

Landraces and scientifically-bred varieties — factors of adaptation

UDC 633.11:58.056:[581.1+575.1]/2

doi: 10.15389/agrobiol.2016.1.68rus

doi: 10.15389/agrobiol.2016.1.68eng

COMPARATIVE CHARACTERISTICS OF ROOT SYSTEMS AND ROOT EXUDATION OF SYNTHETIC, LANDRACE AND MODERN WHEAT VARIETIES

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Acknowledgements:

Study of root exudates isolation was supported by Russian Foundation for Basic Research (15-04-09023-a). Experiments on root exudates chromatography were supported by Russian Science Foundation grant (14-26-00094). Experiments in CIMMYT-Turkey were supported by CRP WHEAT and Republic of Turkey Ministry of Food, Agriculture and Livestock
Received April 24, 2015

doi: 10.15389/agrobiol.2016.1.68eng

Abstract

Finding ways to increase the wheat adaptation to drought is now considered as a major problem in breeding new varieties of this crop. This study was conducted to evaluate genotypic differences in fundamental root traits which may have effect on wheat adaptation to unfavorable environments, including drought. Three wheat genotypes representing various evolution levels of hexaploid bread wheat (*Triticum aestivum* L.) were used: synthetic wheat developed by crossing variety LEUCURUM 84693 of durum wheat (*Triticum durum* Desf., genome AB, Ukraine) with wild Tausch's goat grass (*Aegilops tauschii* Coss., genome D, Turkey), landrace of bread wheat Albostan (genome ABD, Turkey, province Nevşehir), and a modern cultivar Karahan (genome ABD, Turkey). The varieties differed in root diameter, shoot biomass and shoot/root ratio. The removal of above ground biomass caused increase in the root length, number of tips, number of forks, number of crosses and shoot/root biomass ratio of synthetic wheat and Albostan, but decreased these parameters in Karahan. Averaged values of ten measured growth parameters of the plants with removed above ground biomass relatively to the control plants were +28 % for synthetic wheat, 0 % for landrace Albostan and -37 % for cultivar Karahan. These results showed a higher ability of synthetic wheat but lower ability of Karahan to recover from cutting stress and to revegetate. For the first time a comparative analysis of root exudation (amino acids, sugars and organic acids) by wheat genotypes having different levels of evolution was performed. It was shown that Karahan was characterized by high exudation of tryptophan (0.05 mg/g dry roots per day), histidine (0.12 mg/g dry roots per day) and phenylalanine (0.45 mg/g dry roots per day). Total amount of sugars (mostly fructose, glucose and maltose) exuded by Karahan was 55 mg/g dry roots per day, that was 5 and 3 times higher as compared to synthetic genotype and Albostan. The quantum of organic acids in exudates of all studied genotypes was approximately similar and amounted to about 1.8 mg/g of dry roots per day. The results suggested low ability of Karahan to control the flow rate of carbohydrates from roots to the environment. We propose that high root exudation of tryptophane (precursor in biosynthesis of auxins) and sugars may result in deficit of these compounds and involved in impaired shoot regeneration of Karahan. The results demonstrated differences in the functioning of the root system of primitive hexaploid wheat (synthetic) compared to landrace and modern cultivated variety. The nature of these differences requires more investigation.

Keywords: wheat, root exudation, revegetation, drought stress adaptation.

Wheat (*Triticum* spp.) is one of the main crops providing millions of people with food products. It is estimated (<http://www.wheatinitiative.org>) that by 2050 the production of wheat grains must be increased from the current 650-700 tons to 1 billion tons. However, the possibilities of mobilizing the genetic resources of this crop have been considerably exhausted since the Green Revolution. This, in combination with adverse climate changes, can partially explain

the fact that the varieties used have practically reached their biological yield limit. The recent studies on winter wheat in Europe, Central and Eastern Asia and the USA revealed increased average air temperature in periods critical for plant development [1]. Though warmer winters generally led to a higher yield of this crop, the increased temperature in late spring or in summer reduced it because of drought. Now, the adaptation to drought is considered an important task in wheat breeding which gave rise to the International Winter Wheat Improvement Program (IWWIP, <http://www.iwwip.org/>).

Drought resistance in wheat may be evaluated by the crop yield and biochemical composition, and by the traits contributing to high yield at a lack of moisture, for example by the structure of the root system responsible for the absorption and transportation of water to the shoots [2]. It is demonstrated that the efficiency of moisture absorption from arid soils is generally determined by the contact area of the root system which in its turn is determined by root branching and the length of root hairs [3].

