

# The CSR strategies of alpine plants and community functional diversity in the Eastern Qinghai-Tibetan mountains

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### ABSTRACT

Many alpine communities of the Tibetan plateau experience both harsh climates and heavy grazing, and the adaptations to such environment are realized in plant functional traits and strategies. We tested, which leaf traits allow to dominate in the two wide-spread alpine communities of the Eastern Qinghai-Tibetan mountains, *Kobresia* alpine meadows and alpine fens, and do meadows and fens differ by community-weighted dominance-linked traits, strategy affinities, and functional diversity. Lower leaf dry matter content (LDMC) and higher specific leaf area (SLA) provides the species dominance in *Kobresia* alpine meadows, while size traits do not influence the dominance. Both LDMC and SLA have low functional evenness and divergence in the two communities. The prevail of stress-tolerators reflects the abiotic environment of alpine plants, but high affinities to ruderal strategy are possibly related to grazing.

Keywords: functional traits, functional diversity, CSR strategy, alpine plants

### РЕЗЮМЕ

У Ю., Елумеева Т.Г., Казанцева Е.С., У Я., Ван Ц., Дудова К.В., Онипченко В.Г. Эколого-ценотические CSR стратегии альпийских растений и функциональное разнообразие сообществ на востоке Цин-хай-Тибетского нагорья. Многие альпийские сообщества Тибетского нагорья существуют в условиях сурового климата и интенсивного выпаса. Адаптации к таким условиям представлены функциональными признаками растений и стратегиями. Мы изучили, какие признаки листьев позволяют доминировать на альпийских кобрезиевых лугах и на альпийских болотах – сообществах, которые широко распространены в альпийском поясе востока Цинхай-Тибетского нагорья. Мы проверили, различаются ли болота и луга по средневзвешенным признакам, связанным с доминированием, стратегиями и функциональным разнообразием. Более низкое содержание сухого вещества (LDMC) в листьях и более высокая удельная листовая поверхность (SLA) способствуют доминированию видов на альпийских кобрезиевых лугах, тогда как размерные характеристики (площадь и масса листа) не влияют на доминирование. В изученных сообществах признаки LDMC и SLA имеют низкую функциональную выравненность и дивергенцию. Преобладание стресс-толерантов отражает абиотические условия обитания альпийских растений, а большой вклад в рудеральную стратегию, возможно, связан с влиянием выпаса.

**Ключевые слова:** функциональные признаки, функциональное разнообразие, CSR стратегии, альпийские растения

Plant functional traits and functional types or Grime's strategies affinities, measured by standardized protocols, allow to perform rather easy and informative comparative analysis of plant community structure and composition through various vegetation types and geographical zones (Grime 2001, Pérez-Harguindeguy et al. 2013, Garnier et al. 2016, Pierce et al. 2017). The following approaches are often used to study functional composition: 1) the spectrum of plant traits and functional types (strategies); 2) the community weighted means (CWMs) of plant traits or Grime's strategy affinities (Lavorel et al. 2008). The values of CWMs are usually impacted by dominant species and sometimes differ significantly from non-weighted means of the same traits (Onipchenko et al. 2022); 3) the indices of functional diversity (Mason et al. 2005, Schleuter et al. 2010), the most commonly used indices are functional

richness (FRic), functional evenness (FEve) and functional divergence (FDiv). They can be calculated using single traits and as multitrait indices (Laliberté et al. 2014), therefore single trait indices are easier to interpret, as they often better indicate environmental gradients (Butterfield & Suding 2013, Dudova et al. 2019, Onipchenko et al. 2022).

The alpine regions are one of the most extreme environments on the earth. Therefore, alpine species have highly specialized adaptations to such habitats (Körner 1999), and the suits of functional traits, which allow them to withstand the harsh environment of high mountains, were often studied by plant ecologists. Generally, alpine plants experience stress due to high solar radiation, low temperatures, and often low nutrient availability. These factors suggest the stress-tolerators (S) are expected to be the prevailing plant functional type in terms of Grime's CSR

strategies (Grime 2001), as well as the higher affinity to stress-tolerance, calculated by the methods developed by Pierce et al. (2017). Indeed, the dominance of stress-tolerators was observed in the Tibetan plateau (Wang et al. 2018, Zhou et al. 2021, Yu et al. 2022) and increased from humid to arid alpine habitats.

