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Unrevalling phenotypic diversity of root system architecture in ancient wheat species versus modern wheat cultivars

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Abstract

Understanding the phenotypic variability in root system architecture and root-shoot relationships across different growth stages of wheat is of utmost importance for the improvement of genotypes with enhanced nutrient uptake and resource-use efficiency. This study focused on identifying variations and relationships in the root and shoot characteristics of seven modern cultivars and twelve ancient wheat accessions of different species, including T. monococcum, T. turanicum, T. polonicum, T. mirabile, T. durum, and T. aestivum, during the early vegetative growth and stem elongation stages. The results demonstrated significant phenotypic variation among the genotypes for shoot traits, root biomass, rooting depth, R/S ratio, and seminal and nodal root numbers. When considering both growth stages, the dry land-adapted cultivar "Taner' and ancient wheat species, such as *T. turanicum* (2) and *T. monococcum* (1) accessions, exhibited deeper roots, which can enhance access to water in drought-prone areas. Furthermore, it was observed that modern wheat cultivars and *T. turanicum* accessions exhibited increased root biomass, suggesting a higher allocation of resources towards root growth, which could potentially enhance nutrient uptake. Conversely, T. monococcum accessions and *T. mirabile* revealed lower root biomass compared to other ancient species and modern cultivars. Additionally, the unrooted cluster analysis based on root biomass, rooting depth, and root to shoot ratio at both growth stages indicated a distinct separation of T. monococcum accessions and T. mirabile from other genotypes. Overall, these findings underscore the importance of phenotypic diversity in root traits for crop improvement and adaptation to varying environments. Identifying genotypes with desirable root characteristics can enhance nutrient and water uptake efficiencies, leading to increased crop productivity and sustainability.

Keywords: ancient wheat; rooting depth; root biomass; shoot traits; phenotyping

Introduction

Wheat is one of the world's most important staple crops and provides a significant portion of the global population with food and nutrition. The origin and domestication of wheat (*Triticum* spp.) are significant milestones in the development of agriculture and human society. According to Willcox (2005), the domestication of wheat began approximately 10,000 years ago in a region encompassing parts of modern-day

Received: 07 Sep 2023. Received in revised form: 18 Oct 2023. Accepted: 31 Oct 2023. Published online: 16 Nov 2023. From Volume 13, Issue 1, 2021, Notulae Scientia Biologicae journal uses article numbers in place of the traditional method of continuous pagination through the volume. The journal will continue to appear quarterly, as before, with four annual numbers. Iraq, Syria, and Türkiye, where wild grasses were cultivated for food. As explained by Matsuoka (2011), crossing between *Aegilops speltoides* and wild emmer wheat (*Triticum dicoccoides*) resulted in the formation of *T. turgidum* ssp. *dicoccoides*, which served as an important genetic resource for the subsequent domestication of cultivated wheat. The tetraploid (2n = 28) naked-grain wheat species *T. turgidum*, *T. polonicum*, *T. turanicum*, and *T. durum* were developed from *T. dicoccoides*, first as the cultivated hulled *T. dicoccoides* and *Ae. tauschii*. According to research by Kilian *et al.* (2007), the cultivated einkorn wheat, *T. monococcum* ssp. *monococcum*, was domesticated from *T. monococcum* ssp. *boeoticum*, which is its wild parent in the areas of Karacadağ in Southeastern Anatolia.

As demand for food increases with population growth, it is crucial to enhance wheat production and yield potential. One of the key factors influencing wheat productivity is the root system, which plays a vital role in nutrient acquisition, water uptake, and plant anchorage in soil. The diversity of wheat genotypes for root biomass, rooting depth, and root number characteristics provides an opportunity for crop improvement and adaptation to varying environmental conditions. Selecting wheat genotypes with desirable root traits can enhance nutrient and water uptake efficiency, leading to increased crop productivity and sustainability. Moreover, genetic diversity in root characteristics allows the identification and utilization of specific traits through breeding programs and genetic engineering approaches (Manske *et al.*, 2016). One of the most significant root traits, root biomass, is a fundamental trait linked to nutrient acquisition in wheat. Higher root biomass has been associated with an increased nutrient uptake capacity and improved grain yield in wheat genotypes (Gregory *et al.*, 2013). This is supported by a previous study that demonstrated an increase in yield and nutrient use efficacy with root biomass in wheat can inform breeding programs aimed at developing genotypes with improved nutrient uptake and resource-use efficiency.

Another crucial root trait contributing to wheat plant performance is the rooting depth, which is defined as the vertical extent of the root system in the soil profile. Wheat genotypes with deep roots are better equipped to access water stored in deeper soil layers, particularly in drought-prone regions, thereby enhancing their drought tolerance and water-use efficiency (Kulkarni *et al.*, 2017). Odone *et al.* (2009) found that deeprooted wheat genotypes exhibited higher grain yield under water-limited conditions compared to shallow-rooted genotypes. Additionally, deeper roots enable access to nutrients in the lower soil layers, contributing to improved nutrient uptake efficiency (White *et al.*, 2013).

Understanding the root characteristics of wheat is crucial to unravel the complexity of root development and function. The importance and diversity of the root biomass, rooting depth, and root number characteristics of wheat genotypes are essential considerations for crop improvement and sustainable agriculture. The genetic variability present in these traits provides an opportunity to select and develop wheat genotypes with improved nutrient and water uptake efficiency as well as enhanced stress tolerance. Furthermore, advancements in phenotyping and molecular techniques have offered valuable tools for characterizing and manipulating root traits in large-scale breeding programs. This study aimed to explore the variability of root and shoot characteristics between ancient wheat species and wheat cultivars or in each group under greenhouse and laboratory conditions, their potential implications for use in breeding programs, and relationships between roots and shoots in enhancing crop productivity.

