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THE FEATURES OF ROOT FORMATION OF SOME FODDER SEMI-SHRUB AND SHRUB HALOPHYTES IN THE FOOTHILL DESERT OF UZBEKISTAN

E.Z. SHAMSUTDINOVA¹ ✉, N.Z. SHAMSUTDINOV², I.V. SAVCHENKO³,
O.A. STARSHINOVA¹, V.I. AGAFONOV¹, Z.Sh. SHAMSUTDINOV¹

¹Williams Federal Research Center for Fodder Production and Agroecology, 1, Nauchnii Gorodok, Lobnya, Moscow Province, 141055 Russia, e-mail darplant@list.ru (✉ corresponding author), o.starshinova@bk.ru, vladislav@bk.ru, aridland@mail.ru;

²Kostyakov All-Russian Research Institute for Hydraulic Engineering and Land Reclamation, korp. 2, 44, ul. Bolshaya Akademicheskaya, Moscow, Russia 127550, e-mail nariman@vniigim.ru;

³All-Russian Research Institute of Medicinal and Aromatic Plants, 7, ul. Grina, Moscow, Russia 117226, e-mail v-lamii@mail.ru

ORCID:

Shamsutdinova E.Z. orcid.org/0000-0002-8519-9041

Starshinova O.A. orcid.org/0000-0001-9725-6165

Shamsutdinov N.Z. orcid.org/0000-0003-1430-7137

Agafonov V.I. orcid.org/0000-0002-2392-5255

Savchenko I.V. orcid.org/0000-0002-3712-7609

Shamsudinov Z.Sh. orcid.org/0000-0002-1377-457X

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Abstract

Distinguishing feature of halophytes as fodder plants are high nutritional value, stable balance of nutrients over seasons, especially during critical periods of pasturing during autumn and winter, and a high content of essential amino acids. Halophytic fodder dwarf semi-shrubs, *Kochia prostrata* (L.) Schrad. and *Salsola orientalis* S.G. Gmel., and shrubs, *Haloxylon aphyllum* (Minkw.) Iljin and *Aellenia subaphylla* (C.A. Mey) Aellen. perform high and sustainable fodder productivity under xerothermic conditions of the Central Asian deserts. In these conditions, shrub and semi-shrub halophytes can successfully complete a full life cycle due to structural, physiological and biological adaptations. These are a succulent type of the leaf photosynthetic apparatus (R.M. Ogburn et al., 2010), a multilayer epidermis, thickening of the cuticle (R.F. Sage et al., 2011) and the C-4 plants which are more efficient in transpiration compared to C₃ plants and lower water consumption (V.I. Pjankov et al., 1991; V.I. Pankov, 1993). Roots play a central role in the yield formation and now considered key drivers of the second "green revolution". Knowledge of the *Chenopodiaceae* shrubs' and semi-shrubs' root formation in the foothill desert conditions elucidates fundamental peculiarities of these halophytic plant biology and provides the correct placement of the crops in arid zones. We compared parameters of root formation in shrubby and semi-shrubby halophyte species to identify their ecological role in the conditions of the Central Asian foothill desert (Nishan steppe, Kashkadarya region, Republic of Uzbekistan, 2015-2020) in plants of the 1st and 5th year of life. The halophytes of family *Chenopodiaceae* have acquired adaptive properties and increased production functions due to evolutionary developed powerful and deeply penetrating roots capable of the use of precipitation, condensation moisture and shallow ground water. Semi-shrubs *Kochia prostrata* (L.) Schrad., *Salsola orientalis* S.G. Gmel. and shrubs *Haloxylon aphyllum* (Minkw.) Iljin, *Aellenia subaphylla* (C.A. Mey) Aellen. are capable of rapid root growth and development. The roots of 1-year old plants penetrate into the soil to a depth of 235 cm in *H. aphyllum*, 150 cm in *A. subaphylla*, 200 cm in *S. orientalis*, and 215-295 cm in *K. prostrata*. At the age of 5 years, the roots reached a depth of 1240 cm, 600 cm, 550 cm, and 580 cm, respectively. Therefore, the root length exceeds the height of the aerial part in the 1st year by 4-4.5 times, and at the age of 5 years by 6 times. The ability to high growth rates of the root system is an important condition for uninterrupted water absorption by the roots in conditions of moisture deficiency and drought. The depth of penetration of the root system of plants of different life forms (shrubs, semi-shrubs) is strongly influenced by the water-physical properties of the edaphic environment. In conditions of permanent soil moisture deficiency, the root system tends to constantly go deeper into the soil-soil environment, breaking through dense, cemented soil layers. In our opinion, for semi-shrubby, shrubby halophytes can not only uptake water by roots from deep soil but also move it to drier soil horizons where this water can be used by plants with a shallow root system. Therefore, the studied

halophytes can obviously provide a function of hydraulic lift.

Keywords: fodder halophytes, shrubs, semi-shrubs, *Salsola orientalis* S.G. Gmel., *Kochia prostrata* (L.) Schrad., *Aellenia subaphylla* (C.A. Mey) Aellen, *Haloxylon aphyllum* (Minkw.) Iljin, root system, morphology, hydraulic lift

The distinctive features of halophytes as forage plants are high nutritional value, stable balance of nutrients according to the seasons, especially during critical periods of grazing, in autumn and winter, a high content of essential amino acids [1]. The forage shrubs and semi-shrubs are important as protein sources in many regions. Thus, in Western Australia, the crude protein content in *Kochia brevifolia* R. Br. is 20%, in *Atriplex nummularia* L. and *Atriplex vesicaria* Heward ex Benth. 14-18% [2]. An important biological feature of shrubs such as *Haloxylon aphyllum* (Minkw.) Iljin, *Aellenia subaphylla* (C.A. Mey) Aellen and semi-shrubs (*Kochia prostrata*) is rapid growth and development in culture [3, 4].

During haloxerophilization, under the influence of the increasing aridization of the climate, shrubs and semi-shrubs of the *Chenopodioideae* family underwent the deepest adaptive restructuring of various traits and functions, including physiological and biochemical ones. Such a restructuring in xerothermal conditions is primarily the reduction of evaporating vegetative organs and the strengthening of the absorbing (suction) function of the root system [5, 6].

In improving the adaptive properties of shrubby and semi-shrub halophytes, which ensured their successful functioning and reproduction in the harsh xerothermal conditions of the Central Asian desert, root systems that penetrate deeply into the soil are obviously of great importance [7]. It is known that roots are very important for the consolidation and absorption of water and mineral resources, but not all researchers consider roots as an important organ taking an active part in the formation of phytomass (harvest) [8]. Traditionally, most researchers have focused on the study of the aboveground part of plants (stems, leaves, flowers, fruits, and seeds) and overlooked the root system [9]. Nevertheless, many researchers are currently beginning to understand that plant roots play a central role in crop formation. In the review published in 2010 in the Nature journal, V. Gewin [10] notes that the success of the first "green revolution" is associated with the selection of dwarf short-stemmed wheat varieties, in which energy and metabolites are mainly spent on the formation of grains, rather than stems. According to forecasts [10], the key factor of the second "green revolution" is the root system, i.e., the improvement of its architectonics, ecological and physiological functions.

