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Structural and Functional Grounds for *Ephedra sinica* Expansion in Mongolian Steppe Ecosystems

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Abstract—Morphological and structural characteristics of photosynthetic organs, diurnal changes in photosynthetic and transpiration rates, and the efficiency of water use were studied in three plant species from mountain-steppe ecosystems in Mongolia, *Ephedra sinica* Stapf, *Stipa glareosa* P. Smirn., and *Allium polyrhizum* Furcz. ex Regel. The species studied differed in the structural and functional mechanisms for the adaptation of photosynthetic apparatus to arid conditions. *E. sinica* has thick, vertical assimilating shoots, which are characterized by a high density (620 mg/cm^3) and a small proportion of photosynthetic tissues (13%). The proportion of mesophyll in the leaves of *A. polyrhizum* and *S. glareosa* was two and three times higher, respectively. The low content of phototrophic tissues in *E. sinica* shoot was compensated for by a high photosynthetic activity of single chloroplasts (25 mg CO_2/(10^9 chloroplast h)), which was six times higher, than in two other species. Daily course of photosynthesis and transpiration in *E. sinica* differed from those of *A. polyrhizum* and *S. glareosa* by the absence of the midday depression. *E. sinica* had the highest efficiency of water use (45 mg CO_2/g H_2O) due to a low transpiration rate (0.25 g/g fr wt h). It is concluded that, in *E. sinica*, the main strategy for adaptation to arid stress is to develop in the shoot a few photosynthesizing cells of high assimilation activity. Such structural organization of photosynthetic organs in ephedra contributes to its higher efficiency of water use and stability of physiological characteristics under changing environmental conditions. These specific features of the structure of assimilating organs and their functional features contribute to a greater expansion of *E. sinica* with increasing climate aridization in Mongolia.

Key words: Allium polyrhizum - Ephedra sinica - Stipa glareosa - photosynthesis - transpiration - leaf anatomic characteristics - mesophyll - aridization - adaptation - Mongolia

INTRODUCTION

The current trend in environmental changes can be defined as climate aridization and an expansion of the area of arid regions. Changing temperature and water regime can lead to the changes in botanical and geographical zones, the displacement of species area, and the changes in the competition relationships between plants in the ecosystems [1].

Recent studies by the Joint Russian–Mongolian Multidisciplinary Biological Expedition revealed an expansion of Chinese ephedra (*Ephedra sinica*) in several regions of the Gobi Tien Shan [2]. Ephedra actively vegetates on *Stipa gobica*, *S. glareosa*, and *Allium polyrhizum* tussocks, which are the main cenosis-forming species of steppe communities in mountain ecosystems. *E. sinica* becomes not only the dominant and subdominant, but also an edificator species. In the late 1960s–early 1970s, Chinese ephedra was mentioned as a plant species that is rare in these communities [3]. However, according to the data by Gurvantes weather station (Mongolia), the annual precipitation steadily decreased from 180 mm in 1975 to 80 mm in 1990 [2].

Expansion of ephedra, in parallel with the increase in climate aridity, is due to several morphological, anatomical, and physiological adaptations. To date, morphological characteristics of Chinese ephedra are well studied. This plant is a perennial evergreen xeromorphic rhizome-type small shrub of 10–20 cm in height. Various authors studied seasonal and daily changes in photosynthesis [4, 5] and transpiration [6, 7] rates in some representatives of the *Ephedra* genus. Studies of physiological processes provide valuable information about ecological characteristics of plant species. However, these data reflect adaptation of an individual plant function to current growth season or day conditions. Owing to a high lability of physiological characteris-

† Deceased.

Abbreviations: chlp—chloroplast; CMI/V—cell membrane index, or the total area of the cell surface in photosynthetic tissues per unit leaf volume.

tics, they are difficult to use for the assessment of a climate potential of plant species [1]. Rather, invariant features and structures should be analyzed that are related to major physiological functions [1] and characterize the long-term adaptation to a whole complex of environmental conditions. The structure of photosynthetic apparatus was shown to result from long-term adaptation of plant species to environmental conditions and to reflect their functional characteristics [8–11].