Materials and Methods

The purpose of this study was to describe the characteristics of root and shoot parameters and their relationships as two experiments during the early vegetative growth stage (Z11 on the Zadoks scale) and stem elongation (Z31) this year. In the first experiment, the study focused on studying the primary root and shoot

parameters for two weeks after germination. In the second experiment, which was conducted in a greenhouse, root and shoot growth shifted specifically during the nodal root growth stage.

Germplasm samples were chosen to ensure a diverse representation of genetic variations. These samples included seven *T. monococcum* accessions, three *T. turanicum* accessions, one *T. polonicum accession*, one *T. mirabile* accession, and seven modern cultivars. The intention was to encompass a wide range of genetic diversity in these separate experiments (Table 1). Genotypes of non-Turkish origin were obtained from the US Department of Agriculture National Plant Germplasm System. In addition, modern cultivars of Turkish origin were supplied by institutes and local farmers (Table 1).

Taxonomy	CN	Name/Local name	PI/Origin
T. monococcum L. ssp. monococcum (1)	14	Einkorn ('Flavescens')	PI 191381/Ethiopia
T. monococcum L. ssp. monococcum (2)	14	Einkorn	PI 221329/Serbia
T. monococcum L. ssp. monococcum (3)	14	Einkorn ('Laetissimum')	PI 191383/Ethiopia
T. monococcum L. ssp. monococcum (4)	14	Einkorn ('Nigricultum')	PI 221414/Serbia
T. monococcum L. ssp. monococcum (5)	14	Einkorn ('Siyez')	Türkiye, Kastamonu
T. monococcum L. ssp. monococcum (6)	14	Einkorn ('Metzger G68-3288')	Cltr 13965/USA, Oregon
T. monococcum L. ssp. monococcum (7)	14	Einkorn	PI 237659/Kenya, Rift Valley
<i>T. turgidum</i> L. ssp. <i>turanicum</i> Jakubz. (1)	28	Khorasan wheat	PI 68287/Azerbaijan
<i>T. turgidum</i> L. ssp. <i>turanicum</i> Jakubz. (2)	28	Khorasan wheat	PI 67343/Australia, Victoria
<i>T. turgidum</i> L. ssp. <i>turanicum</i> Jakubz. (3)	28	Khorasan wheat	PI 68293/Azerbaijan
T. turgidum L. ssp. polonicum	28	Polish wheat	PI 56262/Portugal, Lisboa
T. turgidum var. mirabile	28	Miracle wheat	Türkiye, Diyarbakır
T. turgidum L. ssp. durum Desf.	28	'Türköz'*/durum wheat	Konya/BDIARI
T. turgidum L. ssp. durum Desf.	28	ʻSırçalı'**/durum wheat	Konya/BDIARI
T. aestivum L. ssp. aestivum	42	'Taner'*/bread wheat	Konya/BDIARI
T. aestivum L. ssp. aestivum	42	'Bozkır'*/bread wheat	Konya/BDIARI
T. aestivum L. ssp. aestivum	42	'Yavuz'**/bread wheat	Konya/BDIARI
T. aestivum L. ssp. aestivum	42	'Tuğra'**/bread wheat	Konya/BDIARI
T. aestivum L. ssp. aestivum	42	'Savatra'**/biscuit wheat	Konya/BDIARI

Table 1. Taxonomy, names, ploidy levels, and origins of genotypes

BDIARI: Bahri Dağdaş International Agricultural Research Institute

* indicates adapted cultivars to dry lands, and ** for irrigated lands.

Laboratory experiment

A controlled experiment was conducted to assess the length of the coleoptile along with the root and shoot traits. Each genotype was represented by three seeds and three replicates were used. The seeds were positioned in the centre of a moist germination towel with a spacing of 5 cm between them. The towels were rolled loosely and secured using a rubber band. The prepared samples were then placed vertically in plastic bags in a dark room maintained at a temperature of 15-16 °C for 15 d (March 15-30).

To measure coleoptile length, a ruler was used to determine the distance from the scutellum to the tip of the coleoptile. Rooting depth, which represents the length of the longest primary root, was measured to assess the depth of the root system. In addition, the total root length was determined by measuring the seminal roots, whereas the seminal root count was performed manually. Root and shoot biomass were recorded following thorough dehydration using an absorbent towel. The proportion of root biomass to shoot biomass was calculated as the root to shoot biomass ratio.

Greenhouse experiment

The second experiment was performed in a greenhouse from March 15 to May 10. Seeds were sown into long columns measuring 100 cm in depth and 12 cm in diameter, which were filled with field soil. The glasshouse climate was monitored using a data logger (T & D Corporation/TR-74Ui), which recorded data at five-minute intervals. In March, the average temperature in the greenhouse during the day was 10 °C, while it was 4 °C at night. In April, the average temperature in the greenhouse during the day was 23.8 °C, while at night it was 11 °C. In May, the average temperature increased to 26.0 °C during the day and 14.5 °C at night.