Most vascular plants are capable of improving their mineral and water nutrition by forming associations and symbioses with soil microorganisms at their roots and in the rhizosphere [4-7]. The main carbon and energy sources for such microorganisms are the organic substances (mostly sugars, organic acids and amino acids) excreted by the roots into the rhizosphere [8]. Root exudates also play an important role in supplying plants with nutrient elements the lack of which may be manifested in drought conditions [9, 10].

At drought, the root to shoot weight ratio increases, but the overall dry weight of roots increases very rarely as compared to that in normal conditions. However, with moisture deficiency the density of the root system per unit of leaf area generally grows [11]. The photosynthates that could be used for the development of new roots are used for the growth of the existing ones, resulting in their penetration into deeper soil layers. For wheat, soil drainage restrained root growth in the upper soil layer (30 cm) and made them spread deeper [12]. After normal soil moisture recovers, the plant roots start to grow quickly again in the upper soil layer and cease developing in deeper layers.

The immediate assessment of the root parameters during research and selection in field conditions is rather labor consuming and requires special equipment. Currently, an indirect indicator, the vegetation cover temperature, is often used to determine the capability of roots to supply plants with nutrient substances and water [13]. Wheat genotypes with good water balance and drought-resistance generally have a lower temperature than the plants growing under drought conditions. However, measuring temperature of the vegetation cover, though a simple and quick, still requires special conditions (i.e., a sunny day without wind) that are not always the case. Another indirect method is measuring plant ability to regenerate after the aboveground parts cut. The removal of aboveground parts in wheat and other crops is a widely used for dual-purpose crop practice on the southern valleys of the USA, in South America and Australia, where fields are used in winter as pastures, after which the crops are grown until grain harvest [14]. However, this technique has never been used in research to assess the adaptation of wheat genotypes to drought and the interrelation between shoot regeneration and root exudation.

The diversity of genetic wheat resources is the basis for enhancing the resistance of plants to abiotic stresses, including drought. More and more researchers and breeders look for new drought-resistance genes beyond the existing and well-described genotypes. The potential sources of such genes are traditional local varieties that have been cultivated for centuries in isolated and arid regions. In Turkey, local primitive wheat varieties are still cultivated throughout the

country, especially in mountainous regions, still being the source of genetic diversity and valuable traits. Synthetic wheat obtained by crossing durum wheat (*Triticum durum* Desf.) and wild Tausch's goat grass (*Aegilops tauschii* Coss.) also possesses a number of useful features, including drought-resistance [15].

Our purpose was to evaluate the root and stem systems of three wheat genotypes (i.e., primitive, modern, and synthetic varieties) representing various stages of the hexaploid wheat evolution in normal conditions and under exposure to stress caused by the removal of aboveground parts. For the first time, root exudation of assimilates (organic acids, sugars, and amino acids) was compared in plant genotypes with identified differences in the root system functioning and shoot regeneration.

Technique. The objects of research were the wheat genotypes received under the IWWIP program from the International Maize and Wheat Improvement Center (CIMMYT, Turkey), corresponding to three levels of the crop evolution: a synthetic form produced by crossing durum wheat (*T. durum* Desf.) of the Ukrainian variety LEUCURUM 84693 (AB genome) and wild Tausch's goat grass (*A. tauschii* Coss.) with genome D; the traditional hexaploid wheat variety (*T. aestivum* L.) Albostan (genome ABD) of local selection in the Turkish province Nevşehir; drought-resistant modern wheat variety (*T. aestivum* L.) Karahan (genome ABD) from Turkey bred in the 1990s through standard methods.

Study of growth of shoots and roots and their response to the removal of shoots was conducted based on the Turkish department CIMMYT (Izmir, Turkey). The plants were grown in pots filled with 1 kg of sand (2 plants per pot, and 4 pots per variant) under natural temperature and light conditions (with night temperature of 8-12 °C and daytime temperature of 20-24 °C) in February to March 2014 to the 4th to 5th leaf before shooting. The plants were watered twice a week (200 ml of water per pot). The plants were treated with the nutrient solution (N₂₀P₂₀K₂₀, 250 g/l, Harmony Imports, USA) three times: at the 2nd to 3rd leaf, before tillering and 1 week after tillering. After five to six weeks, an initial assessment was conducted of the parameters studied. The plants from two pots were removed, and the roots were washed and scanned using an Epson Perfection V700 (Epson America, Inc., USA) and a WinRHIZO (Regent Instruments, Inc., Canada). Then, the roots and shoots were dried up in room temperature until constant dry weight. In the two remaining pots, the shoots were cut and the plants were left for 3-4 weeks for revegetation, after which the parameters of shoots and roots were assessed as described above.