An in-depth understanding of issues related to the root system of plants is associated with solving practical problems in crop production, in particular, more efficient use of fertilizers and water and ensuring sustainable productivity under various biotic and abiotic stresses [11]. Salinization of land creates unfavorable conditions for agricultural production, leading to global annual losses of products in the amount of exceeding 12 billion US dollars [12]. In China, saline-alkaline soils account for 25% of agricultural land and are underutilized. One of the sustainable strategies for more effective involvement of saline lands in agricultural production is the breeding of halophytes that can survive and complete their life cycle in soil environments containing more than 200 mM NaCl [13]. Recently, studies conducted in Iran found that halophytic species of the genus *Suaeda* spp. contain nitrogen-fixing endophytic bacteria in the roots, which can make a significant contribution to providing plants with nitrogen [14].

The study of halophytes is additionally actualized due to climate change and the need to provide food to the growing population of the Earth [15, 16].

According to I.I. Sudnitsyn [17], the rate of water absorption by a plant is directly proportional to the depth of penetration and the density of the root

placement in the soil layer. Therefore, information about peculiarities of the root system formation in shrubs and semi-shrubs of the family *Chenopodiaceae* in the foothill desert conditions (e.g., the growth rate, the depth of penetration into the soil) is very important not only for the knowledge of these halophytic plant life forms but also for the correct placement of crops in arid zones.

This paper for the first time examines the role of the root system in the water supply and water balance maintenance in halophytic shrubs and semi-shrubs under the xerothermal conditions of the Central Asian desert.

The aim of the work is to compare the formation of the root system of shrub and semi-shrub species of halophytes and to reveal their ecological role in the conditions of the Central Asian desert.

Materials and methods. The study was conducted in the area of the foothill desert (Nishan steppe, Kashkadarya region, Republic of Uzbekistan, 38.62624 N, 65.69219 E) in 2015-2020 in the introduction nursery of fodder shrubs and semi-shrubs, founded in 2015. The excavation area of root systems of plants of various life forms is located in the lower belt of the foothill desert at 354 m above sea level. The climatic conditions of the research area are characterized by high dryness and continental climate.

In experiments with the semi-shrub *Kochia prostrata*, three ecotypes were studied: rocky (seeds were collected in the Osh region of Kyrgyzstan), sandy (seeds were collected in the Kyzylkum deserts in Uzbekistan, Muyunkum in Kazakhstan and in the Caspian semi-desert) and solonetzic (the Achikulak Forest Research Experimental Station, Russia).

Phenological observations for each studied species were carried out on 75 plants in three repetitions.

The excavation of the root systems of shrubs *Haloxylon aphyllum* (Minkw.) Iljin, *Aellenia subaphylla* (C.A. Mey) Aellen. and semi-shrubs *Kochia prostrata* (L.) Schrad., *Salsola orientalis* S.G. Gmel. was carried out by the trench method [18]. The excavation of roots of shrubs and semi-shrubs at the age of 1 year was carried out in three plants of each species at different phases of development (seedlings, true leaves, branching, flowering, fruit formation). To excavate the roots systems of the *Haloxylon aphyllum*, *Aellenia subaphylla*, *Salsola orientalis*, *Kochia prostrata* at the age of 5 years, a plant was selected that outwardly corresponded to an average representative of each of the studied species.

Statistical processing of the obtained data was carried out in the Microsoft Excel 2010 program. The results are presented as means (M) and their standard errors (\pm SEM).

Results. In the zone of the foothill desert of Kashkadarya region, the growing season consists of mesothermal and xerothermal periods characterized by a certain temperature and humidification regime [5]. The mesothermal (cool and humid) period falls on November to April. At this time, an average of 224 mm of precipitation falls annually in the research area. The xerothermal (dry) period covers May to October. In summer, the soil dries up due to physical evaporation and transpiration of plants because of high temperatures, insolation and constantly blowing winds. The average annual air temperature is 14.8 °C, +47 °C the maximum, 27 °C the minimum. The temperature transitions through 0 °C predominately occurs at the end of February and the beginning of March. The average air temperature in February is 3.6 °C, in March 9.4 °C, and in April 15.7 °C. Relative humidity over the year is 30% on average, in summer 10% on average.

The soils where the root systems were excavated, as well as the entire lower belt of the foothill desert, are mainly light gray. A characteristic feature of the soil profile is its stratification where horizons of light loam, medium loam, heavy loam and sandy loam alternate.

The soils are largely salinized and can be attributed to saline soils. Only the upper 8-centimeter layer is not salinized, below the salinity is weak, 0.25-0.45%, and at a depth of 94-610 cm the content of water-soluble salts reaches 1.35-2.77%. The gypsum content in the soil of these sections is small and ranges from 0.5-35.8% along the horizons, humus concentration in the root layer is 1.86-2.02%, total nitrogen along the horizons is 0.006-0.12%, total phosphorus 0.02-0.19%. Potassium is present in sufficient quantities throughout the root-inhabited horizon (936 mg/kg in the upper layers, 30 mg/kg in the lower layers).

Salsola orientalis S.G. Gmel. (family *Chenopodiaceae*) is a perennial plant of 40-60 cm in high with a stem of 5-10 cm in high from which 3-6 skeletal axes depart [19]. The *Salsola orientalis* is a haloxerophytic semi-shrub characterized by high tolerance to drought and resistance to salt stress [6]. The ability of the *S. orientalis* to successfully perform a full life cycle under xerothermal arid conditions and high soil salinity is due to structural adaptations and succulent form of leaves [20], including multilayered epidermis, thickening of the cuticle [21] and C4-type photosynthesis to provide more efficient use of water for transpiration than in C3-plants [22, 23].

The data characterizing the growth of the root system of the *S. orientalis* in the first year of life are given in Table 1. At the end of April, at the 0.9-1.0 cm height of the aboveground part of the plant, the roots of the *S. orientalis* penetrate to a depth of 44 ± 5.3 cm, at the end of May they deepen to 80 ± 4.1 cm, at the end of the growing season (2.XII.2016) up to 200 ± 11.2 cm.

1. Root growth and development of *Salsola orientalis* S.G. Gmel. Plants of the 1st year of life ($n = 9$, $M \pm SEM$; introduction nursery, foothill desert zone, Nishan steppe, Kashkadarya region, Republic of Uzbekistan, 2016)

Date and phase of development	Depth of penetration of the root system, cm	Width of the horizontal spread of the root, cm	The ratio of the length of the roots to the height of the aerial part
24.IV. Seedlings	44.0 ± 5.3	16.5 ± 3.3	4.7
31.V. True leaves	80.0 ± 4.1	95.0 ± 2.7	4.1
5.VII. Branching	105.0 ± 7.4	75.0 ± 5.2	2.6
3.IX. Flowering	125.0 ± 5.7	85.0 ± 7.3	2.5
2.XII. Fruiting, the end of growing season	200.0 ± 11.2	145.0 ± 6.4	3.4

Interestingly, the depth of penetration of the roots of the *S. orientalis* is 4.1-4.7 times greater than the height of its aboveground part, and remained 2.5-3.5 times greater in the second half of the growing season. The root coefficient (the maximum depth of root penetration into the soil \times the maximum diameter of its spread) [24] was 726-7600 in the first half of the growing season and 10625-29000 in the second half. In the second and subsequent years of life, the root system continues to develop. According to our observations, in May, the root system of the 5-year-old *S. orientalis* plants was powerful, penetrating the soil to a depth of 550 cm (Fig. 1).