The soil used in the experiment was collected from the field (0-40 cm depth) and characterized as clay loam with low organic matter content (1.7%) and high levels of CaCO₃ (23.7%) and Ca (5491 mg/kg). The electrical conductivity (EC) of the soil was measured at 0.6 mmhos/cm, and the soil pH was determined to be 7.7. Salinity issues were not observed. The concentrations of P₂O₅, Zn, and Mn in the soil were low, with values of 4.58 mg/kg, 0.67 mg/kg, and 8.13 mg/kg, respectively. However, K₂O (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 performed on individual plants grown in separate columns (Figure 1). Morphological characteristics, such as shoot length and number of tillers, were recorded. Rooting depth was determined after the roots were washed and cleaned. The number of nodal roots was counted manually. After drying at $80 \,^{\circ}$ C for three days, the root biomass and shoot biomass were recorded to determine the root to shoot ratio.

Statistical analysis

The experiments were conducted following a completely randomized design with three replicates. Statistical analysis was performed using the Minitab 16 software package, and significant differences between the means were determined using Tukey's test. Subsequently, for the six root morphological data, including root biomass, rooting depth, and root to shoot ratio in both growth stages, an unrooted dendrogram was constructed using the Euclidean distance algorithm and the average cluster algorithm.

Results

The variance analysis results for the root and shoot traits of wheat cultivars and ancient wheat species are provided in Tables 2, 3, and Figure 2A. significant difference was observed between the wheat cultivars and ancient wheat species in terms of the investigated traits (P < 0.001). Furthermore, according to the mean results of cultivars and accessions of each ancient wheat species, significant variations were observed for root and shoot traits in the stem elongation growth stage (P < 0.001), rooting depth (P < 0.05), and shoot length (P < 0.001) (Figure 1).

Root system and shoot traits in the early growth stage <u>Rooting depth</u>

The genotypes exhibited significant variations in rooting depth, ranging from 15.6 to 23.3 cm. 'Taner' and *T. turanicum* (2) had the highest rooting depths at 23.3 cm, while *T. monococcum* (2) and *T. monococcum* (3) had the lowest rooting depths at 15.6 cm and 15.8 cm, respectively. Among ancient wheat species, *T. turanicum* accessions and *T. polonicum* indicated deep rooting compared to *T. monococcum* accessions and *T. mirabile*. In terms of rooting depth, the cultivars 'Türköz', 'Bozkır', and 'Taner' indicated promising characteristics. These genotypes have demonstrated deeper rooting depths, suggesting their potential for better drought tolerance and efficient nutrient uptake from lower soil layers in the early growth stage.

Total root length

The *Triticum* genotypes demonstrated considerable diversity in terms of total root length (TRL), with values ranging from 37.3 cm to 91.3 cm. Among the genotypes studied, 'Türköz' exhibited the highest TRL at 91.3 cm, followed by *T. polonicum* with a TRL of 81.3 cm. 'Sırçalı' and *T. turanicum* (1) demonstrated relatively long TRLs of 72.8 cm and 65.3 cm, respectively. 'Bozkır', *T. turanicum* (2), and 'Savatra' displayed TRLs of 61.5 cm, 61.2 cm, and 60.8 cm, respectively. 'Taner' and 'Yavuz' both reached TRLs of 59.5 cm and 59.4 cm, while *T. turanicum* (3) exhibited a TRL of 56.7 cm.

C	Shoot length Coleoptile		Rooting depth	Total root	Root/shoot	
Genotypes	(cm)	length (cm)	(cm)	length (cm)	(ratio)	
T. monococcum (1)	22.8±0.1 ^{bc}	7.3±0.3 ^{bc}	17.9±0.2 ^{c-h}	49.0±2.3 ^h	0.38±0.01 ^{cf}	
T. monococcum (2)	$20.4 \pm 0.4^{b-h}$	6.1±0.3 ^{cf}	15.6±0.4 ^h	48.3±2.4 ^h	0.52 ± 0.06^{bcd}	
T. monococcum (3)	19.1±0.5 ^{c-h}	$5.1 \pm 0.3^{\text{fgh}}$	15.8 ± 0.6^{h}	37.3 ± 1.5^{i}	0.49±0.05 ^{b-c}	
T. monococcum (4)	21.2±0.3 ^{b-f}	6.6±0.3 ^{cde}	$16.0 \pm 0.0^{\text{gh}}$	47.6±2.2 ^h	0.56 ± 0.03^{b}	
T. monococcum (5)	19.4±0.4 ^{c-h}	5.7 ± 0.2^{efg}	16.7±0.9 ^{fgh}	50.2±0.3 ^{ghi}	0.45±0.03 ^{b-f}	
T. monococcum (6)	22.1 ± 0.8^{bcd}	6.1 ± 0.1^{def}	$18.4 \pm 0.1^{d-g}$	49.7 ± 1.1^{h}	0.53 ± 0.03^{bc}	
T. monococcum (7)	18.9±0.3 ^{c-h}	6.5±0.2 ^{cde}	19.3±0.8 ^{cde}	48.7±2.3 ^h	$0.44 \pm 0.02^{b-f}$	
T. turanicum (1)	24.4 ± 4.7^{ab}	8.3±1.2 ^{ab}	22.0 ± 1.7^{ab}	65.3±9.0 ^{cd}	0.34 ± 0.03^{f}	
T. turanicum (2)	20.2±1.1 ^{c-h}	7.3±0.3 ^{bcd}	23.3±0.6ª	61.2±2.8 ^{def}	0.37 ± 0.02^{f}	
T. turanicum (3)	21.0±0.3 ^{b-g}	6.4±0.3 ^{cde}	20.8 ± 0.8^{bc}	56.7±1.0 ^{d-h}	0.36 ± 0.05^{f}	
T. polonicum	27.3±1.5ª	9.0±0.0ª	20.7±1.5 ^{bcd}	81.3±4.7 ^b	0.43±0.02 ^{c-f}	
T. mirabile	17.9±1.3 ^{c-i}	6.3±0.3 ^{cde}	18.3±0.8 ^{d-h}	53.8±2.5 ^{c-h}	0.41 ± 0.09^{def}	
'Türköz'	17.5±0.6 ^{f-j}	5.9±0.3 ^{cfg}	22.5±0.4 ^{ab}	91.3±2.0ª	0.51±0.03 ^{bcd}	
'Sırçalı'	22.0±1.8 ^{b-c}	4.9±0.2 ^{gh}	19.0±0.9 ^{c-f}	72.8±2.4 ^{bc}	0.51 ± 0.00^{bcd}	
'Taner'	17.0±0.7 ^{g-j}	3.7 ± 0.2^{i}	23.3 ± 1.2^{a}	59.5 ± 1.8^{def}	0.71 ± 0.01^{a}	
'Bozkır'	18.3±0.5 ^{d-i}	6.3±0.3 ^{cde}	21.9 ± 0.2^{abc}	61.5±0.5 ^{de}	0.43±0.03 ^{c-f}	
'Yavuz'	14.7 ± 1.1^{ij}	4.1 ± 0.2^{hi}	17.5±0.4 ^{c-h}	59.4±1 ^{d-g}	0.55±0.01 ^b	
'Tuğra'	13.4±0.5 ^j	3.5 ± 0.4^{i}	18.7±0.8 ^{c-f}	52.2±3.4 ^{f-i}	0.56 ± 0.07^{b}	
'Savatra'	16.3 ± 0.4^{hij}	4.3 ± 0.2^{hi}	17.7±0.3 ^{c-h}	60.8±2.3 ^{d-g}	0.70 ± 0.02^{a}	
Mean	19.7	6.5	19.2	58.3	0.49	
Р	<i>P</i> < 0.001	<i>P</i> <0.001	P < 0.001	P < 0.001	<i>P</i> < 0.001	