The experiments with root exudates were conducted at the All-Russia Research Institute for Agricultural Microbiology using hydroponic culture. To receive root exudates, the seeds were subject to surface sterilization for 6 minutes with 0.1 % HgCl₂, washed with sterile water, and then they germinated for 2 days in Petri dishes in darkness at 27 °C. The sprouted seeds were planted into sterile glass dishes with 100 ml of deionized water and stainless steel meshes (10 seeds per dish, and 3 dishes per genotype). The seedlings were cultivated in the climatic cell ADAPTIS-A1000 (Conviron, Great Britain) for 5 days (at illumination of 200 $\mu\text{lk} \cdot \text{m}^{-2} \cdot \text{c}^{-1}$ and 16-hour photo-period with minimum and maximum temperatures of 18 °C and 22 °C, respectively). After 3 days, 0.1 ml of the solution was taken from each pot and plated on Petri dishes with Bacto Pseudomonas agar (Difco International BV, Netherlands) to control sterility. After 5 days, the plants were taken out of the dishes, dried up, and the dry weight of shoots and roots was determined. The solutions from the three dishes were pooled, vacuum-filtered through nylon filters (0.45 μm ; Coming, Inc., USA) and

vacuum-evaporated to 5 ml using a rotary evaporator BUCHI R-200 (BUCHI Labortechnik AG, Switzerland). Aliquot of 100 μ l was taken from each concentrate of root exudates, and the remaining solution was poured through a column with ion-exchange resin DOWEX 50Wx8 (Sigma-Aldrich Co., USA) to obtain a purified fraction of organic acids and sugars, vacuum-evaporated to dryness, and the residue was dissolved in 0.5 ml of deionized water. The chromatographic analysis was conducted using Waters ACQUITY UPLC H-Class (Waters, USA). Sugars were separated using a SUPELCOSIL LC-NH₂ column (Supelco Gland, Switzerland). To identify sugars, a refraction index detector Waters 2414 (Waters, USA) was used. Amino acids, except L-tryptophan, were analyzed using Waters AccQ-Tag (Waters, USA) with a fluorescence detector by the manufacturer's standard method. L-tryptophan in root exudates was determined by separation using a column Waters UPLC RP-18 Shield (Waters, USA) with a fluorescence detector ACQUITY UPLC (Waters, USA). Organic acids were separated using ACQUITY CSH C18 (Waters, USA) and determined with an UV-detector Photodiode Array ACQUITY UPLC (Waters, USA) at $\lambda = 210$ nm. The freshly prepared mixtures of sugars, organic acids, non-proteinogenic acids (1-amino-cyclopropane-1-carbonic acid, β -alanine, α -aminobutyric acid, β -aminobutyric acid, γ -aminobutyric acid, N-butyryl-DL-homoserine lacton, L-canavanine, L-citrulline, dopamine, DL-homoserine, D-glucosamine, L-mimosine, L-ornithine, serotonin) (analytical grade, Sigma-Aldrich Co., USA), L-tryptophan (analytical grade, Fluka Chemie GmbH, Switzerland) and Amino Acid Hydrolysate Standard H (Thermo Fisher Scientific, Inc., CIIIA) served as standards for identifying components of root exudates. Three replicates were conducted.

For data processing (i.e., determining standard errors, Student's *t*-test LMD, correlation analysis), STATISTICA v. 7.0 (StatSoft Inc., USA) and the dispersion analysis program DIANA were used [16].

