Historia naturalis bulgarica 46 (6): 147–163
ISSN 2603-3186 (online) | ISSN 0205-3640 (print) · nmnhs.com/historia-naturalis-bulgarica
https://doi.org/10.48027/hnb.46.061
Publication date [online]: 3 June 2024

Research article

Species-specific and environment-sensitive functional traits in six steppe plant species with different roles in community

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Abstract: Plant functional traits are often considered as indicators of plant-environment relationship; however, some plant features can be highly taxonomic-specific. The study of intraspecific trait variation is essential to understand what functional traits are influenced by the phylogeny and what traits are more dependent on environment. We studied six common steppe plant species in two natural vegetation plots near lake Baikal in Southern Siberia different in climate aridity and grazing degree: site 1 – native true grass steppe under lower climate aridity, site 2 – high disturbed sagebrush steppe under higher aridity. Plant functional traits showed different relevance to species and environment. Plant height, leaf thickness (LT), mesophyll cell volume (V_{cell}), and the chloroplast number per cell had the greatest contribution to differences between species and varied slightly within a species. Photosynthesis (A_{max}) and transpiration (E) rates, chlorophyll content, mesophyll surface area per leaf area unit (A_{mes}/A) were more dependent on environment than on species. A_{max} and E decreased in all studied species in more adverse conditions of site 2, however plants differed in mechanisms of these changes. In *Stipa krylovii, Artemisia frigida* and *Potentilla acaulis,* most abundant in true steppe (site 1) mesophyll cell sizes, cell and chloroplast number per leaf area decreased in site 2. Other species, *Artemisia scoparia, Potentilla bifurca* and *Allium anisopodium* which were more abundant in disturbed steppe (site 2), had larger cells and showed an increase in cell and chloroplast number per leaf area in site 2 and decrease in the photosynthetic capacity of a chloroplast. We concluded that the leaf thickness and cell size belong to species-specific features, whereas A_{max}, pigment content and integral mesophyll traits as A_{mes}/A are more indicative for plant-environment relationships and their response to growth conditions depend on the ecological strategy of a species.

Keywords: cell volume, chlorophyll content, leaf structure, mesophyll, photosynthesis, plant height

Introduction

Plant functional traits can serve as indicators of plant adaptation to growth conditions (Niinemets, 2001; Poorter et al. 2009; Reich, 2014). These traits are measurable morphological and physiological parameters, closely related to the main functions of plants, but at the same time they should notably vary with environment (Violle et al., 2007; Garnier & Navas, 2012). To be able to survive in changing environment, plants will either shift their ranges or adapt to changing environment (Cornwell & Ackerly, 2009; Jung et

Received: 29 March 2024; accepted: 2 May 2024 · Editor: Stanislav Abadjiev

al., 2014). Therefore, environment impact not only causes the changes in taxonomic diversity, but also can led to functional shifts as species with given traits are replaced by other species with other traits (Grime, 2001; de Bello & Mudrak, 2013). Unlike taxonomic approaches, trait-based methods enable generalisations across regions (Diaz et al., 2004). The study of these mechanisms is of great importance for a deep and comprehensive understanding of environment effects on plants.

Nowadays many studies describe environmental variation in plant traits mostly in strongly controlled manipulative experiments, common gardens (transplant experiment), open-top chambers and rain-out shelters. Natural gradients have been used much less because of methodological reasons. However, it is often inherently difficult to extrapolate the results from controlled but rather artificial experiments to natural conditions in the real world (Poorter et al., 2016). There is certainly a pressing need for other approaches based on "natural" ecosystems (van der Plas, 2019). Thus, the natural variation in plant traits provides an excellent and unique opportunity to study the impact of many ecological factors on the structuring and functioning of plants. Different ecosystems / communities could be used as "natural laboratories" to assess response of terrestrial organisms to climate (de Frenne et al., 2013) or disturbance (Ivanov et al., 2018).

Climate change is one of the most important factors influencing the biodiversity and vegetation traits from individual species up to landscape-scale properties. On the other hand, the anthropogenic impact on ecosystems leads to a deterioration in the overall functional state of vegetation. Numerous studies in recent years have shown that the ecosystems of the Lake Baikal basin are changing under the influence of anthropogenic factors. The observed widespread overgrazing led to the formation of communities with low production and poor feeding quality phytomass (Miklyaeva et al., 2004; Bazha et al., 2012, 2015; Gunin et al., 2012, 2015). The range of functional traits is virtually infinite therefore we need to know what functional traits can be used to assess and monitor vegetation change in response to environmental change (Gillison, 2013). Leaf traits are of prime importance to specify the response of plant species to environment (Loranger & Shipley 2010; Gillison, 2019). Leaf mass per area (LMA) and leaf thickness (LT) were shown to be controlled by climate (Fonseca et al., 2000; Reich et al., 2003; Poorter et al., 2009). At the same time these parameters are linked with main physiological characteristics such as photosynthesis rate, relative growth rate, leaf lifespan and others (Poorter et al., 2009; Hassiotou et al., 2010; Siefert et al., 2015). Leaf thickness determines the amount of light absorbed by the leaf and the diffusion path of CO_2 through the tissues. Chlorophylls and carotenoids are responsible for light absorption and photochemical reactions in chloroplasts. Regulation of chlorophyll concentration and the ratio of pigments in the leaf is a function of photosynthesis adjustment to various environmental factors, first to light and water availability (Ivanov et al., 2004, 2022). Leaf mesophyll traits deserve special attention since they are particularly informative as functional parameters responsible for leaf gas exchange (Evans et al., 2009; Terashima et al., 2011). These parameters are useful for estimating the internal leaf conductance for CO_2 (Laisk et al., 1970; Terashima et al., 2011), studying the adaptation mechanisms of plants to stress (Nobel & Walker 1985; Mokronosov 1981; Pyankov et al., 1999) and examining the response of different plant functional types (PFTs) to their environment (Poorter et al., 2009, 2019; Shipley et al., 2016). Therefore, trait combinations seem to be selected by local environment, disturbance and biotic interactions (Bruelheide et al., 2018).