Table 2. Root and shoot traits of genotypes in early growth stages

Means followed by different letters within columns are significantly different (P < 0.001) according to Tukey's pairwise comparison test.

Comparable TRL values were observed among the *T. turanicum* genotypes, specifically *T. turanicum* (1), *T. turanicum* (2), and *T. turanicum* (3), suggesting similar patterns of root growth and length among these genotypes. *T. monococcum* accessions exhibited lower TRL values compared to other genotypes.

Root biomass

The root biomass (RB) of the *Triticum* genotypes showed significant variation, ranging from 0.043 to 0.122 g. In comparison, the *T. turanicum* genotypes showed a wider range of RB values, ranging from 0.080 to 0.098 g. *T. turanicum* (2) had the highest RB value, indicating a higher accumulation of root biomass, while *T. turanicum* (3) had the lowest RB value among the *T. turanicum* genotypes. Additionally, *T. polonicum* exhibited a relatively higher RB value of 0.115. For root biomass, the genotypes 'Taner', *T. polonicum*, 'Türköz', 'Sırçalı', 'Savatra', and *T. turanicum* (2) exhibited favorable characteristics. These genotypes have shown higher root biomass values compared to other genotypes.

Root to shoot ratio

Our results demonstrated considerable variation in root to shoot ratios among the investigated wheat genotypes. Among the *T. turanicum* accessions, *T. turanicum* (1) exhibited a root to shoot ratio of 0.34, while *T. turanicum* (2) and *T. turanicum* (3) had ratios of 0.36. Among the *T. monococcum* accessions, *T. monococcum* (1) showed a ratio of 0.38, and *T. monococcum* (3) and *T. polonicum* both had ratios of about 0.44. The root to shoot ratio of *T. monococcum* (1) was 0.45, while *T. monococcum* (3) had a slightly higher ratio of 0.48. *T. monococcum* (2) and *T. monococcum* (6) exhibited ratios of 0.52 and 0.53, respectively. 'Türköz' and 'Sırçalı' both displayed a root to shoot ratio of 0.51, and 'Yavuz' (5) had a ratio of 0.55. *T. monococcum* (4) had a ratio of 0.55, indicating a higher allocation of biomass to roots.