However, the alpine environment is variable due to terrain, which may cause stronger differentiation of vegetation than elevation gradient, that's why in alpine belts of humid climate the depressions are characterized by late snowmelt time and short, sometimes extremely short, growing seasons. This requires plant adaptations to rather fast growth, attributed to the ruderal (R) strategy (Onipchenko et al. 2022). The depressions, which do not suffer too late snowmelt, have enough rates of mineralization to support species with traits of competitors (Onipchenko et al. 2022).

Besides the harsh environment, the biotic interactions are also important for alpine plant selection, because nonwoody alpine communities often support wild mammals and/or livestock grazing. In the areas, which develop as pastures for a considerable time, the selection also will lead to the prevailing of traits, which reflect adaptations to growth under heavy grazing. For example, the disturbance is a second important factor determining CWMs of specific leaf area (SLA) in calcareous grasslands of the Bavarian Alps (Rosbach et al. 2015), while in Tibetan rangelands, CWM SLA was not correlated with grazing intensity, but was positively correlated with precipitation and soil nitrogen content (Jäschke et al. 2020). In Tibetan alpine meadows intermediate grazing induced a shift to the ruderal strategy, while high grazing intensity promoted the dominance of species with higher C-affinities (Wang et al. 2018).

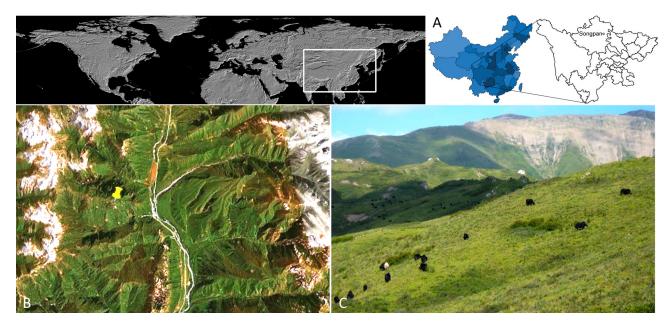
The Tibetan Plateau is an interesting object due to its large areas, covered by alpine vegetation, its high plant diversity and a long history of livestock grazing, mostly by yaks (Bos grunniens Linnaeus 1976). There are an increasing num-

ber of studies concerning functional traits of alpine plants in Tibet, including leaf traits and strategies, life form composition, floristic and functional richness, phytomass structure and CWMs of plant traits (Ma et al. 2010, Elumeeva et al. 2014, Onipchenko et al. 2014, Elumeeva et al. 2015a,b, Ren et al. 2015, Li et al. 2017, Wang et al. 2018, Jäschke et al. 2020, Vandvik et al. 2020, Zhou et al. 2021, Liu et al. 2022, Yu et al. 2022). However, the high species richness of the region and its large area suggests the importance of local studies for further incorporation of these data into large-scale regional studies.

Thus, our study aims to contribute to the investigation of alpine communities at the Eastern Qinghai-Tibetan Plateau by exploring the leaf functional traits and functional diversity of two local alpine communities, *Kobresia* alpine meadows and alpine fens. We tested which leaf traits allow to dominate in the communities and do meadows and fens differ by dominance-linked traits, strategy affinities, and functional diversity.

# MATERIAL AND METHODS Study area

The study was conducted in Mount Kaka (32°98'N 103°67'E). It is located in the West Sichuan Plateau, which is a part of Songpan County, Sichuan province in China (Fig. 1). The altitude of Mount Kaka is around 3950 meters. It belongs to the Min Mountains – the east of the Qinghai-Tibetan Plateau. This area is controlled by warm wet flow coming from southwest and southeast monsoon, it is a typical mountain monsoon climate. The average annual temperature in this area is +5.7°, the average temperature in January is -7.6°, and the average temperature in July is +9.7°. There is no absolute frost-free season and the average annual duration of solar radiation is 1827.5 hours, annual precipitation is 718 mm, and 72 % of precipitations falls from June to August (Hu et al. 2012, Onipchenko et al. 2014).



**Figure 1** Study area: A – Sichuan Province on the map of China and Songpan County on the map of Sichuan Province; B – the satellite image of the study area, marked is the position of observation plots; C – a typical alpine landscape of the study area with yaks pastures at *Kobresia* meadows

The timberline in the study area is at 3800–4000 m and the alpine belt is occupied by alpine meadows, fens and shrubs. The Latin names of plants are given by "Flora of China" (Editorial Board of Flora of China 1994–2013).