Research conducted in natural ecosystems often reveals challenges in discerning precise effects of various factors on the plant's functioning. Typically, in steppe, plants experience the combined effects of multiple adverse factors, including water deficit, high insolation and fluctuating precipitation together known as climate aridity as well as livestock grazing. There is little information on the combined effects of different factors on plant functional traits (Havstad et al., 2008; Hunt, 2010; Xie et al., 2018). Both climate aridity and grazing have a significant impact on plant productivity, but they can act on different groups of functional traits (Ivanov et al., 2018). Trait variations often go beyond interspecific differences and are influenced by intraspecific phenotypic and genetic factors (Nicotra et al., 2010; Siefert et al., 2015). The combined study of intra- and interspecific variation makes it possible to find out what functional traits are determined by the phylogenetic nature of plants (species, taxonomy), and what traits are more dependent on changing environmental factors. The Trans-Baikal region is insufficiently studied in relation to

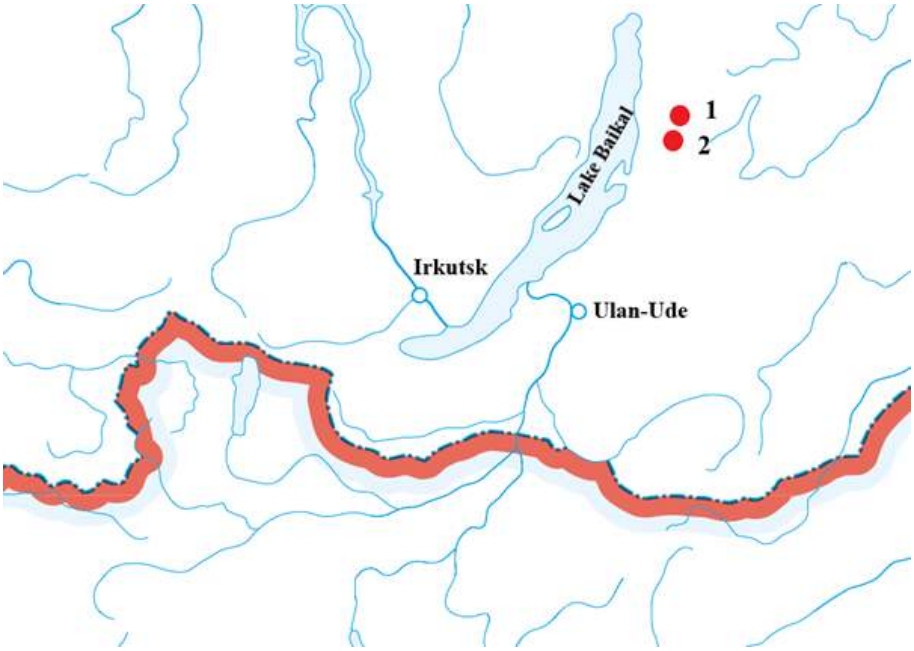


Fig. 1. Map of the locations of two study sites. 1 – Site 1, 2 – Site 2 (see Table 1).

the structural and physiological mechanisms of plant response to environment. We studied six plant species of different taxa and life forms in two steppe sites differed by climate and grazing disturbance. The purpose of the work was to study the interspecific differences and intraspecific variation of plant functional traits. To reveal the degree of species-specificity and dependence on external conditions for biochemical, physiological, and structural traits at the leaf-, tissue- and cell-level we investigated the relationship between plant functional traits and environmental conditions.

Materials and methods

The study was conducted in 2018 in two steppe plant communities in Southern Siberia near Lake Baikal, Republic Buryatia, Russian Federation (Fig. 1). Table 1 presents the description of the studied communities. The material was collected in native true steppe and anthropogenically disturbed steppe during the period of active plant vegetation (budding-flowering) in early July. Data on average annual rainfall and temperature of three regions were taken from the site https://www.worldclim.org/data/worldclim21.html (Table 1). Climate of the study sites is characterised by mean annual precipitation (mm) (MAP) mean annual temperature (°C) (MAT) and the De Martonne aridity index (Ia) (Table 1), calculated using the equation: Ia = MAP/(MAT + 10). The minimum value of the index corresponds to the maximum aridity of the climate.

We studied 6 species of angiosperms of different taxa and growth forms (Table 2). *Artemisia frigida* is a widespread in Europe and Asia species, where grows in the steppes of the Urals, Southern Siberia, Kazakhstan, Mongolia, and China. *Artemisia scoparia* is an annual or biennial herb which is distributed across much of Eurasia from France to Japan, including China, India, Russia, Germany, Poland, central and southwest Asia. *Artemisia scoparia* grows in steppes, steppe meadows, pastures, fallow lands, roadsides, gravelly and sandy slopes, riverbanks, and sparse forests. The native range of *Potentilla acaulis* which is a perennial xerophytic herb is Central Asia, up to Siberia and Northern China. *Potentilla bifurca* is widespread in temperate and alpine zones of the Northern hemisphere, grows on crushed slopes, ramps, and rocks. *Stipa krylovii* is a grass that typically dominates in steppes of Central Asia. *Allium anisopodium* is a herbaceous perennial bulbous plant with succulent-like leaves. This species grows in steppes, dry slopes, and sands. Its natural wide range includes Kazakhstan, Siberia, the Far East (Russia), Mongolia, China, and the Korean Peninsula.



Fig. 2. The study sites: at the top site 1 – true grass steppe with a high abundance of *Stipa krylovii* and *Artemisia frigida,* at the bottom site 2 – highly disturbed sagebrush steppe.

We studied morphological, structural, physiological and biochemical parameters of plants (Table 3). To measure leaf traits, 10 to 20 leaves were harvested from the middle leaf tier of fully developed, healthy individuals per species. Ten to twenty fresh leaves per species were photographed directly in the field for leaf area and LMA measurements. Leaf area was determined using a digital camera and the Simagis Mesoplant™ image analyzer (SIAMS, Ekaterinburg, Russia). Collected fresh leaf material was stored in a

Table 1. Location, climatic and vegetation characteristics of the study sites. Sh – the share of grazing digression active plant species, P – precipitation, T – temperature, Ia – aridity index, SpN – species number, TotC – total coverage of community (%).