Company	Tiller number	Rooting depth	Shoot length	Root/shoot (ratio)	
Genotypes	/plant	(cm)	(cm)		
T. monococcum (1)	7.3±0.6 ^{ab}	$98.0 \pm 3.5^{\text{a-f}}$	41.0±2.6 ^{e-h}	0.66 ± 0.11^{abc}	
T. monococcum (2)	4.0 ± 1.7^{cd}	86.3±6.0 ^{d-g}	39.3±4.2 ^{c-h}	0.92±0.32ª	
T. monococcum (3)	5.3±0.6 ^{a-d}	80.3±5.8 ^{b-g}	38.7±0.6 ^{c-h}	0.56 ± 0.16^{abc}	
T. monococcum (4)	6.7 ± 1.2^{abc}	$91.0 \pm 7.0^{b-g}$	29.0 ± 1.0^{i}	0.72 ± 0.28^{abc}	
T. monococcum (5)	7.0 ± 0.0^{abc}	81.3±3.1 ^g	35±2.6 ^{hi}	0.67 ± 0.12^{abc}	
T. monococcum (6)	6.0±1.0 ^{a-d}	84.3 ± 4.2^{cfg}	38.7±1.5 ^{c-h}	0.59 ± 0.10^{abc}	
T. monococcum (7)	7.7±1.5ª	96.0±2.7 ^{a-f}	44.3±2.1 ^{c-f}	0.73±0.08 ^{abc}	
T. turanicum (1)	4.0±0.0 ^{cd}	98.3±4.5 ^{a-c}	60.3±0.6ª	0.55 ± 0.10^{abc}	
T. turanicum (2)	4.3 ± 0.6^{bcd}	106.3±0.6ª	52.3±2.1 ^b	0.84 ± 0.17^{ab}	
T. turanicum (3)	5.0±1.0 ^{a-d}	89.7±3.5 ^{b-g}	49.0 ± 1.0^{bcd}	0.60 ± 0.14^{abc}	
T. polonicum	3.3±0.6 ^d	99.7±3.8ª-d	65.0±2.0ª	0.39±0.06°	
T. mirabile	4.7±0.6 ^{a-d}	$84\pm4.6^{\mathrm{fg}}$	37.3±3.5 ^{fgh}	0.49 ± 0.08^{abc}	
'Türköz'	$7.0\pm1.0^{\mathrm{abc}}$	81.3±4.9 ^g	41.7±1.2 ^{c-h}	0.55 ± 0.09^{abc}	
'Sırçalı'	6.7 ± 1.2^{abc}	$94.0 \pm 8.5^{a-g}$	42.3±2.1 ^{d-g}	0.68 ± 0.13^{abc}	
'Taner'	6.7 ± 1.5^{abc}	100.7 ± 2.5^{abc}	49.7±1.5 ^{bc}	0.42 ± 0.11^{bc}	
'Bozkır'	7.3±0.6 ^{ab}	84.0 ± 5.3^{fg}	41.7±4.2 ^{e-h}	0.56±0.12 ^{abc}	
'Yavuz'	5.0±1.0 ^{a-d}	88.7±4.7 ^{c-g}	45.0±3.5 ^{cde}	0.53±0.05 ^{abc}	
'Tuğra'	5.0±1.0 ^{a-d}	103.3 ± 1.5^{ab}	37.0±0.0 ^{gh}	0.57 ± 0.05^{abc}	
'Savatra'	4.7±1.2 ^{a-d}	103.0±2.7 ^{ab}	45.7±1.5 ^{b-c}	0.91±0.13ª	
Mean	5.7	92.1	43.8	0.63	
Р	<i>P</i> < 0.001	<i>P</i> < 0.001	<i>P</i> <0.001	<i>P</i> <0.001	

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Means followed by different letters within columns are significantly different (P < 0.001) according to Tukey's pairwise comparison test.

The genotypes 'Savatra' and 'Taner' showed the highest root to shoot ratios among all investigated genotypes, with ratios of 0.69 and 0.72, respectively.

Seminal root number

The genotypes exhibited significant variation in seminal root numbers, ranging from 3 to 5. *T. monococcum* (5), *T. turanicum* (3), and 'Türköz' had the highest seminal root numbers at 4.4, 4.2, and 5.0, respectively, while 'Taner' and *T. monococcum* (1) and (7) had the lowest seminal root numbers at 3.0. Among the *T. monococcum* genotypes, *T. monococcum* (5), *T. monococcum* (1), and *T. monococcum* (4) displayed relatively higher seminal root numbers, ranging from 4.2 to 4.4. These results suggested differences in primary root development within the *T. monococcum* species. *T. turanicum* (2) and 'Sırçalı' genotypes also showed

comparable seminal root numbers, indicating similar root development patterns among these genotypes. Among the genotypes, 'Türköz' and *T. polonicum* exhibited the highest mean root numbers, with values of 5. Conversely, 'Taner' and *T. monococcum* (2) had the lowest mean root numbers, with values of 3.0 each. These genotypes may have limited root proliferation, which could impact their overall growth and nutrient acquisition abilities. 'Sırçalı' demonstrated the highest mean root number among the genotypes, with a value of 4.8. This genotype may possess genetic traits that promote robust root development, contributing to its overall performance.



Figure 1. The image displays a lineup of wheat genotypes, including 'Türköz' (a), *T. polonicum* (b), *T. mirabile* (c), *T. monococcum* (d), and *T. turanicum* (e), arranged from left to right. Figure 1a represents the average data of root and shoot biomass (P<0.001) for various wheat genotypes during the stem elongation stage. The Figure 1a is a representative of root architecture, showcasing seven modern wheat cultivars, seven *T. monococcum* accessions, three *T. turanicum* accessions, *T. mirabile*, and *T. polonicum*. In Figure 1b, the average data of rooting depth (P<0.05) and shoot height (P<0.001) during the stem elongation stage are displayed

Shoot length

The *Triticum* genotypes displayed notable diversity in terms of shoot length (SL) with values ranging from 13.4 cm to 27.3 cm. *T. polonicum* had the highest SL at 27.3 cm, while 'Tuğra' exhibited the lowest value

at 13.4 cm. Among the *T. monococcum* accessions, *T. monococcum* (1) and *T. monococcum* (6) displayed relatively higher SL values, ranging from 22.8 cm to 21.1 cm.

This indicated variations in shoot development and length within the *T. monococcum* species. *T. turanicum* (1) had the highest SL among the *T. turanicum* genotypes, whereas 'Tuğra' had the lowest value in modern cultivars.

Shoot biomass

The shoot biomass (SB) varied significantly among the *Triticum* genotypes, ranging from 0.09 to 0.27 g. Among *T. monococcum* accessions, *T. monococcum* (5) exhibited the highest SB value of 0.14 g, while *T. monococcum* (3) had the lowest value of 0.09 g. In comparison, Triticum *turanicum* genotypes demonstrated consistent SB values, with *T. turanicum* (1) and *T. turanicum* (2) both displaying a SB value of 0.27 g, indicating a relatively higher shoot biomass accumulation in these genotypes. Notably, *T. polonicum* showed substantial shoot biomass accumulation, with an SB value of 0.26 g. SB of modern cultivars was above 0.15 g, and 'Sırçalı' and 'Türköz' had relatively higher RB values of 0.22 g.