We mainly studied two types of communities:

Kobresia alpine meadows (KAMs). These communities occupy gentle southern slopes and ridges. The most abundant herbaceous species (from the most to less abundant) are Kobresia humilis (C.A. Mey ex Trauvt.) Serg., Sibbaldia procumbens Linn., Anaphalis nepalensis (Spreng.) Hand.-Mazz., Gentiana hexaphylla Maxim. ex Kusnez., Trollius farreri Stapf, Festuca orina L., and Ptilagrostis concinna (Hook. f.) Roshev. The cover of shrubs, for instance, Potentilla fruticosa L., Caragana jubata (Pall.) Poir., and Spiraea alpina Pall. range from 5 to 10 %. Kobresia alpine meadows have a well-developed moss layer, however, the lichens are not abundant in this community. The studied meadows are mainly used as pasture with moderate grazing by yaks (Elumeeva et al. 2014).

Alpine fens (AFs). Alpine fens occupy gentle slopes with poor drainage. The coverage of mosses is nearly 35 %, The most abundant vascular plants in AFs are *Carex moor-croftii* Falc. ex Boott, *Carex atrofusca* Schkuhr., *Kobresia humilis* and *Cremanthodium lineare* Maxim. These communities are mainly affected by intensive grazing (Elumeeva et al. 2014).

# Leaf traits measurements and CSR strategies calculation

The field sampling was in July 2012 and July-August 2019. We measured leaf area (LA), leaf fresh mass (LFM), and dry mass (LDM) of 94 plant species, together representing the most common vascular plant species of studied communities at the local site. In 20 species only LA and LDM were measured. Among them, the LFM of Kobresia humilis, Carex cruenta Nees, and Carex parva Nees were derived using regression coefficients of the relationship between LDM and LFM of the Carex and Kobresia species with flat leaves from open habitats (15 alpine and temperate grassland and fen species,  $R^2=0.968$ , p<0.001), the leaf dry matter content (LDMC) of Androsace mariae Kanitz was obtained from Ma et al. (2010), and that of Allium sikkimense Baker was obtained from Ren et al. (2015). For one species, Saussurea stella Maxim., all leaf measurements were extracted from the publication of Ren et al. (2015) from Maqu station, located at 3600 m. a.s.l.

To identify the plant species, we used Flora of China (Editorial Board of Flora of China. 1994–2013), the Moscow Digital Herbarium (Seregin 2022), National Plant Specimens Resource Center (2023) and the atlases of Q. Wang (2016) and Q. Zhou & Y. Gan (2016).

Standard protocols were used to measure the traits (Pérez-Harguindeguy et al. 2013). For measurements, we sampled 10–15 well-developed leaves without signs of damage, pathogenic infection, or senescence. For several species with small leaves (e.g. *Cerastium falcatum* Bunge), we collected 3–5 leaves from one plant per sample, but in all cases, the total number of samples was 10–15. Cutoff leaves were placed in plastic boxes with water and were kept in the fridge for 5–10 hours to get water-saturated status.

To measure the LFM and LDM, we used FA-N Series

Electronic Analytical Balance. We used a scanner (CanoScan LiDE 120) to scan the leaf samples for LA measurements at 300 dpi for medium size leaves and 600 dpi for small leaves. Leaf samples were dried by DHG Series Heating and Drying Oven (DHG-9240B).

Specific leaf area (SLA) was defined as the ratio between LA and LDM. Leaf dry matter content (LDMC) was calculated as the ratio between LDM and LFM.

To calculate the CSR strategy affinities of collected species, based on LA, LDM and LFM, we used the global plant strategy calculator tool StrateFy (Pierce et al. 2017). Thus, strategies were defined for 99 species.

# Community-weighted means

We calculated community biomass weighted means (CWM) of LFM, LDM, LDMC, LA, SLA, and CSR affinities in each plot by Eq.1 (Lavorel et al. 2008):

$$X_{W} = \sum_{i=1}^{n} B_{i} \times X_{i}$$

where  $X_w$  is community-weighted means of traits or strategies;  $X_i$  is the value of the trait of i-species; n means the number of species on the plot and  $B_i$  is the relative abundance (biomass proportion) of i-species.

The data on the biomass of each species was obtained from square plots of 0.0625 m² (25×25 cm), located in typical sites of the communities, in September 2011 and late June-July 2012 (Elumeeva et al. 2015b). There were 53 sampling plots in KAM (the total area was 3.3 m²) and 20 plots in AF (total area 1.25 m²). The distance between plots was at least 1 m. Aboveground biomass was clipped at the surface level, and vascular plants were sorted by species. Air-dried samples were dried in the oven before weighing. In total, 76 species with all measured traits and defined CSR types occurred in biomass sampling plots, accounted in an average 95 % (85–100 %) of aboveground biomass. The number of species with available LA, LDM, and SLA data was 91, and they contributed 94–100 % to the total biomass.