The objective of this work was to study the structure of the photosynthetic apparatus and its functional characteristics in three dominant plant species of steppe ecosystems of Mongolia (*E. sinica, S. glareosa*, and *A. polyrhizum*) and to reveal the causes for the high competitiveness of Chinese ephedra under conditions of arid stress.

MATERIALS AND METHODS

The studies were carried out in a mountain–steppe region of Gobi Tien Shan at an altitude of 2170 m above the sea level, 30 km from Gurvantes inhabited locality (43°12′16″ N, 100°39′35″ E). Climate of the region is extremely continental and dry [12]. An average annual precipitation is equal to 118 mm with an average annual air temperature of 4.4°C and soil temperature of 6.6°C. The absolute maximum of air temperature is 26°C, and the minimum temperature is equal to –18°C. In summer, soil surface is, generally, heated to 50°C, and, in winter, cools down to –39°C. The maximum of precipitation occurs in July–September.

We studied three dominant plant species in the steppe community: *Ephedra sinica* Stapf (the family Ephedraceae), *Stipa glareosa* P. Smirn. (Poaceae), and *Allium polyrhizum* Turcz. ex Regel (Liliaceae). The plants were collected in August 2001, at fruit. In *S. glareosa* and *A. polyrhizum*, the measurements were carried out on leaves, and, in aphyllous species *E. sinica*, assimilating shoots were collected.

Diurnal changes in photosynthesis and transpiration rates were studied simultaneously, using plant material collected in the same habitat. The measurements were performed from 8:00 a.m. to 8:00 p.m. at 2-h intervals. Concurrently, microclimate variables were recorded and temperature of leaf surface was measured with a MT-54 "M" multichannel thermometer with microresistors (Russia), a Yu-117 luxmeter (Russia), and an Assman psychrometer (Russia).

The photosynthetic rate was measured with a radiometric method at a saturating $^{14}CO_2$ concentration, 0.5% (specific activity 1000 MBq/l) [13]. The experiments were performed under natural light and temperature conditions, the exposure time was equal to 3 min, and the measurements were repeated three times. Then, plant material was fixed in boiling ethanol vapors, dried, and its radioactivity was measured under laboratory conditions with a Veb Robotron–Messelektronik 20046 counter (Germany).

The transpiration rate was measured by the method of rapid weighing [14] with a VT-500 torsion balance (Russia) and calculated per fresh and dry weights. Time interval between measurements of the weight of assimilating organs was 5 min. The experiments were done in seven replicates.

The efficiency of water use (mg CO_2/g H_2O) was calculated as the ratio of photosynthetic (mg CO_2/(g dry wt h)) to transpiration rate (g H_2O/(g dry wt h)).

The structural indices of the assimilation apparatus were determined by the method of Mokronosov [13] and by projection method [11]. In these experiments, 5–10 leaves were collected from 10–15 plants of each species. The specific leaf density, i.e. dry weight per unit leaf volume, was measured in ten replicate samples by a gravimetric method. The leaf thickness was measured in ten replicate samples on transversal cross-sections of freshly collected leaves placed in Tris–HCl–sorbitol buffer (pH 7.4). The measurements were done under a Biolam light microscope (LOMO, Russia) with an eyepiece-micrometer.

The numbers of cells were counted in the plant material fixed in 3.5% glutaraldehyde solution in phosphate buffer (pH 7.4). Assimilating organs were macerated by heating in 20% KOH. The numbers of cells per unit leaf volume were counted in a Goryaev's chamber. Mesophyll cell volume was measured by the projection method [11]. To this end, tissues were macerated in 1 N HCl. The projections of mesophyll cells, obtained by microscopic examination of macerated material (magnification ×200–400), were analyzed with the use of a Siams Mesoplant image analysis system (SIAMS, Russia). Projections of 30 randomly selected cell were analyzed. Using the characteristics of two-dimensional cell projections, we reconstructed three-dimensional indices of cells, i.e., the volume and area of cell surface.