Coleoptile length

The coleoptile length varied significantly among the *Triticum* genotypes in a range between 3.5 cm and 9 cm. *T. polonicum* exhibited the longest coleoptile length, with a value of 9 cm. Among the *T. monococcum* genotypes, *T. monococcum* (1) had the highest coleoptile length of 7.3 cm, suggesting relatively greater shoot elongation during emerging compared to other *T. monococcum* genotypes. *T. turanicum* (1) displayed the second-highest coleoptile length among the genotypes, with a value of 8.3 cm, indicating its potential for longer shoot elongation during germination compared to other *T. turanicum* genotypes. Cultivars 'Taner' and 'Tuğra' showed the shortest coleoptile lengths among all genotypes, with values of 3.7 cm and 3.5 cm, respectively.

Root and shoot traits in the stem elongation stage

Rooting depth

The genotypes displayed significant variation in rooting depth, ranging from 80.3 cm to 106.3 cm. *T. polonicum* had a rooting depth of 99.7 cm, 'Taner' reached 100.7 cm, and 'Savatra' and 'Tuğra' exhibited depths of 103 cm and 103.3 cm, respectively. However, 'Türköz' and 'Bozkır' exhibited a shorter depth of 81.3 cm and 84 cm, respectively, compared to other modern cultivars. *T. turanicum* (2) had the highest rooting depth among the analysed genotypes, measuring 106.3 cm. Ancient wheat species, *T. turanicum*, and *T. polonicum* genotypes displayed relatively deeper rooting depths compared to the other ancient wheat species.

Nodal root number

The genotypes exhibited significant variation in nodal root number (NRN), ranging from 3.3 to 9.7. *T. monococcum* (2) had the lowest NRN at 3.3, while *T. turanicum* (2), 'Taner', 'Sırçalı', 'Türköz', and 'Bozkır' displayed relatively higher NRN compared to the other genotypes.

Root biomass

The genotypes showed significant variation in root biomass, ranging from 0.3 to 1.4 g. *T. monococcum* (3) had the lowest root biomass at 0.3 g, while *T. turanicum* (2) displayed the highest biomass with a value of 1.4 g. Among the *T. monococcum* genotypes, *T. monococcum* (1), *T. monococcum* (4), *T. monococcum* (5), *T. monococcum* (6), and *T. monococcum* (7) exhibited similar root biomass values ranging from 0.5 to 0.7 g. These results suggest comparable root biomass development within the *T. monococcum* species. Among the genotypes evaluated, 'Türköz', 'Bozkır', 'Sırçalı', and 'Savatra' exhibited higher root biomass values, ranging from 0.9 to

1.1 g. Comparatively, the ancient wheat species, including *T. monococcum*, *T. mirabile*, and *T. polonicum*, had lower root biomass values ranging from 0.3 to 0.8 g than *T. turanicum* accessions.

Root to shoot ratio

The results indicate considerable variation in root to shoot ratios (R/S) among the different genotypes. *T. monococcum* showed a wide range of ratios, with values ranging from 0.56 to 0.92. This suggests that different accessions of *T. monococcum* may employ diverse strategies in resource allocation between roots and shoots. Notably, *T. monococcum* (2) and *T. monococcum* (7) had notably higher ratios, indicating a preference for shoot development. *T. turanicum* also displayed variation in root-to-shoot ratios, with values ranging from 0.55 to 0.84. Similarly, 'Sırçalı' and 'Savatra' exhibited relatively higher ratios, suggesting a focus on shoot growth in these genotypes. Additionally, 'Taner' and *T. mirabile* also had lower ratios, reflecting a tendency for enhanced root growth.

Shoot height and tiller number

The genotypes revealed significant variation in shoot length, ranging from 29 cm to 65 cm. *T. monococcum* (4) displayed the shortest shoot length at 29 cm, while *T. polonicum* exhibited the tallest plants at 65 cm. 'Sırçalı' reached a height of 42.3 cm, *T. monococcum* (7) had a height of 44.3 cm, and 'Yavuz' and 'Savatra' exhibited heights of 45 cm and 45.7 cm, respectively. *T. turanicum* (3) and 'Taner' displayed shoot lengths of 49.0 cm and 49.7 cm, while *T. turanicum* (2) reached a height of 52.3 cm. Among ancient wheat species, *T. turanicum* accessions and *T. polonicum* demonstrated the tallest shoot length among the genotypes analysed, measuring between 49 cm and 65 cm.





Figure 2. Root biomass and shoot biomass in early growth stage in Figure 2a (P<0.001), in stem elongation stage in Figure 2b (P<0.001), and seminal in early growth stage and nodal root numbers in stem elongation stage in Figure 2c (P<0.001). The names of the genotypes are represented by four-letter abbreviations.

The genotypes exhibited significant variation in tiller numbers, ranging from 3.3 to 7.7. *T. polonicum* and *T. turanicum* (2) displayed the lowest tiller numbers at 3.3 and 4.0, respectively, while *T. monococcum* (7) had the highest tiller number at 7.7.



Figure 3. An unrooted dendrogram, showing the clustering patterns of six significant traits (rooting depth, root biomass, and root to shoot ratio) in both growth stages, was constructed using the euclidean distance and average cluster algorithms.