Besides the community-weighted means, we calculated trait means per plot, assuming that all species occurring in the plot have equal biomass. Function *functomp* in the *FD* package in R (Laliberté et al. 2014) was used.

## Functional diversity indices

We calculated three indices of functional diversity for single traits: functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv). Function *dbFD* in the *FD* package in R (Laliberté et al. 2014) was used for FRic and FEve, and Fdiv was calculated by the exact formula of abundance-weighted functional variance by Eq. 2 (Mason et al. 2005):

FDiv= 
$$\frac{2}{\pi}$$
 arctan  $\left(5 \times \sum_{i=1}^{n} \left[ \left( \ln X_{i} - \overline{\ln X} \right)^{2} \times B_{i} \right] \right)$ 

where n means the number of species,  $X_i$  – trait or strategy value of the i-species,  $\ln X$  is the mean logarithmic trait values, and  $B_i$  is the relative abundance (biomass proportion) of *i*-species.

## Data analysis

Because the numbers of sampling plots were different, to compare the leaf traits between the AF and KAM we used an approximative general independence test in the *coin* package in R (Hothorn et al. 2008). This test was applied for mean trait values, calculated per plot, and for community-weighted means.

To test whether community-weighted means of traits differ from means, we used paired Student's t-test if both the variables in the community were normally distributed following the results of the Shapiro test, and the Wilcoxon signed rank exact test if the data did not comply with normality assumptions. These tests were run separately for AF and KAM.

# RESULTS Leaf functional traits

Most of the studied plants in the Eastern Qinghai-Tibetan Mountains have low leaf fresh mass (<100 mg), small leaf area (<5 cm²) and low leaf dry matter content (<30 %; Table 1). The specific leaf area of the most of leaves is less than 300 cm²/g. The smallest leaves, less than 0.1 cm² were typical for annual gentianas (*Gentiana crassuloides* Bureau et Franch., *G. squarrosa* Ledeb.), *Androsace brachystegia* Hand.-Mazz., and the largest leaves, more than

**Table 1.** The descriptive statistics of leaf functional traits in alpine plants. n – number of species accessed, LFM – leaf fresh mass; LDM – leaf dry mass; LA – leaf area; LDMC – leaf dry matter content; SLA – specific leaf area.

Functional trait	n	Mean	Median	Minimum	Maximum
LFM (mg)	99	84.1	43.8	1.05	542
LDM (mg)	115	16.8	8.5	0.23	112
LA (cm <sup>2</sup> )	115	3.31	1.75	0.062	22.4
LDMC (%)	99	22.0	20.9	4.83	40.4
SLA (g/cm <sup>2</sup> )	115	230	211	54	755

20 cm², were in Angelica apaensis R.H. Shan & C.Q. Yuan and Pleurospermum wilsonii H. Boissieu. The lowest LDMC was in the succulent Sedum rosei Hamet (4.8%). Plants with the highest LDMC were shrubs (Potentilla fruticosa Linn., Salix cupularis Rehd., Spiraea alpina Pall.), Festuca ovina Linn., Carex atrofusca Schkuhr. and some other species of Cyperaceae. SLA varied from 54 cm²/g in Juncus sikkimensis Hook. f. and 99 cm²/g in Rhododendron thymifolium Maxim. to 755 cm²/g in Veronica vandellioides Maxim. Other species with a very high SLA (>400 cm²/g) were Gentiana striata Maxim., Cerastium falcatum Bunge, Sedum rosei Hamet, Lomatogoniopsis alpina T.N. Ho et S.W. Liu, Draba eriopoda Turcz.

The plots of both the communities had similar values of mean LDM, while LA, LFM and SLA were higher and LDMC was lower in KAM (Table 2, Fig. 2). LFM<sub>CWM</sub> was significantly higher in the KAM, and LDMC<sub>CWM</sub> was higher in the AF, but other CWMs did not differ significantly between communities (Table 2, Fig. 2).

Community-weighted means of all the traits, except LDM, differed significantly from the mean trait values per plot in KAM (Table 2). In the contrary, in AF community, only  $\mathrm{LDMC}_{\mathrm{CWM}}$  was significantly higher than the trait mean, and  $\mathrm{LFM}_{\mathrm{CWM}}$  was lower than the trait mean.