The volume of leaf mesophyll was calculated as percentage of the total volume of leaf tissues using the following formula:

$$V_{mes} = N_{cell} V_{cell} \times 100/V_l,$$

where N_{cell} is the number of mesophyll cells per 1 cm^2 of leaf volume, V_{cell} is the average volume of the mesophyll cell, V_l is the volume corresponding to 1 cm^2 of leaf surface (calculated with the use of mean leaf thickness).

The indices of cell and chloroplast numbers were used to calculate photosynthetic rate per unit of mesophyll volume and per chloroplast.

The significance of differences in these characteristics between species was estimated by the nonparametric Mann-Whitney test [15].

RESULTS

Changes in Microclimate Variables

The changes in light intensity and soil temperature were described by unimodal curves with maxima at

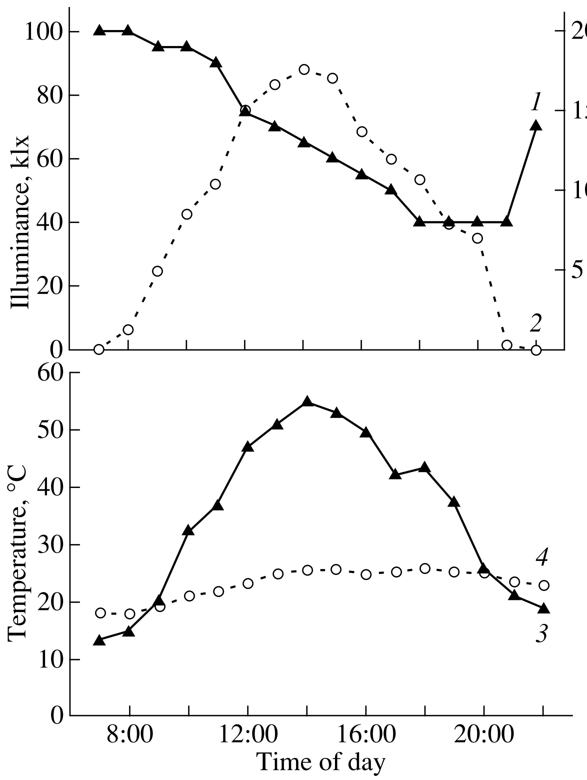

Fig. 1. Changes in major microclimate variables during the period of observations.

(*1*) Relative humidity; (*2*) illuminance; (*3*) temperature of soil surface; (*4*) air temperature.

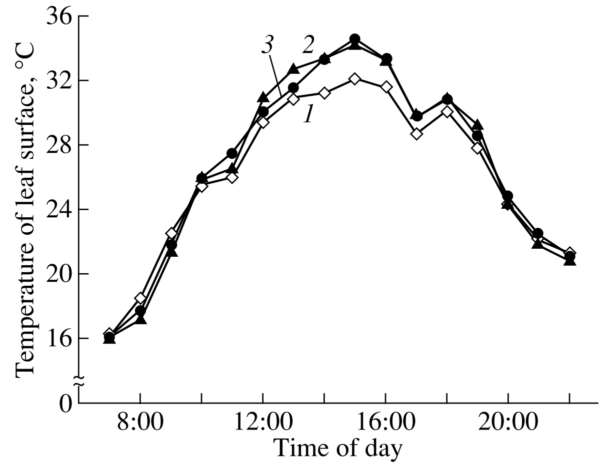

Fig. 2. Diurnal changes in the surface temperature of photosynthesizing organs of (1) *Ephedra sinica*, (2) *Stipa glareosa*, and (3) *Allium polyrhizum*.

12:00 a.m. and 2:00 p.m., respectively (Fig. 1). Air temperature varied insignificantly between 19 and 25°C. A characteristic feature of the study area was low humidity, which decreased from 20% at 7:00 to 8% at 18:00. The changes in the temperature of photosynthetic organs were similar in three species studied and were characterized by a maximum at 15:00 (Fig. 2). However, during the most hot time of day, form 14:00 to 16:00, temperature of the assimilating shoot surface in Chinese ephedra was by 2–3°C lower than the leaf surface temperature in onion (*A. polyrhizum*) and Mongolian grass (*S. glareosa*).