The main root at a depth of 8 cm is divided into two large roots going down at a slight angle to each other. In turn, one of them at a depth of 12 cm, the other at a depth of 17 cm are divided into two, forming four rather large roots. One of them at a depth of 25 cm turns at an angle of 45 degrees to the side by 65 cm, gradually deepening into the ground. At a depth of 140 cm, one of the roots turns sharply to the side, horizontally by approx. 1 m in length, then goes down again, and at a depth of 330 cm, entering a dense fine-grained horizon, goes horizontally to the side. The other, the thinnest of the three roots, goes vertically down, branches strongly into small white tails. The third root at a depth of 340 cm, making a loop, goes slightly up and to the side by 30 cm, and then turns sharply down. The main root of the *S. orientalis* plant, having reached the dense horizon,

turns aside, divides into several roots that diverge along the sides. Some roots even rise up and branch into numerous thin roots, which, in turn, dividing into smaller ones, end in a loose medium-loamy moist horizon. The rapid growth and formation of a powerful root system of the *S. orientalis* are crucial in the rational use of water and mineral resources from the soil to provide high forage and seed productivity under arid conditions of the foothill desert.

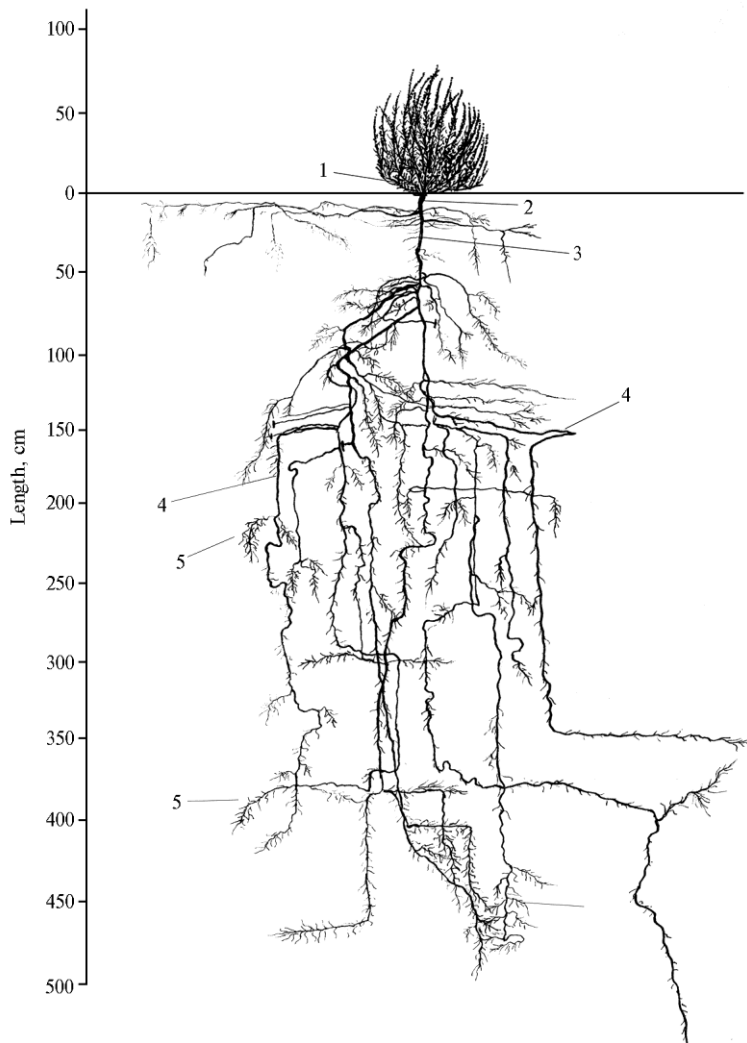


Fig. 1. Root system of *Salsola orientalis* S.G. Gmel. 5-year old plants on medium loamy gray soils: 1 — renewal buds, 2 — root neck, 3 — main root, 4 — lateral roots, 5 — root hairs (introductory nursery, foothill desert zone, Nishan steppe, Kashkadarya region, Republic of Uzbekistan, 2020).

Kochia prostrata (L.) Schrad. (*Chenopodiaceae* family) is a perennial semi-shrub xerogalophyte, according to our observations, it has a height of 75-110 cm, forms 16-25 kg/ha of dry fodder mass which is 16-18% protein. It is intended for cultivation without irrigation to create long-term highly productive pastures in arid areas under low and medium soil salinity. In experiments conducted in the arid regions of the USA (Idaho and Utah), *K. prostrata* turned out to be the best in terms of productivity, nutritional value and digestibility of feeds obtained from it [25-27].

We compared the development of various ecotypes of *K. prostrata* plants in the 1st year of life (Table 2). It was found out that the depth of root penetration

varies significantly depending on the ecotype.

2. Growth and development of *Kochia prostrata* (L.) Schrad. of various ecotypes in the 1st year of life ($n = 9$, $M \pm SEM$; introduction nursery, foothill desert zone, Nishan steppe, Kashkadarya region, Republic of Uzbekistan, 2016)

Ecotype	PH	CW	NS	DRP	HRS	NR1
Rocky (from Kyrgyzstan)	92,0±1,4	100,0±6,3	32,0±4,2	240,0±12,6	115,0±13,6	29,0±2,1
Sandy (from Kyzylkum)	67,0±0,8	65,0±5,2	23,0±3,0	237,0±18,7	130,0±15,8	25,0±1,8
Sandy (from Muyunkum)	73,0±2,7	36,0±2,5	18,0±3,6	270,0±10,5	100,0±19,6	19,0±2,3
Sandy (from Volgograd)	50,0±4,2	47,0±2,8	10,0±2,7	295,0±22,3	90,0±16,1	17,0±2,6
Solonetzic (from Achikulak)	54,0±1,8	67,0±0,4	25,0±3,4	215,0±17,3	135,0±10,5	21,0±1,6

Note. PH — plant height, cm; CW — crown width, cm; NS — the number of shoots; DRP — depth of root penetration, cm; HRS — horizontal root spreading, cm; NR1 — the number of roots of the 1st order.