Figure 4. Correlations between the investigated root and shoot traits at two different growth stages: early growth stage (left side) and stem elongation stage (right side). The traits analysed included SRN (seminal root number), NRN (nodal root number), CL (coleoptile length), TRL (total root length), RD (rooting depth), RB (root biomass), SB (shoot biomass), and R/S (root to shoot ratio)

Shoot biomass

The shoot biomass of the genotypes showed significant variation, ranging from 0.4 to 1.8 g. Genotypes *T. monococcum* (2) and *T. monococcum* (3) had the lowest shoot biomass values at 0.4 g and 0.6 g, respectively, while 'Bozkır' exhibited the highest shoot biomass at 1.8 g. The variations in shoot biomass observed among the genotypes can have implications for their agronomic performance, including high root biomass accumulation. The study indicated positive and significant relationships between root and shoot biomass in both growth stages (Figures 5a and 5b).



Figure 5. Regression analyses to examine the relationship between root and shoot traits at different stages of plant growth. Figures a, c, and f illustrate the analyses conducted during the early growth stage, while figures b, d, and e represent the analyses carried out during the stem elongation stage. The results, including the R and P values, are displayed on the respective images.

Discussion

Rooting depth

The genotypes analysed displayed significant variations in rooting depth in the early and stem elongation growth stages. When evaluated together in both growth stages, 'Taner', T. turanicum (1), and T. turanicum (2) exhibited deeper rooting, potentially attributing them to accessing water and nutrients from deep soil layers (Saengwilai et al., 2014; York et al., 2018; Ober et al., 2021). On the other hand, genotypes such as T. monococcum (3) showed shallower rooting depths, suggesting potential differences in their resource acquisition strategies (Kashiwagi et al., 2017). Compared to a shallow root system, a deeper root system architecture in bread wheat provided enhanced stability for photosynthesis and yield, particularly during periods of terminal drought stress (Kulkarni et al., 2017; Rathod et al., 2022). The possession of a deep root system stands out as the crucial attribute for the ideotype of a drought-tolerant crop, as it enables the utilization of residual water resources and nitrogen (N) from deeper soil layers. The presence of deep root systems contributed to an increase in grain yield by 20% in drought conditions (Jordan et al., 1983). Modern cultivars exhibited an enhanced capacity to extract moisture from deeper soil profiles, particularly at depths of 60-120 cm, especially during grain filling, as observed in the study by Pask and Reynolds (2013). Similarly, in the current study, the rooting depth of modern cultivars during stem elongation ranged between 81.3 cm and 103.3 cm in the stem elongation stage. The deep rooting trait collectively underscores yield increase, drought tolerance, water-use efficiency, and nutrient acquisition. Understanding the variations in rooting depth among different genotypes can aid in the selection and breeding of wheat varieties with improved root characteristics, ultimately enhancing their adaptability and productivity in diverse agricultural environments.

Root biomass and root to shoot ratio

Several studies have highlighted the importance of greater root biomass at deeper levels as an advantage in efficiently capturing soluble nitrogen, preventing its leaching into groundwater (Bakhshandeh et al., 2016; Koevoets et al., 2016; Ober et al., 2021). The combined evaluation of early growth and stem elongation stage root biomasses (RBs) allows us to assess the genotypes' overall root biomass growth patterns. Based on the consistent RB results, 'Yavuz', 'Bozkır', 'Savatra', 'Sırçalı', 'Türköz', 'Taner', and T. turanicum accessions were found to exhibit promising root biomass growth characteristics. Waines and Ehdaie (2007) showed that modern wheat cultivars exhibited smaller root systems compared to landraces. Paschen (2017) revealed that T. turanicum exhibited significantly higher RB in comparison to other ancient wheat species, including T. ispahanicum, T. monococcum, T. dicoccum, and T. carthlicum. In the study, notably, the average root biomass of T. turanicum accessions was approximately two-fold greater than that of T. monococcum (Figure 1a). On the other hand, T. monococcum accessions and T. mirabile for root biomass, rooting depth and root to shoot values in both growth stages were grouped together, forming a distinct group separated from modern cultivars, T. polonicum and T. turanicum accessions (Figure 3). Therefore, it is significant that identifying the variations in root biomass among ancient wheat species and modern wheat cultivars facilitates the discernment of prospective cultivars harbouring exceptional root architectures capable of acclimatizing to diverse environmental stress factors.

The combined analysis of shoot biomass (SB) during early and late growth stages provides valuable insights into the performance of different wheat genotypes. Compared to the early and late growth stages together, it is noteworthy that modern wheat cultivars along with *T. turanicum* accessions and *T. polonicum* indicated higher SB values. In contrast, genotypes like *T. monococcum* accessions and *T. mirabile* exhibited relatively lower SB values during both growth stages. When evaluating the R/S ratio across both growth stages, 'Savatra' exhibited a consistently high R/S ratio of 0.90 in the early stage and 0.70 in the stem elongation stage, respectively. Furthermore, *T. monococcum* (2) and *T. turanicum* (2) demonstrated a significant increase in R/S

ratio in the stem elongation stage when compared to the early growth stage, indicating a shift towards greater root or less shoot development between these growth stages. Conversely, a significant decrease in the R/S ratio was observed in 'Taner' from 0.71 to 0.42 towards the late growth stage. This suggests that different genotypes may employ diverse growth patterns in allocating resources between roots and shoots.