Structure of the Photosynthetic Apparatus

Our studies showed that the assimilating organs of the studied plant species differed in their morphological and structural characteristics. Thick cylindrical aphyllous shoots of *E. sinica* had the lowest volume of photosynthetic tissues, which made up 13% of the total volume of the assimilating shoot (table). This plant species had also the highest specific density of photosynthesizing organs. *S. glareosa* was also characterized by thin leaves with the highest proportion of mesophyll in the leaf (36%). In *S. glareosa*, mesophyll consisted of numerous small cells densely packed with chloroplasts. This species was also characterized by a large internal assimilating surface (index of cell membranes per unit leaf volume, CMI/V) and a high content of chloroplasts per unit leaf volume, which was by an order of magnitude greater than in two other species. *A. polyrhizum* was characterized by a high water content of leaves and by large mesophyll cells and chloroplasts. Both *E. sinica* and *A. polyrhizum* had the small internal assimilating surface.

Diurnal Changes in the Photosynthetic Rate

The time course of diurnal changes in photosynthetic activity differed in the studied plant species. In *S. glareosa*, CO_2 uptake rate drastically increased during the morning in parallel with the increase in light intensity (Figs. 1, 3). In *S. glareosa*, the highest photosynthetic rate was recorded between 10:00 and 12:00, when its value attained 38 mg CO_2/(g dry wt h). During afternoon time, when leaf was markedly heated, the assimilation rate decreased in *S. glareosa* (Figs. 2, 3). The noon maximum in the photosynthetic rate was found in *A. polyrhizum* during morning time, from 8:00 to 10:00, then it markedly decreased (by 4 times), down to 5 mg CO_2/(g dry wt h). The second peak of CO_2 uptake rate was observed in *A. polyrhizum* at 18:00, although its absolute value was lower, 10 mg CO_2/(g dry wt h). In *E. sinica*, photosynthetic rate remained constant from 10:00 to 17:00 (about 15 mg CO_2/(g dry wt h)), even when the temperature of assimilating shoots increased up to 32°C (Figs. 2, 3). Thus, *E. sinica* had a plateau-type of photosynthetic curve, whereas diurnal changes of photosynthesis showed a depression in *A. polyrhizum* and *S. glareosa* [16].

Diurnal changes of photosynthesis were somewhat different when calculated as carbon dioxide uptake per chloroplast (Fig. 3b). As calculations showed, the highest rate of CO_2 assimilation per chloroplast was typical of *E. sinica* and equal to 27 mg $CO_2/(10^9$ chlp h), Quantitative characteristics of the photosynthetic apparatus structure in studied Mongolian plant species

Characteristic*	Species			Differences**
	Ephedra sinica (Es)	*Allium polyrhizum* (Ap)	*Stipa glareosa* (Sg)	
Leaf water content, %	49.0 ± 0.3	84.5 ± 0.6	58.2 ± 2.2	Es vs. Ap Es vs. Sg Ap vs. Sg
Leaf thickness, μm	1290 ± 43	897 ± 31	220 ± 6	″
Leaf density, mg/cm^3	620 ± 71	103 ± 11	397 ± 41	″
Mesophyll cell volume, 10^3, μm^3	13.8 ± 0.9	48.9 ± 3.9	4.2 ± 0.5	″
Number of mesophyll cells, $10^3/cm^3$	9445 ± 283	5032 ± 251	87750 ± 2377	″
Number of chloroplasts per mesophyll cell	39 ± 2	75 ± 1	30 ± 1	″
Number of chloroplasts, $10^6/cm^3$	364 ± 28	377 ± 35	2656 ± 185	Es vs. Sg Ap vs. Sg
Chloroplast volume, μm^3	19 ± 2	38 ± 2	22 ± 3	Es vs. Ap Sg vs. Ap
CMI/V, cm^2/cm^3 leaf	274 ± 30	383 ± 41	1413 ± 125	Es vs. Ap Es vs. Sg Ap vs. Sg
Mesophyll volume, %	13 ± 2	25 ± 1	36 ± 3	″

Note: Ap—*Allium polyrhisum*; Es—*Ephedra sinica*; Sg—*Stipa glareosa*.
* In *E. sinica* these characteristics were measured in assimilating shoot.
** The data show pairwise comparison of species by the Mann–Whitney test. The differences are significant at $p \le 0.05$.

whereas it amounted to only 5 mg $CO_2/(10^9$ chlp h) in *S. glareosa*, and between 1 and 5 mg $CO_2/(10^9$ chlp h) in *A. polyrhizum*.