Study site	Geographical location	Type of community	Dominant species	P	T	Ia	SpN	TotC
Site 1 N53.34° E110.61°	Kurumkan, Russia	True grass steppe	*Stipa krylovii, Artemisia frigida*	345	-3.5	53	19	75
Site 2 N53.73° E110.27°	Barguzin, Russia	Highly disturbed sagebrush steppe	*Artemisia scoparia*	358	-2.8	50	17	55

Table 2. Studied plant species, their characteristics and relative abundance in studied communities (coverage, %): SN – short symbols of species used in figures, Site 1 – true grass steppe, Site 2 – highly disturbed sagebrush steppe (see Table 1). GF – growth form, DS – dwarf shrub, HA – herb annual, HP – herb perennial.

Plant species	SN	Family	GF	Coverage, %	
				Site 1	Site 2
Stipa krylovii Roshev.	SK	Poaceae	HP	26	3
Artemisia frigida Willd.	AF	Asteraceae	DS	13	11
Potentilla acaulis L.	PA	Rosaceae	HP	9	9
Potentilla bifurca L.	PB	Rosaceae	HP	1	5
Artemisia scoparia Waldst. et Kit.	AS	Asteraceae	HA	7	29
Allium anisopodium Ledeb.	AA	Amaryllidaceae	HP	1	3

refrigerator in wet filter paper for 2–3 h. Nine to twelve leaves were taken for measurements of chlorophyll and carotenoid contents and 20–30 leaves were fixed in tubes in a solution of glutaraldehyde (3.5% glutaraldehyde in 0.15M phosphate buffer, pH 7.4) for anatomical measurements.

Gas exchange was measured under field conditions on intact mature leaves of three individuals in each species per community. The maximal photosynthetic rate (A_{max}) and transpiration rate (E) were determined using a portable photosynthetic system Li-6400 XT (Li-COR, USA). Measurements were taken in the first half of the day from 9 to 12 hours. Water use efficiency (WUE) was calculated as the ratio of maximal rate of photosynthesis to transpiration rate, μmol $mmol^{-1}$: $WUE = A_{max}/E$. To determine the content of photosynthetic pigments, cuttings were made from 20–30 leaves of 10–15 plants of each species. Pigments were extracted with 80% acetone, then chlorophyll content (C_{ab}/A, mg/dm^2) and carotenoid content per leaf area unit (Car/A, mg/dm^2) were measured using the Odyssey DR/2500 portable spectrophotometer (Hach, USA). C_{ab}/A was calculated according to Lichtenthaler and Wellburn (1983): C_a (mg/l) = 11.63· D665 – 2.39 · D649, Cb (mg/l) = 20.11·D649 – 5.18·D665, Car = 4.695·D440,5 – 0.268(C_{ab}/A), where C_a – chlorophyll *a* concentration, C_b – chlorophyll *b* concentration, D665, D649 and D440.5 – optical densities of the extract at the wavelengths 665, 649 и 440.5 nm, C_{ab}/A – chlorophyll *a*+*b* content per unit leaf area. In addition, the ratio of chlorophylls *a/b* and the ratio of chlorophylls/carotenoids (Chl/Car) were calculated.

For anatomical and biochemical analyses, the central part of the leaf avoiding main veins was taken. The main leaf structural traits will be obtained according to Leaf Mesostructure Method of Ural School of Ecophysiology (Pyankov et al., 1999; Ivanova et al., 2016, 2018a). The number of cells per unit leaf area was determined in 20 replicates using a hemocytometer (Goryaev chamber; Minimed, Bryansk, Russia) in cell suspension obtained after heating to 90°C and after maceration of leaf pieces of known area (ca. 1 cm^2) in 2–3 ml of 20% KOH (described in detail by Ivanova et al., 2016, 2018a). Chloroplast number per cell was determined in 30 replicates in the same cells

Table 3. The list of studied traits and units.

Abbreviation	**Explanation**	**Units**
PlantH	Plant height	cm
LT	Leaf thickness	μm
LMA	Leaf mass per area	mg dm^{-2}
LD	Leaf density	g cm^{-3}
V_{cell}	Cell volume	10^3 μm^3
N_{cell}/A	Number of cells per unit leaf area	10^6 cm^{-2}
V_{chl}	Chloroplast volume	μm^3
Chl per cell	Number of chloroplasts per cell	items
N_{chl}/A	Number of chloroplasts per unit area	10^6 cm^{-2}
A_{mes}/A	Total mesophyll cell surface area per unit leaf area	cm^2 cm^{-2}
A_{chl}/A	Total chloroplast surface per unit leaf area	cm^2 cm^{-2}
A_{max}	Maximal rate of photosynthesis per leaf area	μmol m^{-2} s^{-1}
E	Transpiration rate per leaf area (mass)	mmol/m^{-2} s^{-1}
WUE	Water use efficiency	μmol $mmol^{-1}$
C_{ab}/A	chlorophyll a+b content per unit leaf area	mg dm^{-2}
Car/A	carotenoid content per unit leaf area	mg dm^{-2}
Chl/Car	chlorophylls/carotenoids ratio	non-dimensional
a/b	chlorophyll a/b ratio	non-dimensional
A_{max}/Chl	Maximal rate of photosynthesis per chloroplast	10^{-10} μmol CO_2 s^{-1}
C_{ab}/Chl	Chlorophyll a+b content per chloroplast	10^{-9} mg
TR_{mes}	Rate of CO_2-transfer through the mesophyll surface	μmol m^{-2} s^{-1}

that were measured for cell sizes. Cell sizes were determined in 30 replicates in cell suspension after maceration of leaf pieces in 1M HCl heated to 40–50°C. Cell projection area (A_{cell}) and perimeter (P_{cell}) are measured with a light microscope (Axiostar plus, Zeiss, Germany) using the Simagis Mesoplant™ image analyzer (SIAMS, Ekaterinburg, Russia). The mesophyll cell volume (V_{cell}) and cell surface area (S_{cell}) were calculated separately for each type of photosynthetic tissue (palisade and spongy mesophyll cells, bundle sheath cells, and segmented mesophyll cells of grasses) using the projection method described in Ivanova et al. (2018a). Cell volume was calculated using the formula:

$$Vcell = \frac{Scell^2}{Pcell}\sqrt{b^3 * K_p}$$

where V_{cell} – cell volume (μm^3), S_{cell} – average cell projection area (μm^2), P_{cell} – average cell projection perimeter (μm); *b* and *Kp* – proportionality coefficient depending on the cell shape, for majority of mesophyll cells, b ranges from 3.2 to 4.0, Kp – ranges from 0.9 to 0.11 (described in Ivanova et al., 2018a). Chloroplast number per unit leaf area (N_{chl}/A) was calculated by multiplying chloroplast number per cell and cell number per unit leaf area for palisade and spongy mesophyll, or for total mesophyll in the case of uniform or irregular cells. Total cell surface area per unit leaf area (A_{mes}/A) was determined by multiplying the average cell surface area and cell number per unit leaf area. Total chloroplast surface area per unit leaf area (A_{chl}/A) was determined by multiplying the average chloroplast surface area and the chloroplast number per unit leaf area. The chlorophyll a+b content per chloroplast (C_{ab}/chl, 10^{-9} mg) was obtained by dividing the pigment content per unit leaf area (C_{ab}/A) by the chloroplasts number per unit area (N_{chl}/A). Photosynthetic activity of the chloroplast (A_{max}/chl, 10^{-10} μmol CO_2 s^{-1}) was calculated by divid-

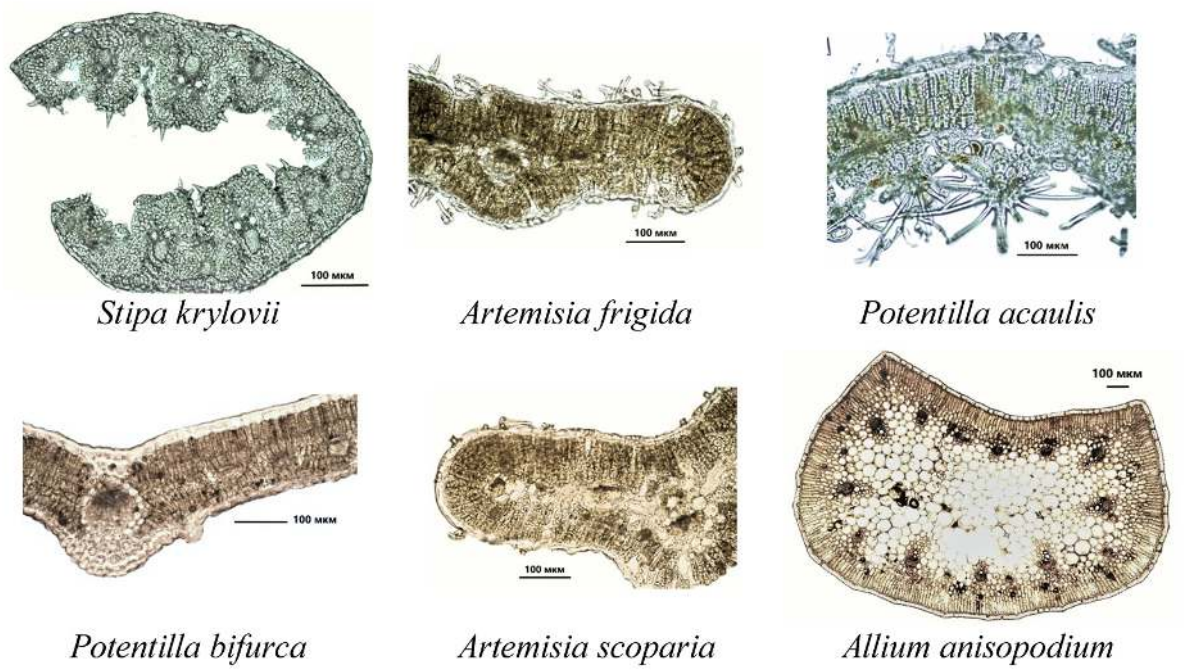


Fig. 3. Pictures of the leaf cross-sections for studied plant species. Scale is 100 μm.

ing the photosynthetic rate per unit leaf area (A_{max}) by the number of chloroplasts per leaf area (N_{chl}/A). The rate of CO_2-transfer through mesophyll surface area (TR_{mes}) and chloroplast surface area (TR_{chl}) were calculated by dividing the maximum rate of CO_2-uptake per leaf area (A_{max}) by A_{mes}/A or A_{chl}/A, respectively.

Statistical analysis was performed using STATISTICA 13.0 (USA). Data analysis was made using variance analysis (ANOVA) by factors "Species" and "Site". Paired t-Test was performed to reveal differences between samples of two communities inside the same species.

Results

Table 1 presents the characteristics of two steppe communities, in which 6 plant species were studied. The studied communities varied significantly in grazing disturbance, species composition, and total coverage. Highly disturbed sagebrush steppe had similar species richness, but lower total coverage in comparison to true steppe (Table 1). The studied species played different roles in communities. First three species in Table 2: *Stipa krylovii, Artemisia frigida* and *Potentilla acaulis* belonged to the most abundant species of non-disturbed true grass steppe and decreased their abundance in site 2. Other three species: *Artemisia scoparia, Potentilla bifurca* and *Allium anisopodium* were less abundant in true grass steppe and increased their abundance in disturbed steppe of site 2, moreover *Artemisia scoparia* became a dominant species at site 2.

Anatomical analysis revealed a high variation in leaf morphology among the studied species (Fig. 3). Two species of genus *Artemisia – A. frigida* and *A. scoparia* – had a typical for steppe dicotyledonous xerophytic herb isopalisade type of mesophyll with palisade tissue on both leaf side (Ivanova et al., 2018a, b). Two species of genus *Potentilla – P. acaulis* and *P. bifurca* – possessed a dorsoventral type of mesophyll with palisade tissue on the upper and spongy tissue on the lower side of a leaf. Grass *S. krylovii* characterised by long rolled leaves of graminoid type. Leaves of onion *A. anisopodium* were hemy-cylindrical with isopalisade-peripherical type of mesophyll and water-storing parenchyma in the centre of the leaf. Studied species also distinguished by values of gas exchange rate, pigment content and traits of a whole leaf and of a mesophyll (Figs 4, 5).