Results. In the synthetic wheat obtained due to crossing durum wheat (*T. durum* Desf.) of the LEUCURUM 84693 variety (genome AB) and goat grass

Root and shoot growth in the wheat genotypes representing various levels of the crop evolution (pot test with and without shoot removal)

Parameter (per plant)	Control			Plants with removed shoots					
				total			vs. control, %		
	1	2	3	1	2	3	1	2	3
Root length, cm	823 ^a	923 ^a	1373 ^a	1274 ^a	1404 ^a	1052 ^a	+55	+52	-23
Root area, cm ²	144 ^a	206 ^a	204 ^a	160 ^a	153 ^a	103 ^a	+11	-26	-50
Root volume, cm ³	2.1 ^{ab}	3.7 ^{ab}	2.4 ^{ab}	1.6 ^{ab}	1.3 ^{ab}	0.8 ^a	-22	-64	-67
Average root diameter, mm	0.55 ^c	0.71 ^d	0.48 ^{bc}	0.40 ^{ab}	0.35 ^{ab}	0.31 ^a	-27	-51	-34
Number of root tips	1596 ^a	2022 ^a	2311 ^{ab}	2365 ^{ab}	3398 ^b	2534 ^{ab}	+48	+68	+10
Root fork number	6650 ^a	9723 ^a	11069 ^a	9529 ^a	10268 ^a	6299 ^a	+43	+6	-43
Number of root overlaps	926 ^a	1213 ^a	2121 ^a	1963 ^a	2318 ^a	1618 ^a	+112	+91	-24
Dry root weight, g	0.29 ^{ab}	0.53 ^b	0.31 ^{ab}	0.19 ^a	0.17 ^a	0.12 ^a	-35	-69	-63
Dry shoot weight, g	0.56 ^a	1.30 ^b	1.19 ^b	0.64 ^a	0.54 ^a	0.43 ^a	+15	-59	-64
Shoot to root weight ratio	2.0 ^a	2.5 ^{ab}	4.0 ^b	3.5 ^{ab}	3.2 ^{ab}	3.7 ^b	+78	+32	-8

Note. 1 — synthetic form created by crossing durum wheat (*Triticum durum* Desf.) of the Ukrainian variety LEUCURUM 84693 (genome AB) and wild Tausch's goat grass (*Aegilops tauschii* Coss.) (genome D); 2 — traditional variety of hexaploid wheat (*T. aestivum* L.) Albostan (genome ABD) of local Turkish selection; 3 — modern Turkish drought-resistant wheat variety (*T. aestivum* L.) Karahan (genome ABD). In an experiment two replicates were performed per each variant. Different Latin characters are used to indicate significant differences between the variants for each parameter (LMD test, $P < 0.05$).

(genome D), the resulting hexaploid genotype (genome ABD) reconstructs semi-wild wheat that existed 4,000-6,000 years ago when it was cultivated in the Middle East in the area of the so-called Fertile Crescent. The genotype is resistant to abiotic and biotic stresses due to the genes received with genome D. Albostan (genome ABD) is a local ancient traditional primitive variety of hexaploid wheat (*T. aestivum* L.) well adapted to drought that was cultivated in Turkey hundreds

years ago without any improvements through modern breeding methods. Karahan (*T. aestivum*) (genome ABD) obtained by standard breeding is drought-resistant and used in Turkey in development of drought-resistant varieties.

The vegetation experiment showed that Albostan had a bigger root diameter as compared to the synthetic genotype and Karahan (by 29 % and 48 %, respectively), while the shoot weight and the shoot to root ratio in Albostan and Karahan plants were higher than those of the synthetic genotype (by 130 % and 113 %, and by 25 % and 100 %, respectively) (Table).

Shoot removal resulted in a 27-50 % decrease in the root diameter of all genotypes, and in a 68 % increase in the number of new roots in Albostan plants. The weight of shoots in Albostan and Karahan plants reduced 2.4-fold and 2.8-fold, respectively, and the weight of roots in Albostan plants reduced 3.1-fold (see the Table). With shoot removal, some characteristics of the root system (e.g., root length, root number, number of forks, shoot to root ratio) changed depending on the wheat genotype, namely increased in the synthetic form and the Albostan variety, but decreased in Karahan plants (see the Table). These data can be considered as an evidence that even in modern scientifically-bred varieties with effective root system its recovery after stressing caused by shoot removal is still problematic. In the control variant, the shoot weight in the modern cultivar Karahan was 4.0 times higher than the root weight (see the Table), while in synthetic wheat plants and in the traditional local variety Albostan it was only 2.0 times and 2.5 times higher, respectively. After shoot removal, the root system of the synthetic wheat form and the Albostan variety demonstrated high efficiency in re-vegetation and contributed to the growth of new shoot weight to the values that are 3.2-3.5 times higher than the root weight. Comparing average growth values of the control plants exposed to stress confirmed that the effect of the shoot removal depends substantially on wheat genotype (Fig. 1). For synthetic wheat, seven parameters out of those ten studied (see Table) demonstrated a positive reaction to the shoot removal, the Albostan variety under stress showed higher values of five parameters, while in the modern variety Karahan only one parameter changed positively.