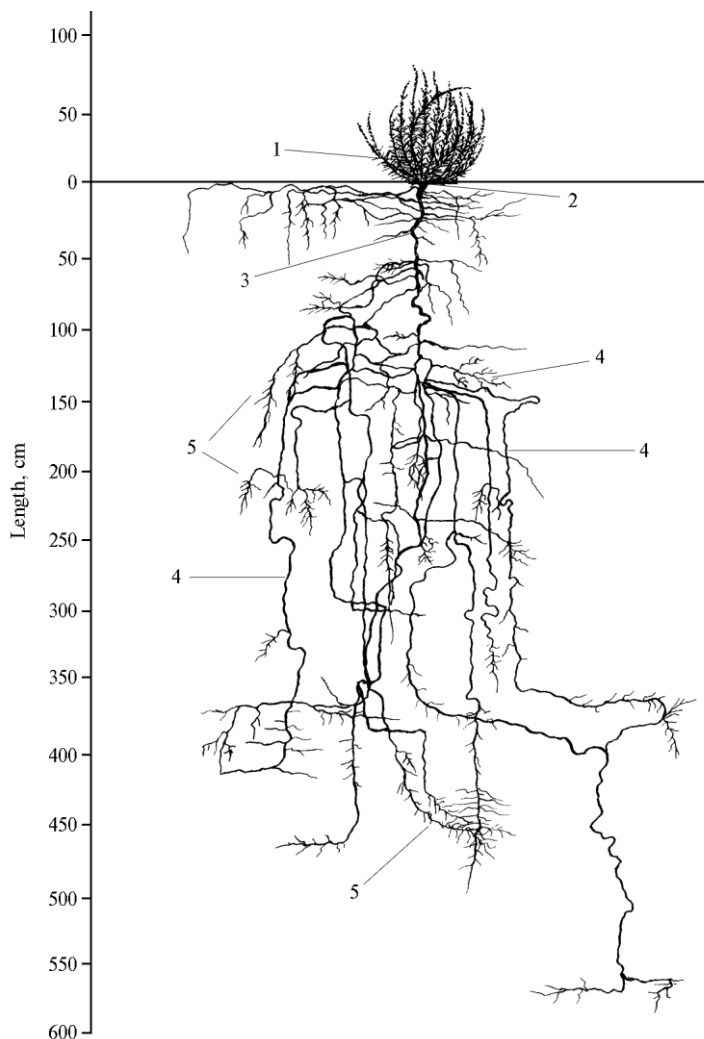


Fig. 2. Root system of *Kochia prostrata* (L.) Schrad. 5-year old plants on medium loamy gray soils:: 1 — renewal buds, 2 — root neck, 3 — main root, 4 — lateral roots, 5 — root hairs (introduction nursery, foothill desert zone, Nishan steppe, Kashkadarya region, Republic of Uzbekistan, 2020).

There were differences in the structure of the root system between ecotypes. The *K. prostrata* rocky ecotype has a pronounced main root. In sandy ecotypes, root systems are quite powerful and deeply penetrating. However, at a depth of 80–100 cm, their main root in size and development becomes similar to the lateral roots of the 1st order. The root system of the *K. prostrata* solonetzic ecotype is the weakest of all.

In the 5-year-old *K. prostrate* (rocky ecotype) plants, the roots penetrate to a depth of 580 cm under the conditions of the Nishan steppe (Fig. 2). The main root is vertically directed downward. The diameter of the root neck is 4 cm. At a depth of 10 cm, a large root departs from the main root, going in a horizontal direction. It does not go deep into the soil and branches strongly. The main root deepens, while forming small bends and turns. At a depth of 50-75 cm, many small and several large lateral roots appear on the main root. Small roots in these layers end, and large ones go down. At a depth of 75 cm, the main root is noticeably thinned, at a depth of 120-125 cm, it branches strongly and forms many thin roots directed downward. Up to a depth of 300 cm, large lateral roots carry a large number of living thin roots. Most of the roots heading down at a depth of 400 cm penetrate into the dense forest horizon, here they are greatly thinned, breaking up into a large number of small ones, and in a layer of 450-470 cm from the surface, they end, forming a dense network of root hairs. Only one root of the *K. prostrate* plant passes through the sedimentary horizon and is buried in a loose medium loamy layer at a depth of 580 cm.

In the morphology of the root system of *K. prostrate*, growing in the conditions of the foothill desert (Nishan steppe), there are three clearly distinguishable tiers. The first tier is ephemeral roots located in a layer of 0-25-30 cm, the second tier is located at a depth of 120-150 cm in the zone of strong lateral branching of the roots. The third tier is the zone of the end of the roots where they are strongly branched and carry many sucking small roots.

Thus, the root system of the *K. prostrata* cultivated in the foothill desert can be characterized as powerful and deeply penetrating, capable of utilizing water and mineral resources from a large volume of soil and soil solution.

Aellenia subaphylla (S.A. Meu) Aellen (*Chenopodiaceae* family) is a perennial haloxerophytic shrub with stems covered with light gray bark [19]. The plants are strongly branched, with branches inclined mostly away from the stem, having a light green color, sometimes with a bluish tinge. The plant height can reach 1.5-2.0 m. The species is exceptionally polymorphic and found in various ecological conditions of the arid zone. A distinctive feature of the *Aellenia subaphylla* is its high drought resistance and ability to grow on saline soils. In the initial growth phases, the root system develops vigorously and deepens into the soil (Table 3).

3. Growth and development of *Aellenia subaphylla* (C.A. Mey) Aellen in the 1st year of life ($n = 75$, $M \pm SEM$; introduction nursery, foothill desert zone, Nishan steppe, Kashkadarya region, Republic of Uzbekistan, 2016)

Date and stage of development	Seedling and plant height, cm	Depth of root penetration, cm	The number of roots of the 1st order a
24.IV. Seedlings; seed leaves	2.0±0.2	21.0±2.0	
30.V. Appearance of true leaves:			
two	2.5±0.5	30.4±1.8	5.6±1.4
four (5.VI.)	6.4±0.4	36.0±4.3	7.4±1.1
six (13.VI.)	8.0±1.2	43.0±2.8	11.8±2.0
eight (20.VI.)	9.6±1.6	46.0±3.3	12.8±1.5
5.VII. Branching begins	20.0±2.6	46.0±2.8	21.0±2.7
3.IX. Flowering begins	55.0±1.4	53.0±1.5	50.0±5.8
2.XII. Fruit formation	77.0±3.3	150.0±3.7	58.0±3.6

In the phase of cotyledon leaves, a plant height is 2.0 ± 0.2 cm, the roots deepen into the soil by 21.0 ± 2.0 cm, at a height of 2.5 ± 0.5 cm by 30.4 ± 1.8 cm, at 8.0 ± 1.2 cm by 43.0 ± 2.8 cm. At the end of the growing season in the 1st year of life (in the fruiting phase), the roots penetrate to a depth of 150.0 ± 3.7 cm.

In May, we excavated the underground part of the *A. subaphylla* plant of the 5th year of vegetation. The main root, which was 6 cm thick, goes vertically down. At a depth of 12-15 cm, two powerful lateral roots, spreading apart, are

directed vertically downwards (Fig. 3). The main root at a depth of 37 cm is divided into two roots. The latter, in turn, were divided into smaller ones several more times as they went deeper into the soil. All the *A. subaphylla* roots of the 1st order, with the exception of some small ones, have very few lateral branches in the 0-140 cm layer, and only from a depth of 140 cm the number of lateral roots increases. In all strongly compacted horizons, for example at a depth of 170-180 and 220-230 cm, there are loose layers with a thickness of 5-15 cm. The roots, once in these layers, creep in a horizontal direction, moving away from the main root to the sides (at a distance of up to 2 m or more). They have many branches in the vertical direction, which, in turn, branch into many small roots. At a depth of 300-320 cm, there are many living and dead root hairs on the roots. At a depth of 500 cm in the soil, there are often empty or containing loose rocks cracks. The roots, falling into them, form bundles of thin roots that fill these spaces. Below 600 cm there is a dense, as if cemented gravel horizon. The roots of *A. subaphylla*, having reached this horizon, do not penetrate into it, but branching strongly, creep over it, forming a dense network of small roots.