We analysed the influence of environmental conditions of site 1 and site 2 on different functional traits. Some functional traits were largely species-specific and hardly influenced by environment changes

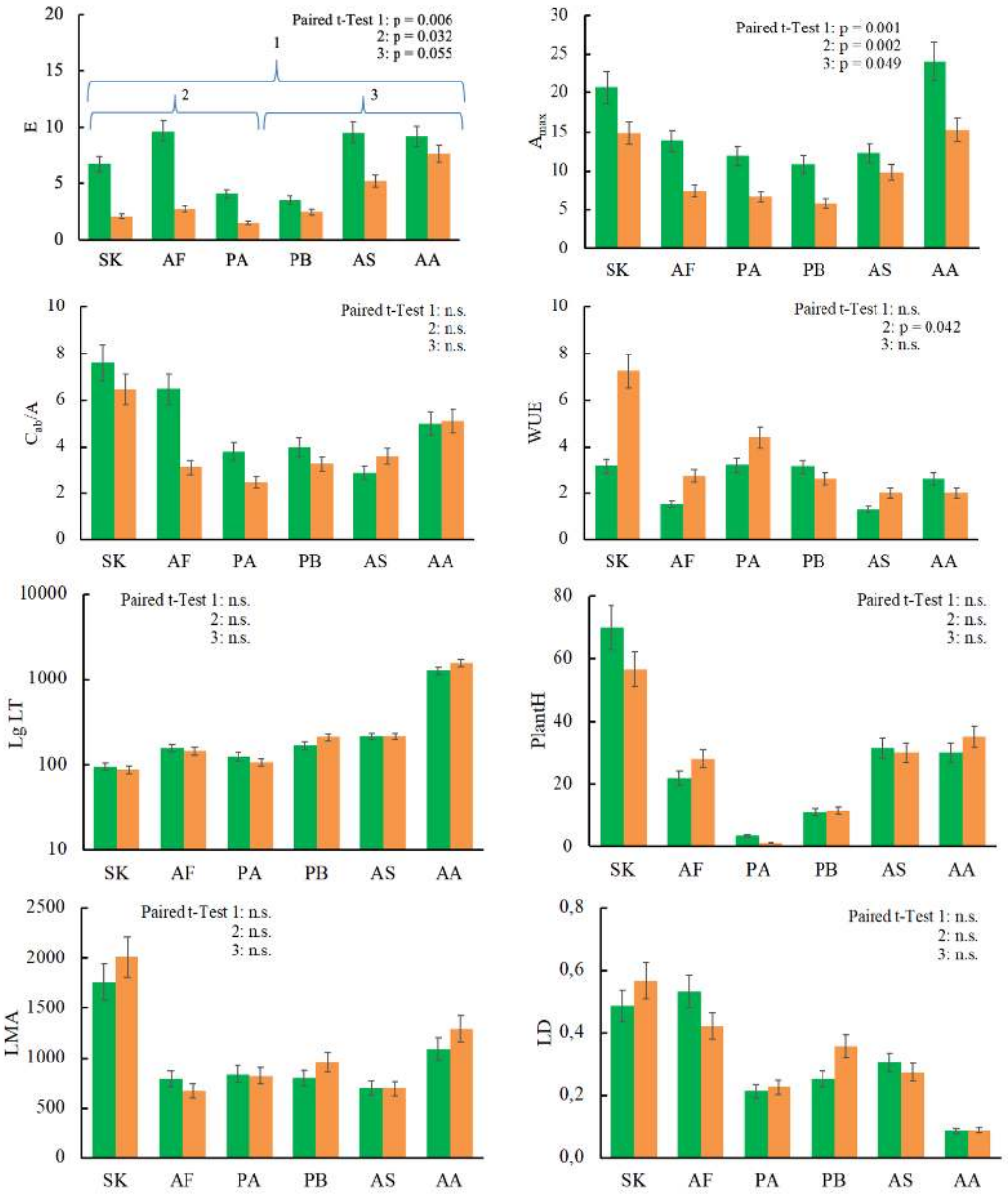


Fig. 4. Plant functional traits of 6 studied species at two study sites: the first column (green) presents site 1, the second column (orange) presents site 2. Horizontal axis presents species names (full species names see Table 2). The results of paired t-Test are presented in three variants: 1 – all species, 2 – the first group of species (SK, AF, PA) which are the most abundant in native true steppe, 3 – the second group of three species (PB, AS, AA) which increase their abundance in disturbed community on site 2. n.s. – not significant. Species names see Table 2. Leaf traits and units on vertical axes see Table 3.

(Table 4). Thus, plant height, leaf thickness and density (LMA, LD) were determined mostly by plant species and did not differ between study sites in all variants of ANOVA analysis: both for all studied species and for two different groups of species divided on their roles in community. The first group – true steppe dominants (*S. krylovii, A. frigida* and *P. acaulis*) had thinner leaves (Fig. 4) and smaller mesophyll cells (Fig. 5) in comparison to other three species which were more abundant in site 2 (disturbed steppe abundant). Such traits as maximum photosynthesis rate (A_{max}) and transpiration (E) were more de-