# CSR strategies of alpine plants

The prevailing strategies of plants were ruderal R-strategy (ca. 38 %; Table 3) and combined ruderal and stress-tolerant SR-strategy (28 %). The most of plants (97 out 99 species) had expressed R-strategy scores, while S and competitive C-strategies were assigned to 66 and 55 species, respectively. There were no species with C-strategy. The typical R-selected (ruderal) species are *Galium elegans* Wall. ex Roxb. (C:S:R= 0:0:100 %) and *Koenigia islandica* Linn. (C:S:R= 0:0:100 %), which have a very small area of leaves.

**Table 2.** Community weighted means (CWM) and trait means of species in *Kobresia* alpine meadows and alpine fens. SE – standard error; \* – p < 0.05; \*\* – p < 0.01; \*\*\* – p < 0.001, n.s. – not significant. Approximative general independence test was used to check between-community differences, and paired Student's t-test or Wilcoxon signed rank exact test were used to check within-community differences.

Trait	Value	Kobresia alpine meadow (Mean ± SE, n=53)	Alpine fen (Mean ± SE, n=20)	Between-community differences, p
Leaf area, cm <sup>2</sup>	Trait mean	2.77±0.06	2.27±0.12	<0.001***
	CWM	2.55±0.11	$2.27\pm0.12$	0.169 n.s.
	Within-community differences, <i>p</i>	0.015*	0.956 n.s.	
Leaf fresh mass, mg	Trait mean	63.0±1.8	51.5±2.5	<0.001***
	CWM	54.5±3.4	41.9±2.9	0.034*
	Within-community differences, <i>p</i>	<0.001***	<0.001***	
Leaf dry mass, mg	Trait mean	13.6±0.3	12.5±0.7	0.131 n.s.
	CWM	$13.2 \pm 0.6$	$12.9\pm0.9$	0.764 n.s.
	Within-community differences, <i>p</i>	0.089 n.s.	0.622 n.s.	
Leaf dry matter content, %	Trait mean	25.0±0.1	26.2±0.4	<0.001***
	CWM	29.2±0.4	$31.5 \pm 0.5$	0.003**
	Within-community differences, p	<0.001***	<0.001***	
Specific leaf area, cm <sup>2</sup> /g	Trait mean	218±1	194±2	<0.001***
	CWM	196±2	191±5	0.275 n.s.
	Within-community differences, <i>p</i>	<0.001***	0.674 n.s.	

**Table 3.** Summary of different CSR strategies of total 99 plant species measured.

Strategy	Number of species	Percentage (%)	
CR	8	8.1	
CS	1	1.0	
CSR	5	5.1	
R	38	38.4	
S	19	19.2	
SR	28	28.3	
Total	99	100	
Total with C	55	55.6	
Total with S	66	66.7	
Total with R	97	98.0	

Mean S-strategies scores of species, occurring in biomass sampling plots were higher in AF and R-scores were higher in KAM, while C-scores did not differ between communities (Table 4). The community-weighted means of all C and R affinities were higher in KAM, while S-strategy CWMs were higher in AF. Therefore, in both the communities CWM values of S-strategy exceeded mean values, and CWMs of C-and R-strategies were lower than trait values, so from the available local species pool in both the communities' dominant species with the better-expressed stress-tolerance (Fig. 3).

# DISCUSSION Plant functional traits

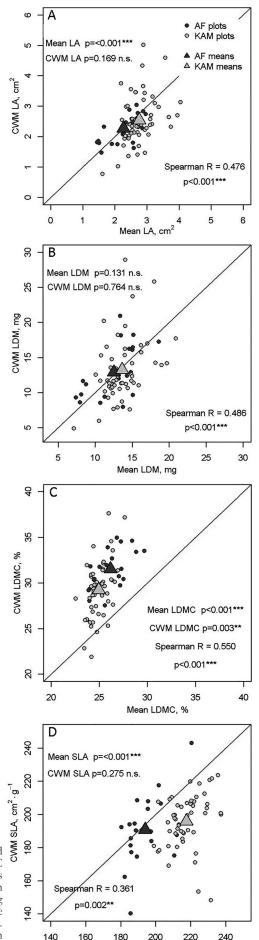
The plants in the study area have general characteristics, typical for alpine plants at the global scale. Almost all studied plant species were shrubs or herbs with generally light and small leaves. Among other mountain systems, the mean values of leaf traits were close to those in the Northwestern Caucasus (Onipchenko et al. 2022) and the Alps (Körner 2003).

# The CSR-types of alpine plants

The total vascular plant species pool of alpine communities at Mt. Kaka is not still estimated, though earlier we obtained 108 species from the total 375 m² recorded plots in KAM and 60 species from the total 100 m² in AF (Elumeeva et al. 2015a), with the maximum species richness of 82 per 100 m² in KAM (Onipchenko et al. 2014). Indeed, there are many species not covered by sampling plots, therefore our data by leaf traits include the most known diversity and the most common species at the altitude range of 3930–3960 m a.s.l.

