fed experiments in central europe. Agricultural Water Management 104: 203-209.

Subbiah B, Katyal J, Narasimham R, Dakshinamurti C (1968). Preliminary investigations on root distribution of high yielding wheat varieties. The International Journal of Applied Radiation and Isotopes 19: 385-390.

Ullah S, Bramley H, Daetwyler H, He S, Mahmood T, Thistlethwaite R, Trethowan R (2018). Genetic contribution of emmer wheat (T*riticum dicoccon* Schrank) to heat tolerance of bread wheat. Frontiers in Plant Science 9: 1-11.

Wang H-J, Huang X-Q, Röder M, Börner A (2002). Genetic mapping of loci determining long glumes in the genus *Triticum*. Euphytica 123: 287-293.