The use of a new method for measurement of cell volume [11], in addition to mesostructure analysis [13], allowed us to accurately calculate mesophyll volume in the leaf and determine photosynthetic activity per unit mesophyll volume (Fig. 3c). The highest values of this characteristic were found also in *E. sinica*, 75 mg $CO_2/(cm^3$ mesophyll h), whereas the lowest values were found in *A. polyrhizum* (2 mg $CO_2/(cm^3$ mesophyll h)). *S. glareosa* had intermediate photosynthetic rates per unit of mesophyll volume during daytime, between 30 and 40 mg $CO_2/(cm^3$ mesophyll h).

Diurnal Changes in Transpiration and in the Efficiency of Water Use

The largest changes in the transpiration rate were observed during daytime in *S. glareosa*, with the highest values at noon, 0.90 g H_2O/(g dry wt h), and a drastic decrease during afternoon time to 0.30–0.35 g H_2O/(g dry wt h). *A. polyrhizum* and *E. sinica* had similar transpiration rates, which were significantly lower than in *S. glareosa*. Chinese ephedra differed from two other species by most stable transpiration rate during daytime (Fig. 4a).

The assessment of the efficiency of water use (the ratio of the photosynthetic to transpiration rate) has shown that the studied species used different amounts of water for uptake of one milligram of carbon dioxide (Fig. 4b). *E. sinica* fixed the highest amount of carbon dioxide per gram of transpired water, up to 45 mg CO_2/g H_2O. The lowest efficiency of water use was characteristic of *A. polyrhizum*, below 15 mg CO_2/g H_2O. Midday depression of water use efficiency was found in all species studied, however, the most strong decrease (up to 5 times) was observed in *A. polyrhizum*.

DISCUSSION

Ecological characteristics of a plant species allow it to occupy a specific type of habitat and position in a plant community. Under arid conditions, when plants are subjected to a complex of adverse factors (high temperatures and insolation, low amount of precipitation, poor soils, etc.), plants develop various structural and functional mechanisms of adaptation. In the terms of the structural adaptation of photosynthetic organs to arid conditions, three major plant groups are identified: sclerophytes, succulents, and aphyllous species [17].