Haloxylon aphyllum (Minkw.) Iljin] (*Chenopodiaceae* family) is a leafless shrub (or semi-tree) with a height of 3-4 m. The assimilating function belongs to annually falling twigs, succulent halophyte [19]. The ability of the *H. aphyllum* to successfully perform a full life cycle at high concentrations of salts in the soil is largely realized due to transformation of lamellar leaves into cylindrical photosynthetic organs, the layering of the epidermis and thickening of the cuticle. *H. aphyllum* has broad ecological resistance to soil salinization, it grows on both sandy and clay and gravelly soils with varying degrees of salinity. *H. aphyllum* withstands mineralization of groundwater up to 40 g/l. The root system is powerful, penetrating deeply into the soil. It occurs mainly in areas with close groundwater occurrence, but can also grow in automorphic conditions. The eaten parts of *H. aphyllum* plants in the autumn-winter period are annual shoots, last year's twigs, fruits. The shoots contain 10-12% protein (fruits are up to 20% protein), 2.2-2.7% fat, 21.2-38.6% ash substances, 39.3% nitrogen-free excretory substances, 14.9% fiber.

In the 1st year of life, the roots of the *H. aphyllum* plants at the beginning of the growing season (25.IV.) penetrate to a depth of 29-36 cm and are 4-5 times longer than the aboveground part. By the end of the growing season, they spread to a depth of up to 235 cm, and in the horizontal direction up to 160 cm. In the foothill desert (Nishan steppe) the *H. aphyllum* 5-year old plant forms a powerful root system which deeply penetrates into the soil (Fig. 4). The main root at a depth of 30-40 cm branches into three roots with a diameter of 8-10 cm, and at a depth of 50 cm one of the roots divides, in turn, into three more parts. The soil in the 0-75 cm layer is quite dense, then it becomes looser, and at a depth of 300-360 cm it compacts again. When they reach the compacted horizon, the roots branch out strongly and pass through cracks deep into the soil. At a depth of 400-500 cm, there is a slight increase in soil moisture. Here, the structure of the soil is layered. In these layers, the roots branch little, going deep into the soil. The root system as a whole tends vertically downwards. At a depth of 800 cm, a very dense layer with a thickness of 30 cm lies. In this layer, the roots thin out, flatten, passing through a dense layer, take a rounded shape. From a depth of 860 cm, a small-granulated layer begins, turning into a homogeneous sandy horizon. Here, the soil is moist, a lump forms when compressed. At a depth of 1130-1200 cm, the soil is sandy loam and very moist. Here the root branches strongly and forms a large number of living white roots. At a depth of 1240 cm, the soil becomes very moist, water droplets are exposed in the lumps when breaking. At this depth, salty water has been accumulating for some time.

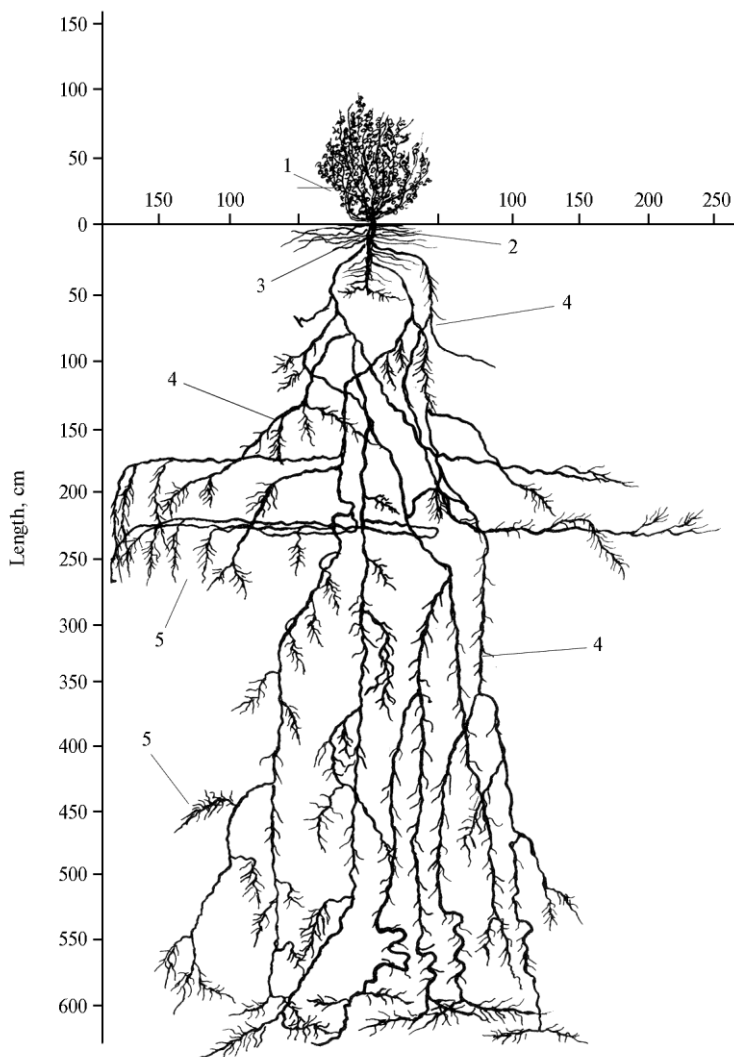


Fig. 3. Root system of *Aellenia subaphylla* (C.A. Mey) Aellen 5-year old plants on medium loamy gray soils: 1 — renewal buds, 2 — root neck, 3 — main root, 4 — lateral roots, 5 — root hairs (introduction nursery, foothill desert zone, Nishan steppe, Kashkadarya region, Republic of Uzbekistan, 2020).

Thus, at the age of 5 years, *H. aphyllum* plants form a powerful root system of a universal type, adapted to the use of atmospheric precipitation, condensation moisture and groundwater.

Analyzing the results obtained, it should be noted that plants of different life forms, in which we studied the peculiarities of the formation of root systems, have different types of adaptive strategies according to the Ramensky-Grime classification. *Haloxylon aphyllum*, *Aellenia subaphylla*, *Kochia prostrata*, being “violents” according to L.G. Ramensky [28] or “competitors” according to J. Grime [29], have a high competitive ability characterized by rapid growth, the ability to capture and hold territory for a long time, suppressing the opponent, and fully use the resources of the environment.

Salsola orientalis, according to the adaptive strategy, refers to tolerators. Stress-tolerators [28, 29] are species that exist not due to high energy of vital activity, but due to endurance under the influence of stressful environmental factors. Therefore, tolerant plants, depending on the growing conditions, are resistant to low water availability, soil salinity or other unfavorable environmental factors.

The ability to restrict moisture use for transpiration plays an essential role in the formation of the plants' properties of *Haloxylon aphyllum*, *Aellenia subaphylla*, *Kochia prostrata* and the halophytes' properties of *Salsola orientalis* in the xerothermal conditions of the Central Asian desert. According to our data (4) obtained in the Central Asian Karnabchul desert, in April, the average daily transpiration intensity in *Haloxylon aphyllum*, *Aellenia subaphylla*, *Salsola orientalis* was 301.6-492.0 mg/h. Under the same conditions, salt-loving *Aremisia halophila* Krasch., a typical representative of the desert flora consumes 2 times more water for transpiration, 957.7 mg/h..