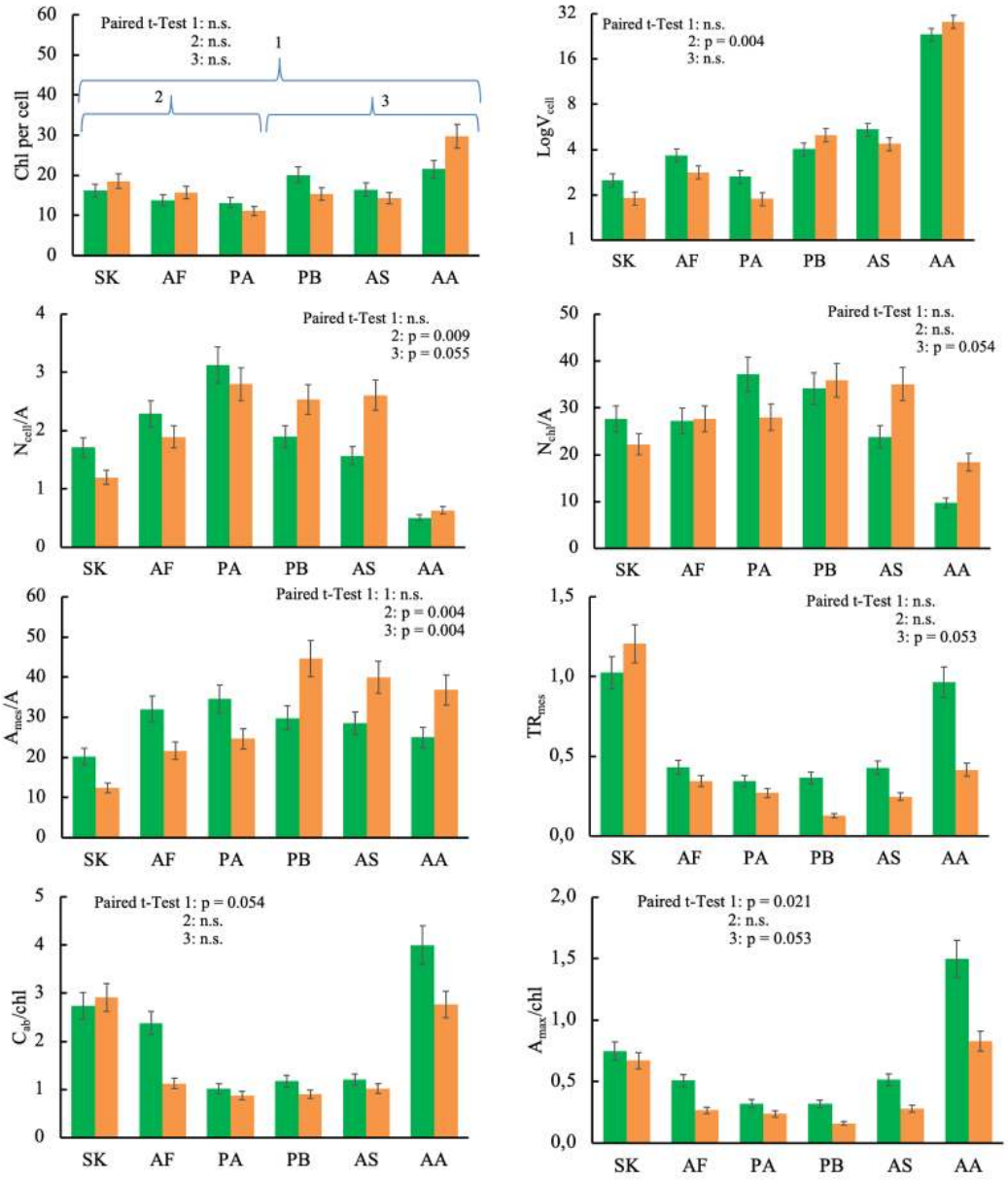


Fig. 5. Leaf mesophyll and cell-level functional traits of 6 studied species at two study sites: the first column (green) presents site 1, the second column (orange) presents site 2. Horizontal axis presents species names (full species names see Table 2). LogVcell – logarithmic values of cell volume (on the base of 2). The results of paired t-Test are presented in three variants: 1 – all species, 2 – the first three species (SK, AF, PA) which are the most abundant in native true steppe, 3 – the last three species (PB, AS, AA) which increase their abundance in disturbed community on site 2. n.s. – not significant. Species names see Table 2. Leaf traits and units on vertical axes see Table 3.

pendent on environment, but total mesophyll surface area per leaf area (A_{mes}/A) was dependent on environment in the case of dividing plant species in two groups: true steppe dominants and disturbed steppe abundant (Table 4). Mesophyll cell volume and cell number per leaf area unit were highly dependent on species in all three variants and influenced by both species and environment in the first group of species (true steppe dominants).

Despite high diversity in morphological and anatomical features among studied species, we found similar intra-specific trends in physiological changes

Table 4. Values of F-criterion in an analysis of variance (ANOVA) by the factors 'Species (6 plant species)', 'Environment (two plots)' and the statistical significance of these factors: *, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$, ns – not significant. Variant 1 – all species were included in the analysis, Variant 2 – three species with the most abundance in true steppe at site 1 (*Stipa krylovii, Artemisia frigida* and *Potentilla acaulis*) were included in the analysis, Variant 3 – three species, which were rare at site 1 and increased their abundance in disturbed steppe (*Artemisia scoparia, Potentilla bifurca* and *Allium anisopodium*), were included in the analysis. See Table 3 for definitions of variables.

Variable	**Variant 1**		**Variant 2**		**Variant 3**	
	Species	**Environment**	**Species**	**Environment**	**Species**	**Environment**
PlantH	37***	ns	40*	ns	52*	ns
LT	71***	ns	156**	ns	76*	ns
LMA	38***	ns	44*	ns	21*	ns
LD	90***	ns	141**	ns	168**	ns
V_{cell}	62***	ns	93*	112**	63*	ns
N_{cell}	7*	ns	248**	55*	ns	ns
A_{max}	21**	44***	62**	308**	ns	ns
A_{mes}/A	ns	ns	103**	138***	ns	132**
E	ns	15*	ns	ns	ns	ns
Chl/Car	ns	18**	ns	42*	ns	14*
A_{max} per chl	10*	7*	23*	ns	16*	ns
C_{ab}	12**	ns	ns	ns	21*	ns

in response to environment. Photosynthetic capacity and transpiration rate decreased in all studied plant species in highly disturbed and more arid steppe (site 2) compared to true steppe community (site 1) (Fig. 4). However, in true steppe dominants transpiration rate decreased in a greater degree than photosynthesis that is confirmed by an increase in water use efficiency (WUE) which is defined as the ratio of photosynthesis and transpiration. In the second group of species which were more abundant in disturbed steppe and did not change their WUE, the proportional changes of A_{max} and E were noted. A_{max} did not relate to pigment content, leaf density and chloroplast number per leaf area, the last one, on the opposite, increased in the second group of species (variant 3 on Fig. 5). The main grounds of a diminishing in A_{max} included microstructural changes of mesophyll as well a decrease in stomatal conductance evidenced by the data on transpiration. Changes in mesophyll structure differed between two groups of plant species. In the first group of true steppe dominants – *S. krylovii, A. frigida* and *P. acaulis,* a decrease in mesophyll cell number and size and as a result to a sharp decrease in A_{mes}/A was caused by the influence of conditions of site 2. On the opposite, in *A. scoparia, P. bifurca* and *A. anisopodium,* more abundant in disturbed steppe, increased cell number and A_{mes}/A in site 2 were observed and they also decreased the CO_2 transport rate per mesophyll surface (TR_{mes}) and photosynthetic capacity of a chloroplast (A_{max}/chl) by 40–60% (Fig. 5).