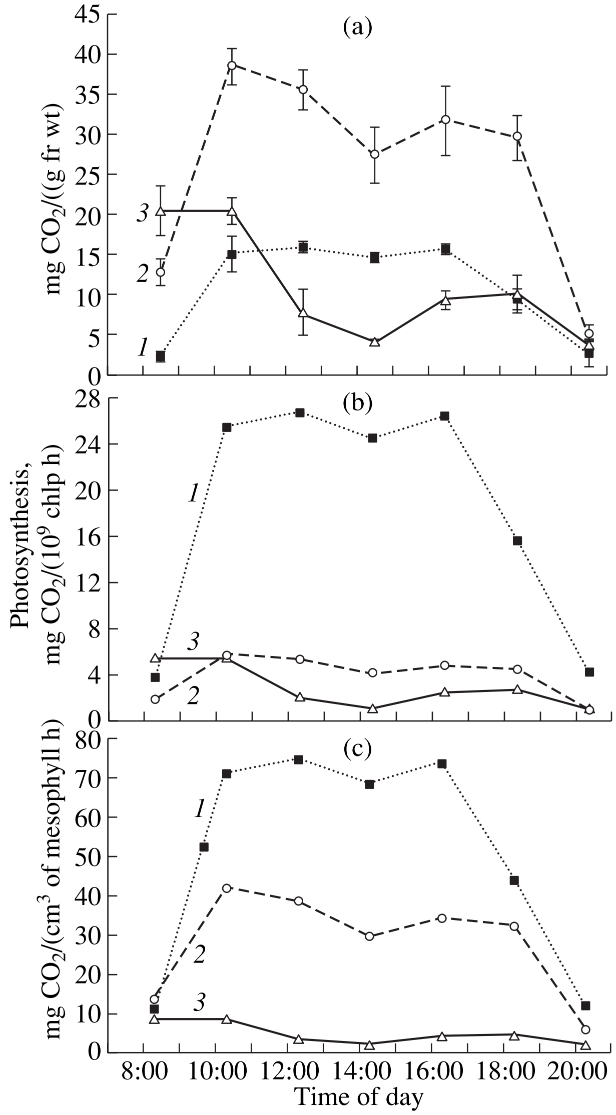

Fig. 3. Diurnal changes in photosynthesis of (*1*) *Ephedra sinica*, (*2*) *Stipa glareosa*, and (*3*) *Allium polyrhizum.*

The pattern of diurnal course of photosynthesis is also dependent on environmental conditions. Diurnal changes may also exhibit a depression in hot time of day or have a plateau [4, 16].

Three studied dominant species from a mountain-steppe ecosystem in Mongolia had different mechanisms of adaptation to environmental conditions. They differed in the morphology and anatomical structure of leaves, as well as the intensity and time course of physiological processes.

E. sinica is a small evergreen xeromorphic bush with a well-developed root system, which penetrates soil to a depth more than 2 m [2]. In this plant species, photosynthesis is performed by cylindrical aphyllous shoots. Our studies showed that the assimilating tissues in Chinese ephedra occupied in total 13% of the volume of the photosynthesizing organ, and the water content

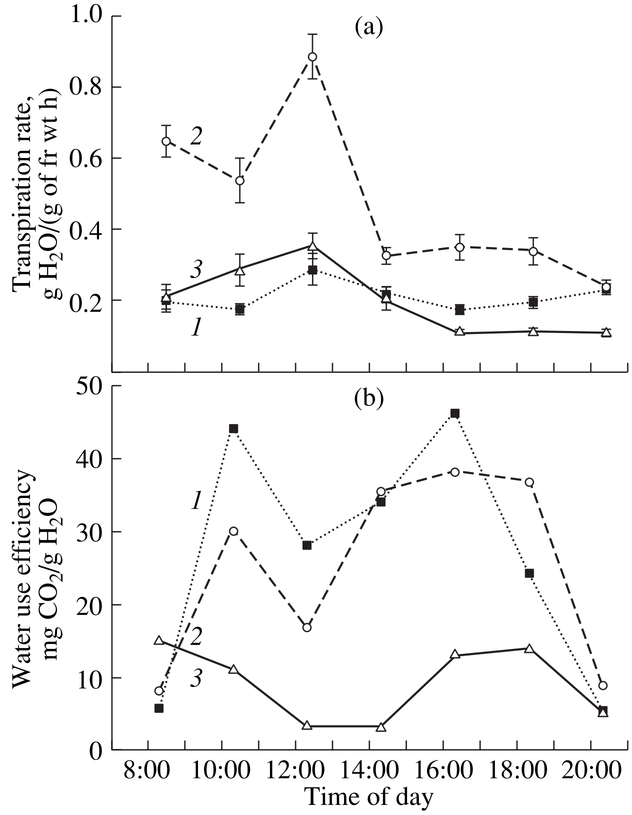

Fig. 4. Time course of transpiration and the efficiency of water use in (*1*) *Ephedra sinica*, (*2*) *Stipa glareosa*, and (*3*) *Allium polyrhizum.*

Method for calculation of water use efficiency is described in the Materials and Methods section.

was 49% (table). The most part of the shoot was represented by mechanical and conducting tissues and exodermis. It seems likely that the predominance of nonphotosynthesizing tissues and a low water content in assimilating shoots of ephedra contributed to a decrease in their heat conductivity and partly to a decreased shoot temperature [18]. Our data show that, in Chinese ephedra, shoot surface temperature was by 3°C lower than that of onion and Mongolian grass leaves (Fig. 2).