The KAM are richer than AF both floristically (Onipchenko et al. 2014) and functionally (Table 5), and this reflects specific ecological conditions of alpine fens with a high water saturation of soils and lower aeration. For example, alpine fens of the Northwestern Caucasus also have a rather low species richness (Onipchenko & Semenova 1995). Lower functional richness indicates that there are fewer species can take advantage from this environmental condition (Tilman et al. 1997). The comparison of the local functional richness with other studies seems not to be relevant because the studies from different regions are based on different species pools.

**Figure 2** The relationships between trait means per plot and community-weighted means (CWM) of plant functional traits. LA – leaf area, LDM – leaf dry mass, LDMC – leaf dry matter content, SLA – specific leaf area of dry leaves. The line shows the linear relationship between means and CWMs if they were equal. The position below the line indicates the decrease of CWM in comparison with the corresponding trait mean for the given sampling plot, and the position above indicated the increase of CWM. Spearman correlation coefficients are given for CWMs and trait means. The significance of differences between communities is based on permutation approximative general independence test



Mean SLA, cm<sup>2</sup> · g

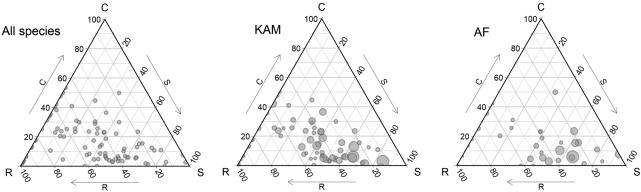


Figure 3 CSR strategies of alpine plants in Eastern Qinghai-Tibetan Mountains (KAM – *Kobresia* alpine meadows, AF – alpine fens). The symbol size for KAM and AF plots is proportional to species abundance (small <1 %, medium 1–5 %, large >6 %).

Both communities have rather low functional evenness, which suggests the existence of one or more groups of species with similar trait values, which dominate the community. The lowest functional divergence is observed for SLA, thus the dominance is shifted to a single group of species. In contrary, the size traits have high FDiv indices and there can be two or more functionally distinct groups.

The differences between mean trait values reflect the differences in ecological conditions between sites, which influence the selection of species that are able to survive in a given environment, while differences between CWMs reflect the dominance of species with certain trait values. In the case of the studied KAM and AF, our data suggests, that there can be the same factor, which acts on selection by the SLA and leads to the similar CWMs of this trait (196 and 191 cm<sup>2</sup>/g, respectively). This selection to dominance can be caused by intensive grazing, which both affects meadows and fens. These CWMs of SLA are close to the value, reported for alpine snowbeds in the Caucasus (Elumeeva et al. 2015a, Onipchenko et al. 2022), which structure is supposed to be due to overgrazing and kept despite long-term reservation. In contrary, Li et al. (2017) found that SLA<sub>CWM</sub> of alpine swamps in the eastern part of the Tibetan plateau north of our site, where standing water is present during the growing season, is ca. 120–130 cm²/g and lower than that of swamp meadows and typical meadows, where its values are also close to ours (ca. 180–190 cm²/g). They also reported lower LDMC $_{\rm CWM}$  of the alpine swamp (25-30%), which kept the range of our values for both communities.

In contrast to "economics" traits, the size traits show high functional divergence, which suggests the dominance of at least two groups with small and relatively large leaves.

The plants of alpine communities of the studied site suffer from two factors, which in opposite ways influence SLA. Intensive grazing promotes species with high SLA, which is usually associated with a high relative growth rate (Wright & Westoby 2001) and is important for fast regrowth. On the other hand, grazing reduces plant height and the growth of shrubs, which improves light availability and increases ultraviolet stress in high altitudes, promoting the species with lower SLA (Li et al. 2010). The higher mean values of SLA show that many species of KAM are comfortable to withstand light shading of alpine shrubs such as *Potentilla fruticosa* or *Spiraea alpina*, but grazing disturbance shifts down CWMs of SLA with the corresponding increase of affinities to stress-tolerance, while, for example, SLA<sub>CWM</sub> decreases under *Potentilla fruticosa* shrubs (Wang et al. 2021).