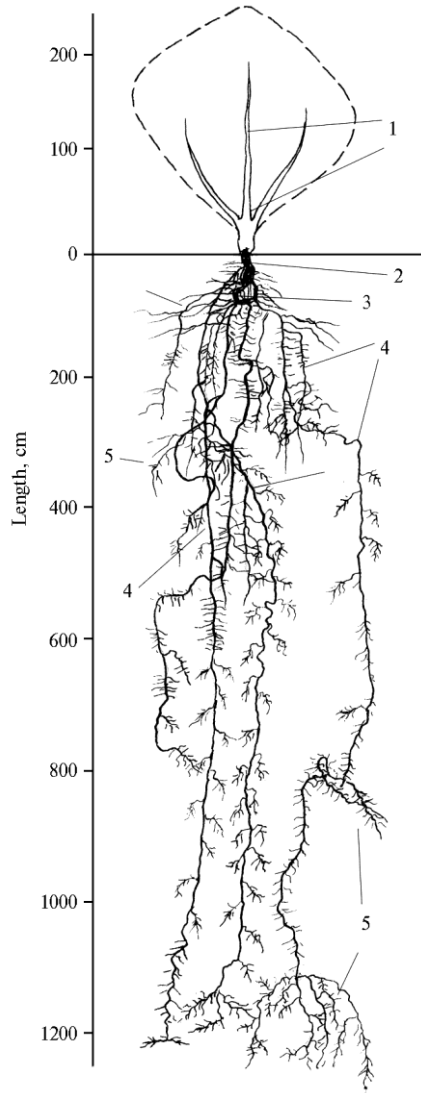


Fig. 4. Root system of *Haloxylon aphyllum* (Minkw.) Iljin 5-year old plants on medium loamy gray soils: 1 — renewal buds, 2 — root neck, 3 — main root, 4 — lateral roots, 5 — root hairs (introduction nursery, foothill desert zone, Nishan steppe, Kashkadarya region, Republic of Uzbekistan, 2020).

Thus, our data and the results of other researchers confirm the position that forage shrubs (*Haloxylon aphyllum*, *Aellenia subaphylla*) and semi-shrub halophytes (*Kochia prostrata* (L.) Schrad., *Salsola orientalis*) are characterized by economical consumption of water for transpiration. During the long-term evolution of plants from true mesophytes to xerogalophytes, a profound adaptive

transformation of their morphology occurred, which was primarily expressed in the reduction of producing organs [30]. As a result, in the *Kochia prostrata* and *Aellenia subaphylla* species, the lamellar leaves turned into small pubescent leaves, and in the *Salsola orientalis* and *Haloxylon aphyllum* species, the leaves turned into cylindrical assimilating succulent fleshy leaves with a multilayer cuticle [31], which reduces the evaporation surface and the intensity of transpiration [20].

In the formation of various types of adaptive strategies during evolution under the xerothermal conditions of the Central Asian desert, along with the development of haloxerophilized properties of photosynthetic organs, the ability to form a rapidly growing and deeply penetrating root system played an important role in forage shrubs and semi-shrubs. The results obtained by us (see Fig. 1-4) show that under moisture deficiency, excessively high temperature and dry air, *Salsola orientalis*, *Kochia prostrata* (semi-shrubs), *Haloxylon aphyllum* and *Aellenia subaphylla* (shrubs) are able to maintain normal hydration of tissues [4] due to increased water absorption by roots [32]. It follows that the ability of plants to continuously absorb water is associated with the activation of the growth of their roots [10]. It turned out that the lack of soil moisture causes increased root growth, thereby increasing the possibility of water absorption [33]. Thus, the ability of the roots to continuously grow plays a decisive role in adapting to water scarcity, since thanks to this the plant receives water in the required amount [34].

The data obtained show that *Salsola orientalis*, *Kochia prostrata*, *Haloxylon aphyllum* and *Aellenia subaphylla* have a high growth rate of the root system which penetrates deeply into the soil. In the 1st year of life, the depth of the root system of these semi-shrubs and shrubs is more than 4-5 times higher than the height of their aboveground part. The fast-growing and deeply penetrating roots of semi-shrub and shrub halophytes ensures their successful functioning in the harsh conditions of the Central Asian desert and allows them to survive a long dry summer period. We found that the roots of semi-shrubs and shrubs during growth and development penetrate through very dense layers of soil, comparable in density to concrete. The scientific literature discusses the ability of plants to penetrate dense layers of soil. It is associated with the structural features of the root tip which provides overcoming the resistance of dense dry soils. It is assumed that one of the mechanisms of this may be the formation of root hairs that act as an anchor when the root moves through dry dense soil layers [35]. Water transport along the phloem to the root tip can play an important role in maintaining continuous root growth in dense dry soil layers. Its role was established using three-dimensional modeling of water distribution depending on the location of phloem endings [36].

V.G. Onipchenko [37] described the phenomenon of the so-called hydraulic lift, when a plant is able not only to lift water by its roots, but also to release it into drier soil horizons. The phenomenon of hydraulic lift is widespread in arid regions [38]. In desert conditions, plants with their roots penetrating deeply into the soil raise water into the surface layers, where plants with a shallow root system can use this water. Similar results were obtained in other studies in the forests of *Acer saccharum* Marshall where plants of the lower tiers received water due to a hydraulic lift provided by maple. It is shown that during the night an adult sugar maple tree can pump about 100 l of water from the lower soil horizons to the upper ones [39]. One tree of the umbrella acacia *Acacia tortilis* (Forssk.) Hayne in Africa raises from 70 to 235 l of water per night [40]. Currently, more than 90 plant species with this ability have been described [41, 42].

Hydraulic lifting is the passive movement of water from the roots into the

soil layers with a lower water potential, while other parts of the root system in the wetter soil layers, usually at depth, absorb water [43, 44]. Hydraulic redistribution ensures the passive movement of water between different parts of the soil through the root systems of plants, caused by gradients of water potential at the soil—plant interface. Hydraulic redistribution can have important consequences on a community scale, affecting net primary productivity, as well as the dynamics of water reserves and growth development. On a global scale, it can affect hydrological and biogeochemical cycles and, ultimately, the climate. The results obtained by comparing the features of the formation of the root system of shrubs and semi-shrubs give reason to assume that *Salsola orientalis*, *Kochia prostrata*, *Haloxylon aphyllum* and *Aellenia subaphylla* are capable of performing the function of a hydraulic lift due to the formation of a root system that penetrates deeply into the soil. The release of water in the soil due to a hydraulic lift ensures better absorption of mineral nutrition elements by plants from the upper dry soil horizons and increased activity of soil microorganisms [37].

The importance of the root systems of halophytes for their resistance to salinization has been revealed. The ability of plants to tolerate a saline environment is determined by a variety of physiological and biochemical processes that contribute to the retention and/or absorption of water, protect the functions of chloroplasts and maintain ion homeostasis. Halophytes synthesize osmotically active metabolites, specific proteins and certain enzymes that capture free radicals. Many halophytes accumulate methylated metabolites which play a crucial role as osmoprotectors and neutralize free radicals [45].

The variety of microorganisms associated with the roots of halophyte plants is enormous. This complex microbial community, which is called the second genome of a plant, is crucial for its stress resistance. Plants are able to form their own rhizospheric microbiome, as evidenced by the fact that different species of plants are hosts of certain microbial communities on the same soil [46].