The low proportion of photosynthesizing tissues in the shoots of Chinese ephedra was the cause of its low photosynthetic rate per unit shoot weight. However, *E. sinica* had the highest efficiency of water use among plant species studied. The importance of this characteristic in Chinese ephedra is due to the low transpiration rate in this species (Fig. 3). *E. strobilacea* was shown to have a low rate of water loss in eastern Kara Kum [6, 7]. The ratio of photosynthesizing to nonphotosynthesizing tissues may be an important factor, which regulates the transpiration level [19]. The marked predominance of nonphotosynthesizing tissues in *E. sinica* contributes to plant protection from water loss. Previously, the proportion of photosynthetic tissues in plants of the boreal zone was shown to be an important index, which characterizes the resistance of plant species to environmental stress [8]. Stress-tolerant plant species had low proportion of chlorenchyma in the leaf, between 10 and 25%. The proportion of nonphotosynthesizing tissues in steppe plants was shown to increase with increasing climate aridity [20]. Thus, we suppose that the low proportion of photosynthetic tissues may be characteristic of *E. sinica* as a plant species the most tolerant to arid stress. However, the development of large amount of nonphotosynthesizing tissues is associated with large energy expenditures. The maintenance of positive carbon balance, given the low proportion of phototrophic tissues in *E. sinica*, is possible due to a high photosynthetic activity of stem parenchyma. This is attained due to a high photosynthetic rate per single chloroplast with a small number of chloroplasts per unit shoot volume (Fig. 4).

S. glareosa, in terms of its anatomical and morphological characteristics, can be related to typical sclerophytes [17]. Our studies showed that the leaves of Mongolian grass had all the features of the highly effective photosynthetic system: a low thickness, high content of cells and chloroplasts, and a large internal assimilating surface (table). Indeed, *S. glareosa*, had a high photosynthetic rate per unit leaf weight, although it varied to a great extent, depending on microclimatic conditions (Figs. 1, 3). This species had also the high transpiration rate, which greatly varied during daytime. The high photosynthetic rate in *S. glareosa* was the cause of the high efficiency of water use in this species.

A. polyrhizum is a herbaceous perennial plant with linear cylindrical leaves, which are characterized by a high water content (table). Onion leaves are of succulent type and have no sclerenchyma elements [17]. Leaf shape is maintained due to cell turgor, and the cell size is several times greater than in Mongolian grass and Chinese ephedra. The assimilation apparatus of *A. polyrhizum* was characterized by a small number of chloroplasts, both per unit of leaf volume, and per mesophyll cell (table). The major feature of onion photosynthetic activity was an enhanced rate of CO_2 assimilation in morning, when humidity is at its highest, and a drastic decrease of CO_2 assimilation upon decrease of humidity in the noontime (Figs. 1, 3). Slemnev and Tsoozh [21] found that *A. polyrhizum* is the most demanding as to watering conditions, and the photosynthetic activity of onion diminishes even upon a small decrease in the leaf water content. Thus, the low humidity limits the photosynthetic activity of onion as a consequence of spending water to maintain tissue turgor. Because of low rates of CO_2 assimilation, the efficiency of water use in *A. polyrhizum* was the lowest among the plant species studied (Figs. 3a, 4b).

Our data showed that the studied plant species are well adapted to arid condition; however, they have different structural and functional mechanisms of adaptation. For example, *S. glareosa* developed a powerful photosynthetic apparatus (great number of cells and chloroplasts in the leaf and a large leaf assimilation surface), which provides for greater photosynthetic rates and efficiency of water use. *A. polyrhizum* is characterized by water storage in a photosynthesizing cell and by the high photosynthetic rate under conditions of sufficient water supply. In *E. sinica*, the major strategy of adaptation is the development in the shoot of relatively few photosynthesizing cells, with elevated assimilation activity. Such structural organization of photosynthetic organs in *E. sinica* contributes to a higher efficiency of water use and stabilization of physiological characteristics upon diurnal microclimate changes. As compared to Chinese ephedra, Mongolian grass and onion rapidly respond to changing environmental conditions and manifest a pronounced depression upon decrease in humidity and temperature elevation.

Thus, the specific features of the structure of the photosynthetic apparatus and its functional characteristics suggest that *E. sinica* is the most tolerant to arid stress. In the case of further climate aridization, ephedra will show a greater competitive advantage, as compared with other dominant species of the mountain-steppe community.

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