**Table 4.** Community weighted means and strategies means of species in *Kobresia* alpine meadows and alpine fens. SE – standard error. C – C-selected proportion of species; S – S-selected proportion of species; R – R-selected proportion of species. Different letters indicate significant difference between CWMs and strategies means in the same community at p < 0.05. \* – p < 0.05; \*\* – p < 0.01, \*\*\* – p < 0.001, n.s. – not significant. Approximative general independence test was used to check between-community differences, and paired Student's t-test or Wilcoxon signed rank exact test were used to check within-community differences.

Strategy affinity, %	Value	Kobresia alpine meadow (Mean ± SE, n=53)	Alpine fen (Mean ± SE, n=20)	Between-community differences, p
С	Mean CWM Within-community	13.0±0.2 11.7±0.6	12.4±0.4 9.6±0.3	0.161 n.s. 0.032*
	differences, p	0.003**	<0.001***	
	Mean	41.0±0.4	46.9±1.4	<0.001***
c	CWM	52.6±1.3	60.7±1.9	0.001**
S	Within-community differences, <i>p</i>	<0.001***	<0.001***	
R	Mean	45.9±0.4	40.6±1.2	<0.001***
	CWM	$35.6\pm0.8$	$29.7 \pm 1.8$	<0.001***
	Within-community differences, <i>p</i>	<0.001***	<0.001***	

### CONCLUSION

The leaf traits of plants in the communities of the eastern Qinghai-Tibet plateau are typical for the alpine belt and are affected by local environmental factors, such as grazing by yaks and excess water availability. KAMs are more functionally rich than alpine fens, but both have low functional evenness. The abiotic environment causes the prevalence of stress-tolerant strategy, while grazing enhances the role of R-selection and dominance of species with a narrow value range of some traits. The most indicative trait was SLA, where means in AF were significantly lower than in KAM, but SLA<sub>CWM</sub> were similar.

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# LITERATURE CITED

- Butterfield, B.J. & K.N. Suding 2013. Single-trait functional indices outperform multi-trait indices in linking environmental gradients and ecosystem services in a complex landscape. *Journal of Ecology* 101(1):9–17.
- Dudova, K.V., G.G. Ataballyev, A.A. Akhmetzhanova, D.M. Gulov, S.V. Dudov, T.G. Elumeeva, A.M. Kipkeev, et al. 2019. Functional diversity of alpine plant communities: a case study of plant height. Zhurnal Obshchei Biologii 80(6):439–450 (in Russian). [Дудова К.В., Атабаллыев Г.Г., Ахметжанова А.А., Гулов Д.М., Дудов С.В., Елумеева Т.Г., Кипкеев А.М., и др. 2019. Опыт изучения функционального разнообразия альпийских сообществ на примере анализа высоты растений // Журнал общей биологии. Т. 80, № 6. С. 439–450].
- Editorial Board of Flora of China. 1994–2013. Flora of China, vol. 2–80. Available from: http://www.efloras.org (last accessed 01.11.2022).
- Elumeeva, T.G., D.K. Tekeev, Y. Wu, Q. Wang & V.G. Onipchenko, 2014. Life-form composition of alpine plant communities at the Eastern Qinghai-Tibetan Plateau. *Plant Biosystems An International Journal Dealing with all Aspects of Plant Biology* 148(5):988–994.
- Elumeeva, T.G., V.G. Onipchenko, E.N. Rovnaia, Y. Wu & M.J. Werger 2015. Alpine plant communities of Tibet and Caucasus: in quest of functional convergence. *Botanica Pacifica* 4(1):7–16.
- Elumeeva, T.G., V.G. Onipchenko & Y. Wu 2015. Leaf functional traits of plants of alpine pastures at the Eastern Qinghai–Tibetan Plateau. *Moscow University Biological Sciences Bulletin* 70(1):46–52.
- Garnier, E., M.L. Navas & K. Grigulis 2016. *Plant functional diversity*. Oxford UP, Oxford, 249 pp.
- Grime, J.P., 2001. *Plant strategies, vegetation processes, and ecosystem properties. 2nd Edition.* John Wiley and Sons, Chichester, 417 pp.
- Hothorn, T., K. Hornik, M.A. van de Wiel & A. Zeileis 2008. Implementing a class of permutation tests: The coin package. *Journal of Statistical Software* 28(8):1–23.
- Hu, X., N. Wu, Y. Wu, W. Zuo, H. Guo & J. Wang 2012. Effects of snow cover on the decomposition and nutrient