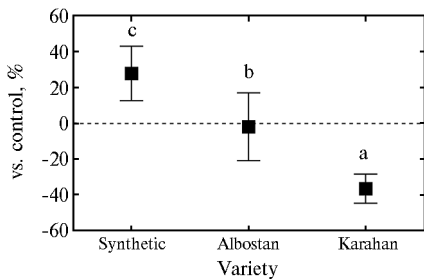


Fig. 1. Average values of growth parameters in wheat plants with removed shoots versus the control ones (%). The forms representing various levels of the crop evolution have been studied: synthetic, traditional landrace Albostan, and modern Turkish cultivar Karahan. The data and variety descriptions are provided in the Table. The vertical sections indicate the standard error of mean. Different Latin characters indicate significant differences between the variants (LMD test, $P < 0.05$).

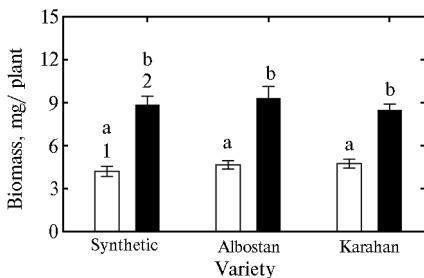


Fig. 2. Dry weight of roots (1) and shoots (2) in hydroponic wheat plants. The forms representing various levels of the crop evolution have been studied: synthetic, traditional landrace Albostan, and modern Turkish cultivar Karahan. Average data of three experiments are provided in one replication for each variant. The vertical sections indicate the standard error of mean. Different Latin characters indicate significant differences between the variants (LMD test, $P < 0.05$).

Hydroponic plants of the studied wheat genotypes practically do not differ in the root and shoot weight (Fig. 2), which suggests that the plant biomass has no effect on the root exudation. The analysis of sugars in root exudates showed that the plant roots in all the three genotypes exuded mostly fructose,

glucose, and maltose (Fig. 3). The sugar exudation was minimum in synthetic wheat plants, and the modern cultivar Karahan plants excreted more glucose and maltose than the other two genotypes. The root exudates of the three genotypes also contained an insignificant amount of arabinose, ribose, and xylose (see Fig. 3).

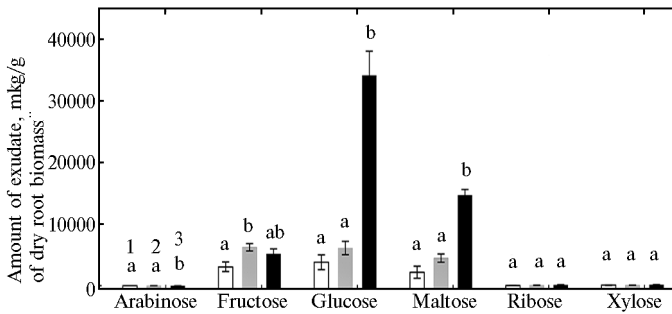


Fig. 3. Root exudation of sugars in hydroponic wheat plants: 1, 2, 3 — the forms representing various levels of the crop evolution (synthetic wheat, landrace Albostan, and modern Turkish variety Karahan). Average data of three experiments are provided in a replication for each variant. The vertical sections indicate the standard error of mean. Different Latin characters indicate significant differences

between the variants (LMD test, $P < 0.05$).