Discussion

Our study is among a few studies which perform simultaneous analysis of morphological, structural, physiological, and biochemical changes in response to combine effect of climate aridity and grazing. Typically, only several traits or single factor are used to reveal the plant functional response due to laboriousness of such research in natural ecosystems. Detailed analysis of structural, chemical and physiological traits combined with ecological variables can reveal what plant functional traits from whole-plant to tissue- and cell-level are the best predictors of functional response of plants to environment. For example, the main adaptive features of xerophytes to a short period of growth are miniaturising of the leaf blade and

higher leaf tissues density (Gamalei, 1984; Mokronosov, 1981; Galmes et al., 2012; Ivanova, 2014). The main leaf tissue – mesophyll is the material basis of photosynthesis and represents a system of structures providing photosynthesis. In this regard, plant adaptation to environment is closely related to the rearrangement of mesophyll cells and chloroplasts (Mokronosov, 1981; Nobel & Walker 1985; Pyankov et al., 1999; Terashima et al., 2011; Ivanova, 2014, 2016). Steppe xerophytes often possess isopalisade leaf structure which is an adaptation to high insolation. Isopalisade mesophyll type is characterised by the high concentration of cells and chloroplasts per unit leaf area (Pyankov et al., 1999; Zvereva, 2000; Ivanova, 2014). Xerophytes of the Karakum Desert had 60–90 million of chloroplasts per 1 cm^{-2} of leaf area (Mokronosov, 1981) that is two-three-fold higher than that in steppe plants (Zvereva, 2000; Ivanova et al., 2018a, 2019) and 6–8 times higher than in boreal mesophytes (Ivanova, 2014). Steppes often are dominated by xerophytic grasses as *Stipa* species which also have high concentration of photosynthetic cells and chloroplasts per leaf area (Ivanova et al., 2019). A special type of leaf adaptation to aridity is succulence. Succulent plants in addition to chlorenchyma, have a water-storing tissue or their mesophyll along with photosynthesis can perform a water-storage function and differ by large cell volume and low leaf density (Rozentsvet et al., 2016; Ivanova et al., 2019). Our species studied belong to different morphological leaf types – isopalisade (both *Artemisia* species), graminoid, dorsovental (*Potentilla* species), succulent-like (*Allium*), however they showed similar functional response to environment.

Our study shows that plant functional traits have different relevance to interspecific variation and growing conditions. Such traits as leaf thickness, cell volume and chloroplast number per cell were highly species-specific and had minimal intraspecific variation. Indeed, a high species-specificity of these traits has been indicated earlier for other plant species including steppe plants (Mokronosov, 1981; Yudina et al., 2017, 2020). Previous studies of *Artemisia frigida* showed, that mesophyll cell volume in different steppe regions of Mongolia ranged from 2 to 6 thousand μm^3 and LT for this species varied between 145 and 200 μm (Ivanova et al., 2019), which is fully consistent with our data for this species (Fig. 5). The data available in the literature for *Artemisia scoparia* and *Allium anisopodium* is also within the values we identified in this study: V_{cell} 4–5 thousand μm^3 and 20–30 thousand μm^3 accordingly. The same conclusion about species-specificity of cell volume and leaf thickness can be made for *Potentilla* species and *Stipa krylovii,* which we studied earlier in steppe communities of Northern Mongolia (Ivanova et al., 2019).

Mesophyll cell volume is a key parameter of leaf structure which is strongly coordinated to photosynthetic function. Cell volume can influence on gas exchange of the whole leaf due to a strong dependence of surface-volume ratio (S/V ratio) on cell size. It was shown that small cells with a volume of less than 10 thousand μm^3 have higher S/V ratio and more dramatic change of S/V ratio with volume change (Ivanova et al., 2014; Migalina et al., 2014). Larger cells have lower S/V ratio, which negatively affects the metabolic transport rate, including the mesophyll diffusion of CO_2 from the intercellular space into the cell (Migalina et al., 2014). Besides, V_{cell} positively correlates with leaf thickness as it was shown for many plant species from steppe (Ivanova et al., 2018a) and high mountains (Pyankov et al., 1999). On the other hand, V_{cell} has inverse relationship to cell number per leaf area and partial share of intercellular air space within a leaf (Ivanova et al., 2014; Rosentsvet et al., 2016), that could also affect gas exchange within mesophyll (Flexas et al., 2012; Ivanova et al., 2018b). Further, there is a high positive correlation between V_{cell} and chloroplast number per cell that allows plants with larger cells inexpensively and quickly to enhance chloroplast number per leaf area and thereby to optimise leaf photosynthesis. Moreover, in previous studies of 193 plant species of Central Asia, we showed that leaf thickness, cell volume and chloroplast number per cell were closely linked with plant functional type (PFT), which combines species with similar functional traits (Ivanova et al., 2019). Thus, we suppose that LT and V_{cell} are not only species-specific as our data showed, but these traits are also highly indicative of functional features of a species, i.e. ecological or life strategy (Grime, 2001; Adler et al., 2014). Obviously, these three traits – mesophyll cell volume, chloroplast number per cell and leaf thickness – were the most informative traits which differentiated studied plant species into two groups according to their roles in the community.