Recent studies have shown that the use of rhizobacteria halophytes has a beneficial effect on the growth of agricultural plants and increases their yield. Five salt-resistant bacteria were isolated from the roots of the halophyte *Arthrocnemum indicum*. Under conditions of salt stress, inoculated peanut seedlings maintained ionic homeostasis, accumulated less reactive oxygen species, and showed enhanced growth compared to non-inoculated seedlings [47]. Inoculation with the rhizospheric bacterium *Azospirillum brasilense* NH, originally isolated from saline soil in northern Algeria, significantly increased the growth of durum wheat (*Triticum durum* var. *waha*) under saline soil conditions. In inoculated plants, the germination rate, stem height, ear length, dry weight of roots and shoots, chlorophyll a and b content, 1000 seed weight, the number of seeds per ear and seed weight were significantly higher than in non-inoculated plants [48].

Halotolerant bacteria are able to adapt to the increased salinity of the environment and maintain normal functioning thanks to effective osmoregulatory mechanisms. Rhizobacteria of halophytes stimulate the growth of plant roots at high salinity by the synthesis of indoleacetic acid, gibberellins, cytokinins, abscisic acid, solubilization of insoluble phosphate, synthesis of 1-aminocyclopropane-1-carboxylate deaminase (ACC-deaminase), which reduces the ethylene content in plants during salt stress [49].

So, forage halophytic *Kochia prostrata*, *Salsola orientalis* (semi-shrubs), and *Haloxylon aphyllum*, *Aellenia subaphylla* (shrubs) when grown in xerothermal conditions, form powerful root systems that penetrate deep into the soil. In the first years of life, the roots deepen to 200-295 cm. On the light gray soils of the Central Asian foothill desert zone (Nishan steppe), at the plant age of 5 years, the

roots penetrate to the depth from 500–600 cm for *Salsola orientalis*, *Kochia prostrata*, and *Aellenia subaphylla* up to 1200 cm (that is, 2 times deeper) for *Haloxylon aphyllum*. These crops form root systems of a universal type adapted to the use of atmospheric precipitation, condensation moisture and shallow groundwater. Plants are characterized by rapid growth and development of root systems. In the 1st year of life roots are 4–4.5 times longer than the aboveground part, at the age of 5 years 6 times longer. This ensures the absorption of water in the amount necessary for the plant despite the moisture deficiency and drought. The depth of root penetration in plants of different life forms (i.e., shrubs, and semi-shrubs) is strongly influenced by the water-physical properties of the edaphic environment. With a constant lack of soil moisture, the root system continuously tends to deepen, breaking through dense, “cemented” soil layers. We believe that semi-shrub and shrub halophytes have the function of a so-called hydraulic lift when the plant is able not only to lift water by its roots, but also to release it into drier soil horizons. In the conditions of the Central Asian desert, forage semi-shrubs (*Kochia prostrata*, *Salsola orientalis*) and shrubs (*Haloxylon aphyllum*, *Aellenia subaphylla*) with fast-growing and deeply penetrating roots raise water into the surface soil layers where plants with a shallow root system can use it.

REFERENCES

1. Nechaeva N.T., Nikolaev V.N. *Khimicheskii sostav, pitatel'nost' i biologicheskaya polnotsennost' pastbishchnykh kormov podgornoj ravniny Turkmenistana* [Chemical composition, nutritional value and biological usefulness of pasture forage in the piedmont plain of Turkmenistan]. Ashkhabad, 1985 (in Russ.).
2. Barret-Lennard E.G., Malcolm C.V. *Saltland Pastures in Australia: a practical guide*. Bulletin 4312. Dept. of Agriculture. Western Australia. South Perth, 1995.
3. Nechaeva N.T., Vasilevskaya V.K., Antonova K.G. *Zhiznennyye Formy Rastenii pustyni Karakumy* [Life forms of plants of the Karakum desert]. Moscow, 1973 (in Russ.).
4. Shamsutdinov Z.Sh., Shamsutdinov N.Z. *Galofitnoe rastenievodstvo (ekologo-biologicheskie osnovy)* [Halophytic crop production (ecological and biological bases)]. Moscow, 2005 (in Russ.).
5. Korovin E.P. *Rastitel'nost' Srednei Azii i Kazakhstana* [Vegetation of Central Asia and Kazakhstan]. Tashkent, 1961 (in Russ.).
6. Akzhigitova N.I. *Galofil'naya rastitel'nost' Srednei Azii i ee indikatsionnyye svoystva* [Halophilic vegetation of Central Asia and its indicative properties]. Tashkent, 1982 (in Russ.).
7. Shamsutdinov N.Z., Shamsutdinova E.Z., Orlovsky N.S., Shamsutdinov Z.Sh. Halophytes: ecological features, global resources, and outlook for multipurpose use. *Herald of the Russian Academy of Sciences*, 2017, 87: 1–11 (doi: 10.1134/S1019331616060083).
8. Bazzaz F.A., Ackerly D.D., Reekie E.G. Reproductive allocation in plants. In: *Seeds: the ecology of regeneration in plant communities*. M. Fenner (ed.). CAB International, Oxford, 2000.
9. Waines J.G., Ehdaie B. Domestication and crop physiology: roots of green-revolution wheat. *Annals of Botany*, 2007, 100(5): 991–998 (doi: 10.1093/aob/mcm180).
10. Gewin V. Food: an underground revolution. *Nature*, 2010, 466: 552–553 (doi: 10.1038/466552a).
11. Geldner N., Salt D.E. Focus on roots. *Plant Physiol.*, 2014, 166(2): 453–454 (doi: 10.1104/pp.114.900494).
12. Shabala S. Learning from halophytes: physiological basis and strategies to improve abiotic stress tolerance in crops. *Ann. Bot.*, 2013, 112(7): 1209–1221 (doi: 10.1093/aob/mct205).
13. Liu L., Wang B. Protection of halophytes and their uses for cultivation of saline-alkali soil in China. *Biology (Basel)*, 2021, 10(5): 353 (doi: 10.3390/biology10050353).
14. Alishahi F., Alikhani H.A., Khoshkolgh-Sima N.A., Etesami H. Mining the roots of various species of the halophyte Suaeda for halotolerant nitrogen-fixing endophytic bacteria with the potential for promoting plant growth. *Int. Microbiol.*, 2020, 23(3): 415–427 (doi: 10.1007/s10123-019-00115-y).
15. Nikalje G.C., Nikam T.D., Suprasanna P. Looking at halophytic adaptation to high salinity through genomics landscape. *Curr. Genomics*, 2017, 18(6): 542–552 (doi: 10.2174/1389202918666170228143007).
16. Flowers T.J., Muscolo A. Introduction to the Special Issue: halophytes in a changing world. *AoB Plants*, 2015, 7: plv020 (doi: 10.1093/aobpla/plv020).
17. Sudnitsyn I.I. *Dvizhenie pochvennoi vlagi i vodopotreblenie rastenii* [Movement of soil moisture and water consumption of plants]. Moscow, 1979 (in Russ.).
18. Shalyt M.S. V knige: *Polevaya geobotanika* /Pod redaktsiei E.M. Lavrenko, A.A. Korchagina [Field geobotany. E.M. Lavrenko, A.A. Korchagin (eds.)]. Moscow-Leningrad, 1960, vol. 2: 369–