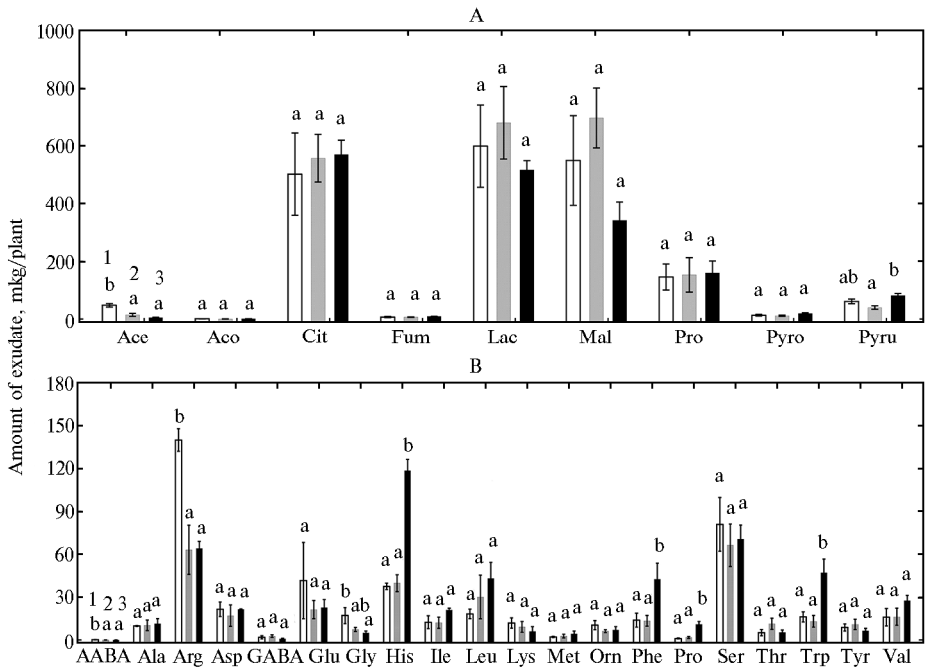


Fig. 4. Root exudation of organic acids (A) and amino acids (B) in hydroponic wheat: 1, 2, 3 — the forms representing various levels of the crop evolution (synthetic wheat, traditional landrace Albostan and modern Turkish cultivar Karahan); Ace, Aco, Cit, Fum, Lac, Mal, Pro, Pyro, and Pyru — acetic, aconitic, citric, fumaric, lactic, malic, propionic, pyroglutamic, and pyruvic acids, respectively; AABA and GABA — α -aminobutyric and γ -aminobutyric acids, and generally accepted abbreviations are indicated for proteinogenic amino acids. Average data of three experiments are provided in a replication for each variant. The vertical sections indicate the standard error of mean. Different Latin characters indicate significant differences between the variants for each acid or amino acid (LMD test, $P < 0.05$).

The content of organic acids was similar in all the genotypes (Fig. 4). The main components were citric, lactic, malic and propionic acids. The genotype differences included increased root exudation of acetic acid in synthetic wheat plants and pyroracemic acid in Karahn as compared to Albostan plants.

The root exudates of the wheat genotypes studied contained 17 proteinogenic amino acids mostly presented by arginine, asparaginic and glutamic acids, histidine, leucine, phenylalanine, serine, tryptophan and valine (see Fig. 4), and

only three of the 13 analyzed non-proteogenic amino acids, the α -aminobutyric, γ -aminobutyric acids and L-ornithine, were found. Synthetic wheat differed from other forms by increased exudation of α -aminobutyric acid, arginine and glycine, while the modern cultivar Karahan was characterized by intensive exudation of histidine, phenylalanine and tryptophane.

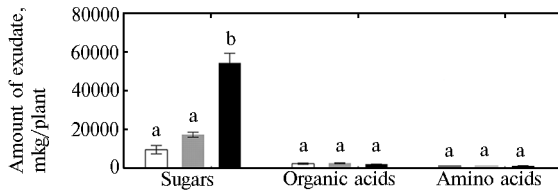


Fig. 5. Total amount of sugars, organic acids and amino acids in root exudates of hydroponic wheat: 1, 2, 3 — the forms representing various levels of the crop evolution (synthetic wheat, landrace Albostan, and modern Turkish variety Karahan). Average data of three experiments are provided in a replication for each variant. The vertical sections indicate

the standard error of mean. Different Latin characters indicate significant differences between the variants (LMD test, $P < 0.05$).

The total amount of sugars secreted by the roots of the Karahan variety plants was 5- and 3-fold higher, respectively, compared to synthetic wheat and Albostan plants, however, we identified no genotype differences by the total exudation of organic acids and amino acids (Fig. 5). The comparison of the total amounts in three analyzed fractions of root exudates showed sugars to be the main component in all the genotypes.