Since plant distribution in the nature is also affected by multispecies interactions, we need to consider not only the presence of species but also their abundance in the community (Grime, 1998; Garnier

et al., 2004). Many past studies (with only several exceptions) that assessed how traits vary across climatic gradients typically have not combined species trait values with species abundances (Wieczynski et al., 2018). Determining the functional traits of species while accounting for the species coverage or phytomass allows proceeding from the species to the ecosystem level (Garnier et al., 2004) as the effect of species on ecosystem properties will depend on their proportional abundance in the community (Grime, 1998). Studied plant species were divided into two groups on their abundance in studied communities. First three species *Stipa krylovii, Artemisia frigida* and *Potentilla acaulis* which are among the most abundant species of true grass steppe had smaller cells and thinner leaves (Figs 4, 5). Other species with larger cells – *Artemisia scoparia, Potentilla bifurca* and *Allium anisopodium* – were less abundant in true grass steppe and had higher abundance in disturbed steppe of site 2. Larger V_{cell} in species of the second group corresponded to higher LT and to a lower leaf tissue density (LD) (Fig. 4). Leaves with lower LD are less resistant to water deficit (Gamalei, 1984; Galmés et al., 2012). In this regard, lower LD reduces the resistance of these species to drought and unfavorable temperatures that inhibits their competitive advantage in steppe conditions and does not allow them to occupy a dominant position in true steppe communities. In the opposite, at grazing disturbed steppe at the site 2, where total vegetation coverage was less and intra-specific competition was minimal due to higher consumption of true steppe dominants by herbivores (Xie et al., 2018; Jäschke et al., 2019), species of the group 2 get an advantage. More favourable conditions at site 2 for plants of group 2 are confirmed by increasing coverage, an increase in cell number and A_{mes}/A. An integral mesophyll trait A_{mes}/A can serve as indicator of optimal conditions for given species because this characterises the size of exchange surface area for CO_2 uptake inside a leaf. We suppose that more favourable water regime, for instance, increased precipitation, should facilitate CO_2 diffusion into leaves, and species with higher A_{mes}/A abundant in disturbed steppe (group 2) could improve their photosynthesis and productivity in areas highly disturbed by overgrazing.

The most variable indicators at the intraspecific level included physiological parameters as photosynthesis rate, transpiration and A_{mes}/A. All species decreased their photosynthesis and transpiration in more adverse conditions at the site 2, however plants of different groups differed in changes A_{mes}/A. Other sources reported a significant level of intraspecific variation in A_{mes}/A (Yudina et al., 2017), chlorophyll content per unit leaf area (Ivanov et al., 2022) and per chloroplast (Yudina et al., 2017; Ivanova et al., 2018a). It has been shown that the number of cells and chloroplasts, A_{mes}/A, the ratio of chlorophylls a/b and chl/car in steppe plants depend on climate aridity and were less influenced by taxonomic position (Yudina et al., 2017, 2020).

Plant adaptation to arid climate is aimed at reducing transpiration and maintaining plant water relations (Galmés et al., 2012). Both aridity and grazing affect can water use efficiency (WUE) (Ivanov et al., 2018). This parameter specifies the amount of absorbed carbon dioxide per unit of transpiration loss and is an indicator of plant resistance to drought (Lambers et al., 1998). In our study species of group 1 increased their WUE under higher aridity and disturbance whereas species of the group 2 did not change WUE in different environment. Other study also revealed an increase in WUE with aridity in *Artemisia frigida* due to a twofold decrease in transpiration (Ivanov et al., 2018). We have not found any data on photosynthesis and WUE for other species studied in literature. We suppose that intraspecific changes of these physiological parameters could be highly coordinated with the response of integral mesophyll traits such as A_{mes}/A that reflects the ecological properties of species. For example, in the study in West Siberia, the response of A_{mes}/A to drought depended on the ecological properties of the species. Thus, A_{mes}/A increased under drier conditions in leaves of steppe xerophyte, whereas it decreased in meadow mesophytes (Ivanova, 2014). In our study, most species decreased the CO_2 transfer rate through the mesophyll surface area unit, chlorophyll content per chloroplast and photosynthetic activity of chloroplast under increasing aridity and disturbance. Chlorophyll content per chloroplast varies among plant species depending on their ecological properties (Mokronosov, 1981). Desert sclerophytes typically contain low chlorophyll at the means of 0.2–0.3 10^{-9} mg per chloroplast (Mokronosov, 1981). For comparison, mesophytic herbaceous plants of deciduous forests possess 4–10 10^{-9} mg per chloroplast, and in steppe plants, the value of this trait varied between 0.4–3 mg per 10^9 chloroplasts (Mokronosov, 1981; Zvereva, 2000). Thus, a decrease of chlorophyll content per single chloroplast

can serve as the adaptation of steppe plants to an increased insolation and water deficit. Declined photosynthetic activity of a single chloroplast in studied species is a consequence of a chlorophyll loss and delayed CO_2 diffusion into a leaf in drier and disturbed conditions. However, species with different roles in communities had different functional adaptation to aridity and grazing. The true steppe dominants decreased mesophyll cell size and number, which led to reduction of A_{mes}/A, that allowed to economise for construction cost and enhanced WUE. In opposite, in abundant in disturbed steppe species increased cell and chloroplast number per leaf area caused an increase in A_{mes}/A, that made it possible to optimise the photosynthetic performance of these species at disturbed areas. The results of this study will enable future research with similar plant functional types to differentiate the effects of phylogeny and environment and predict plant functional response to environmental change.

Availability of data and material

All raw data is available as a Supplementary material 01.

Acknowledgements

The reported study was performed within the framework of the state assignment FEWZ-2024-0007 from Ministry of Education and Science of the Russian Federation and in accordance with the budget theme of the Botanic Garden of the Ural Branch of the Russian Academy of Sciences, and partly by budget theme of A.N. Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences, project of FFER-2024-0025.

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Supplementary materials

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Document title: Raw data
Kind of document: Microsoft Excel (OpenXML)
MIME type: application/vnd.openxmlformats-officedocument.spreadsheetml.sheet
Document name: 000551000462024-01.xlsx
https://doi.org/10.48027/hnb.46.061/01