Total root length

The genotypes analysed displayed significant variations in TRL in the early growth stage, indicating differences in the development and architecture of their root systems. Bakhshandeh *et al.* (2016) provided evidence that longer root length positively influenced both ammonium uptake and water uptake. Genotypes with longer TRLs, such as 'Türköz', *T. polonicum*, 'Sırçalı', and *T. turanicum* (1), may possess more extensive and well-developed root systems, enabling them to explore larger soil volumes and potentially acquire more nutrients and water.

On the other hand, genotypes with relatively shorter TRLs, such as *T. monococcum* accessions, may have less extensive root systems. Paschen (2017) indicated a positive correlation ($r^2 = 0.60$) between root biomass and root length. Similarly, we observed a remarkably significant and positive correlation ($r^2 = 0.67$) between the two variables in the early growth stage (Figure 5e).

Number of seminal and nodal roots

The initial type of roots to emerge, known as seminal roots, play a crucial role in absorbing nutrients and water for seedlings. Consequently, they significantly influence seedling strength and the early establishment of plants, ultimately impacting their competitiveness against weeds.

On the contrary, nodal roots are borne from the shoot and emerge shortly after tillering in wheat plants. Their primary function is to anchor the plant and facilitate the uptake of essential resources, particularly during the reproductive phase of wheat growth (Manske and Vlek, 2002).

Under drought and mechanical stresses, seminal roots may assume greater importance due to their ability to penetrate deeper into the soil layers compared to nodal roots, thereby facilitating the plant's access to water in the deeper soil layer (Araki and Lijima, 2001; Manschadi *et al.*, 2013). A combined analysis of the number of seminal and nodal roots revealed that durum wheat cultivars, 'Sırçalı' and 'Türköz' consistently exhibited the highest values for both root parameters, indicating a tendency towards a more focused and efficient branched root system. On the other hand, *T. monococcum* (2) demonstrated a consistently lower value for seminal and nodal root numbers. In the study, seminal root numbers varied between 3 and 5 per plant. However, wheat varieties may have a sixth seminal root as well (Shorinola *et al.*, 2019).

Root number, referring to the number of roots per plant, is a key component of root system architecture. Increased root number facilitates enhanced soil exploration, nutrient uptake, and anchorage, leading to improved overall plant performance. A previous study demonstrated positive correlations between root number and nutrient acquisition in wheat (Wang *et al.*, 2016). Higher root number density in the soil profile was found to be positively correlated with a lesser decline in leaf photosynthesis rate during drought conditions (Rathod *et al.*, 2022).

The number of seminal roots exhibited a significant correlation with thousand kernel weight (TKW) under stress conditions, as reported by Ruiz *et al.* (2018) and Xu *et al.* (2021). On the contrary, Koevoets et al. (2016) showed that accessions with more nodal roots had a higher yield and biomass. In the present study, the seminal root number was comparatively low for *T. turanicum* accession (1) at 3.7 and medium for *Triticum turanicum* accessions (2) and (3) at 4.2, whereas *T. polonicum* and 'Türköz' exhibited the highest number of seminal roots. It is worth noting that in previous studies conducted by Wang *et al.* (2002) and Akman and Karaduman (2021), *T. polonicum* and *T. turanicum* genotypes displayed notably higher thousand-grain weight compared to other genotypes. Therefore, the observations differ from the findings indicating a positive relationship between thousand kernel weight and seminal root number reported by Ruiz et al. (2018) and Xu

et al. (2021), suggesting some inconsistencies in the results. These variations might be attributed to the diverse environmental conditions, genetic backgrounds, and experimental designs among different studies. Further investigations are warranted to gain a comprehensive understanding of the complex interactions between root number with thousand grain weight, and grain yield in wheat genotypes under varying conditions.

Conclusions

This study sheds light on the critical role of root characteristics in wheat genotypes during early vegetative growth and stem elongation, offering valuable insights into the enhancement of crop productivity. The observed phenotypic diversity among the evaluated genotypes, particularly in root biomass, rooting depth, root number, and shoot traits, underscores the significance of these traits for selecting and developing wheat genotypes with improved nutrient and water uptake efficiency, stress tolerance, and overall agronomic performance. Notable genotypes like wheat accessions T. monococcum (1) and T. turanicum (2), with their deep-rooting abilities, have the potential to facilitate better access to water and nutrients, particularly in regions susceptible to drought. Conversely, the shallow rooting depth of *T. mirabile* presents a distinct profile among the evaluated genotypes. Moreover, modern wheat cultivars and *T. turanicum* accessions, displayed higher root biomass in both growth stages, indicating a greater investment in root growth, potentially enhancing nutrient acquisition. Furthermore, the findings highlight the importance of genetic diversity in root traits as a foundational resource for advancing crop improvement and adaptation to varying environmental conditions. The identification of genotypes with desirable root characteristics can significantly enhance nutrient and water uptake efficiency, ultimately leading to increased crop productivity and sustainability. These improved root characteristics can contribute to more resilient and productive wheat cultivars, which are essential for meeting the increasing grain yield. With the advancement of phenotyping technologies and molecular approaches, the potential for crop improvement in the realm of root traits appears promising, paving the way for more sustainable and efficient agricultural practices.

Authors' Contributions

Conceptualization: HA, EY and SAB; Data curation: HA and EY; Formal analysis: HA and EY; Funding acquisition: EY; Investigation: HA and SAB; Methodology: HA; Project administration: HA and SAB; Resources: HA, EY, and SAB; Supervision: HA; Visualization: HA; Writing - original draft: HA; Writing - review and editing: HA and SAB. All authors read and approved the final manuscript.

Ethical approval (for researches involving animals or humans)

Not applicable.

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Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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