Thus, the basic initial hypothesis in the pot experiment was the assumption that shoot removal is a stress resulting in the mobilization of plant regeneration. Its rate depends on the ability of the root system to supply the plant with water and nutrients. Consequently, more active functioning of the root system will probably lead to accelerated and effective plant regeneration. Shoot removal demonstrated higher stress resistance in synthetic wheat as compared to Albostan and Karahan plants. Accordingly, the regeneration efficiency determined by the biomass of new shoots and the plant growth parameters under stress as compared to control turned out to be better in synthetic wheat. At the same time, in the control the modern cultivar Karahan produced 2-times more aboveground biomass per root weight unit. It can be assumed that long-term wheat breeding indirectly contributed to higher efficiency of plant root system. Our results showed that Karahan was unable to increase the shoot to root ratio in response to stress. Moreover, the average ratio in stressed and control Karahan plants was substantially lower than that of synthetic wheat and Albostan (see Fig. 1). The root systems of the synthetic genotype and Albostan plants demonstrated higher stability in response to stress caused by shoot removal. It is probable that these genotypes are more drought-resistant than Karahan. Currently, field experiments are being conducted to verify this assumption. Previously, the research comparing the root systems of old and modern wheat varieties showed that in modern forms the root weight and size are somewhat less at blooming [17]. If the shoots of winter wheat are eaten by animals, it does not have a substantial effect on the development of the root system in mature plants [18]. However, comparing these data with our results is problematic, as we analyzed the parameters of the root system before shooting. It is possible that the effective response of the synthetic wheat root system to shoot removal is unique and may be attributed to the mechanisms of adaptation to abiotic stresses.

Substantial variety differences in the root exudation of sugars, organic acids and amino acids were described for various plants, including tomato [19], pea [20] and potato [21] which indicates a high variability of genotypes by these traits. A characteristic feature of Karahan plants is a very intensive exudation of sugars (fructose, glucose, and maltose) that accounted for the main amount of

carbohydrates secreted into the rhizosphere. In Karahan plants, as was already mentioned, it is 5- and 3-times higher, respectively, compared to synthetic wheat and Albostan plants (see Fig. 5). Earlier, we showed that modern varieties of hexaploid wheat (*T. aestivum* L.) exude sugars in the rhizosphere more intensively than diploid genotypes *T. boeoticum* Boiss. and *T. monococcum* L. [22]. Based on these data, it can be assumed that the modern cultivar Karahan has a lower capacity of controlling sugar exudation through the root into the soil. It would also be appropriate to assume that after shoot removal the high intensity of sugar exudation in Karahan plants can result in reduced transportation of carbon sources from the root to the aboveground part and, thus, slowing down the re-vegetation. Therefore, it is of interest to compare the root exudation in the studied varieties with removed shoots, and the amount and composition of xylem sap coming to the regenerated shoot. In particular, we demonstrated stronger exudation of xylem sap in the cadmium-resistant pea mutant SGECD⁴ [23] and intensive transportation of nutrients from the root to the shoot [24] resulting in better growth of plants when exposed to cadmium stress [23]. Thus, the increased transportation of nutrition and energy resources from roots to shoots can at least partially explain the high re-vegetation potential of synthetic wheat plants.

In our research, we have for the first time compared the root exudation of organic substances (sugars, organic and amino acids) in wheat genotypes corresponding to the main levels of wheat evolution. The most significant result was the identification of substantial differences in the intensity of sugar exudation. The character of organic acids exudation in the studied varieties was similar, but there were certain genotype peculiarities in the exudation of amino acids. Thus, the roots of synthetic wheat plants exuded more arginine, while the modern cultivar Karahan demonstrated increased exudation of histidine, phenylalanine, and tryptophane. Tryptophane is known as a precursor in the biosynthesis of auxins [25], the phytohormones playing an important role in many physiological processes of plants, including root formation and growth, cell division, xylem tissue formation, shoot regeneration and sugar transportation to the stem meristem [26, 27]. The need for tryptophane and auxins increases under stress caused by the loss of shoot tops (in our experiment this stress was caused by shoot removal), and these compounds are required to repress apical domination and induce a new shoot growth [27]. Intensive exudation of tryptophane by Karahan plants can reduce its content in tissues resulting in reduced biosynthesis of auxins and their transportation to the regenerating shoots. Moreover, the deficiency of auxins can influence negatively the transportation of sugars from the roots to the regenerating shoots. To verify this hypothesis more detailed research is required, including the determination of auxin level in tissues and xylem sap.

So the obtained results show that there are difference in the root systems of the three studied wheat genotypes (primitive, modern, and synthetic varieties), which represent various stages of hexaploid wheat evolution, with regard to the re-vegetation of shoots and the root exudation. The nature of the identified differences is subject to further investigation.

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