- 447 (in Russ.).
19. *Botanicheskaya geografiya Kazakhstana i Srednei Azii (v predelakh pustynnoi oblasti)* /Pod redaktsiei E.I. Rachkovskoi, E.A. Volkovoi, V.N. Khramtsova [Botanical geography of Kazakhstan and Central Asia (within the desert region). E.I. Rachkovskaya, E.A. Volkova, V.N. Khramtsov (eds.)]. St. Petersburg, 2003 (in Russ.).
 20. Ogburn R.M., Edwards E.J. The ecological water-use strategies of succulent plants. *Advances in Botanical Research*, 2010, 55: 179–225 (doi: 10.1016/S0065-2296(10)55004-3).
 21. Sage R.F., Christin P.A., Edwards E.J. The C₄ plant lineages of planet earth. *Journal of Experimental Botany*, 2011, 62(9): 3155–3169 (doi: 10.1093/jxb/err048).
 22. P'yankov V.I., Mokronosov A.T. *Problemy osvoeniya pustyn'*, 1991, 3–4: 161–170 (in Russ.).
 23. P'yankov V.I. *Rol' fotosinteticheskoi funktsii v adaptatsii rastenii k usloviyam sredy. Avtoferat doktorskoi dissertatsii* [The role of photosynthetic function in plant adaptation to environmental conditions. DSc Thesis]. Moscow, 1993 (in Russ.).
 24. Rotmistrov V.G. *Zhurnal opytnoi agronomii*, 1907, V(VIII): 499–522 (in Russ.).
 25. Waldron B.L., Greenhalgh L.K., ZoBell D.R., Olson K.C., Davenport B.W., Palmer M.D. Forage Kochia (*Kochia prostrata*) increases nutritional value, carrying capacity, and livestock performance on semiarid rangelands. *Forage & Grazinglands*, 2011, 9: 1–6 (doi: 10.1094/FG-2011-0301-01-RS).
 26. Erin C.G., Patricia S.M. Does *Kochia prostrata* spread from seeded sites? An evaluation from Southwestern Idaho, USA. *Rangeland Ecol. Manage*, 2013, 66: 191–203 (doi: 10.2111/REM-D-11-00177.1).
 27. Wang X., Wu J., Yang Z., Zhang F., Sun H., Qiu X., Yi F., Yang D., Shi F. Physiological responses and transcriptome analysis of the *Kochia prostrata* (L.) Schrad. to seedling drought stress. *AIMS Genet.*, 2019, 6(2): 17–35 (doi: 10.3934/genet.2019.2.17).
 28. Ramenskii L.G. *Izbrannye raboty. Problemy i metody izucheniya rastitel'nogo pokrova* [Selected works. Problems and methods of studying the vegetation cover]. Leningrad, 1971 (in Russ.).
 29. Grime J.P. *Plants strategies and vegetation processes*. John Wiley and Sons Ltd., Chichester, 1979.
 30. Grigor'ev Yu.S. *Problemy osvoeniya pustyn'*, 1968, 5: 3–13 (in Russ.).
 31. Breckle S.W. How do halophytes overcome salinity? In: *Biology of salt tolerant plants*. M.A. Khan, I.A. Ungar (eds.). Karachi, 1995.
 32. Kudoyarova G.R., Kholodova V.P., Veselov D.S. *Fiziologiya rastenii*, 2013, 60(2): 155–165 (in Russ.).
 33. Skobeleva O.V., Ktitorova I.N., Agal'tsova K.G. *Fiziologiya rastenii*, 2010, 57: 520–529 (in Russ.).
 34. Ivanov V.B. *Kletochnye mekhanizmy rosta rastenii* [Cellular mechanisms of plant growth]. Moscow, 2011 (in Russ.).
 35. Bengough A.G., McKenzie B.M., Hallett P.D., Valentine T.A. Root elongation, water stress, and mechanical impedance: a review of limiting stresses and beneficial root tip traits. *Journal of Experimental Botany*, 2011, 62(1): 59–68 (doi: 10.1093/jxb/erq350).
 36. Wiegiers B.S., Cheer A.Y., Silk W.K. Modeling the hydraulics of root growth in three dimensions with phloem water sources. *Plant Physiology*, 2009, 150: 2092–2103 (doi: 10.1104/pp.109.138198).
 37. Onipchenko V.G. *Funktsional'naya fitosenologiya: sinekologiya rastenii* [Functional phytocenology: synecology of plants]. Moscow, 2013 (in Russ.).
 38. Mirkin B.M., Naumova L.G. *Vvedenie v sovremennuyu nauku o rastitel'nosti* [Introduction to modern vegetation science]. Moscow, 2017 (in Russ.).
 39. Emerman S.H., Dawson T.E. Hydraulic lift and its influence on the water content of the rhizosphere: an example from sugar maple, *Acer saccharum*. *Oecologia*, 1996, 108(2): 273–278 (doi: 10.1007/BF00334651).
 40. Ludwig F., Dawson T.E., Kroon H., Berendse F., Prins H.H. Hydraulic lift in *Acacia tortilis* trees on an east African savanna. *Oecologia*, 2003, 134(3): 293–300 (doi: 10.1007/s00442-002-1119-x).
 41. Ryel R.J. Hydraulic redistribution. In: *Progress in botany*. 65. K. Esser, U. Lüttge, W. Beyschlag, J. Murata (eds.). Springer, Berlin, Heidelberg, 2004.
 42. Liste H.H., White J.C. Plant hydraulic lift of soil water — implications for crop production and land restoration. *Plant and Soil*, 2008, 313(1–2): 1–17 (doi: 10.1007/s11104-008-9696-z).
 43. Caldwell M., Dawson T., Richards J. Hydraulic lift: consequences of water efflux from the roots of plants. *Oecologia*, 1998, 113: 151–161 (doi: 10.1007/s004420050363).
 44. Prieto I., Armas C., Pugnaire F.I. Water release through plant roots: new insights into its consequences at the plant and ecosystem level. *New Phytologist*, 2012, 193: 830–841 (doi: 10.1111/j.1469-8137.2011.04039.x).
 45. Asish K.P., Anath B.D. Salt tolerance and salinity effects on plants: a review. *Ecotoxicology and Environmental Safety*, 2005, 60: 324–349 (doi:10.1016/j.ecoenv.2004.06.010).
 46. Berendsen R.L., Pieterse C.M., Bakker P.A. The rhizosphere microbiome and plant health. *Trends Plant Sci.*, 2012, 17(8): 478–486 (doi: 10.1016/j.tplants.2012.04.001).
 47. Sharma S., Kulkarni J., Jha B. Halotolerant rhizobacteria promote growth and enhance salinity tolerance in peanut. *Front. Microbiol.*, 2016, 7: 1600 (doi: 10.3389/fmicb.2016.01600).
 48. Nabti E., Sahnoune M., Ghoul M., Fischer D., Hofmann A., Rothballer M., Schmid M., Hartman A. Restoration of growth of durum wheat (*Triticum durum* var. waha) under saline conditions

- due to inoculation with the rhizosphere bacterium *Azospirillum brasilense* NH and extracts of the marine alga *Ulva lactuca*. *J. Plant Growth Regul.*, 2010, 29: 6-22 (doi: 10.1007/s00344-009-9107-6).
49. Nabti E., Schmid M., Hartmann A. Application of halotolerant bacteria to restore plant growth under salt stress. In: *Halophiles. Sustainable development and biodiversity*, vol. 6. D. Maheshwari, M. Saraf (eds.). Springer, Cham, 2015: 235-259 (doi: 10.1007/978-3-319-14595-2_9).