- dynamics of *Sibiraea angustata* leaf litter in western Sichuan plateau, Southwest China. *Yingyong Shengtai Xuebao* 23(5): 1226–1232 (in Chinese with English summary).
- Jäschke, Y., G. Heberling & K. Wesche 2020. Environmental controls override grazing effects on plant functional traits in Tibetan rangelands. Functional Ecology 34(3):747–760.
- Körner, C. 1999. *Alpine plant life: Functional Plant Ecology of High Mountain Ecosystems*. Springer-Verlag, Berlin Heidelberg, New York.
- Körner, C. 2003. Alpine plant life: Functional plant ecology of high mountain ecosystems, 2nd edn. Springer, Berlin.
- Laliberté, E., P. Legendre & B. Shipley 2014. FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0–12.
- Lavorel, S., K. Grigulis, S. McIntyre, N.S.G. Williams, D. Garden, J. Dorrough, S. Berman, et al. 2008. Assessing functional diversity in the field methodology matters! *Functional Ecology* 22(1):134–147.
- Li, F.-R., S.-L. Peng, B.-M. Chen & Y.-P. Hou 2010. A metaanalysis of the responses of woody and herbaceous plants to elevated ultraviolet-B radiation. *Acta Oecologica* 36:1–9.
- Li, W., H.E. Epstein, Z. Wen, J. Zhao., J. Jin, G. Jing, J. Cheng & G. Du 2017. Community-weighted mean traits but not functional diversity determine the changes in soil properties during wetland drying on the Tibetan Plateau. *Solid Earth* 8(1):137–147.
- Liu, M., G. Zhang, F. Yin, S. Wang & L. Li 2022. Relationship between biodiversity and ecosystem multifunctionality along the elevation gradient in alpine meadows on the eastern Qinghai-Tibetan plateau. *Ecological Indicators* 141:109097.
- Ma, L., Z.H. Zhang, B.Q. Yao, Z. Ma, X.T. Huang, B.R. Zhou, M. Xu, et al. 2021. Effects of drought and heat on the productivity and photosynthetic characteristics of alpine meadow plants on the Qinghai–Tibetan Plateau. *Journal of Mountain Science* 18(8):2079–2093.
- Ma, W., P. Shi, W. Li, Y. He, X. Zhang, Z. Shen & S. Chai 2010. Changes in individual plant traits and biomass allocation in alpine meadow with elevation variation on the Qinghai—Tibetan Plateau. *China Life Sciences* 53(9):1142–1151.
- Mason, N.W.H., D. Mouillot, W.G. Lee & J.B. Wilson 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos* 111:112–118.
- National Plant Specimens Resource Center 2023. *Chinese Virtual Herbarium CDBI Branch*. Available from: http://cdbi.cib.ac.cn/biology-mis/page/index.jsf (last accessed 01.11.2022).
- Onipchenko, V.G. & G.V. Semenova 1995. Comparative analysis of the floristic richness of alpine communities in the Caucasus and the Central Alps. *Journal of Vegetation Science* 6(2):299–304.
- Onipchenko, V., A. Shulakov, A. Zernov, T. Elumeeva, Y. Wu, Q. Wang & M.J. Werger 2014. Contrasting floristic richness of alpine plant communities on the eastern Qinghai-Tibetan Plateau. *Botanica Pacifica* 3(1):33–37.
- Onipchenko, V.G., K.V. Dudova, D.M. Gulov, A.A. Akhmetzhanova, D.K. Tekeev & T.G. Elumeeva 2022. Leaf functional traits are important for the formation of alpine plant communities composition. *Zhurnal Obshchei Biologii* 83(2):127–137 (in Russian). [Онипченко В.Г., Дудова К.В., Гулов Д.М., Ахметжанова А.А., Текеев Д.К., Елумеева Т.Г. 2022. Функциональные признаки листьев растений важны для формирования состава аль-

- пийских растительных сообществ // Журнал общей биологии. Т. 83, № 2. С. 127–137].
- Pérez-Harguindeguy, N., S. Díaz, E. Garnier, S. Lavorel, H. Poorter, P. Jaureguiberry, M.S. Bret-Harte, et al. 2013. New handbook for standardized measurement of plant functional traits worldwide. *Australian Journal of Botany* 61:167–234.
- Pierce, S., D. Negreiros, B.E.L. Cerabolini, J. Kattge, S. Diaz, M. Kleyer, B. Shipley, et al. 2017. A global method for calculating plant CSR ecological strategies applied across biomes world-wide. *Functional Ecology* 31(2):444–457.
- Ren, Q.J., H.L. Li & H.Y. Bu 2015. Comparison of physiological and leaf morphological traits for photosynthesis of the 51 plant species in the Maqu alpine swamp meadow. *Chinese Journal of Plant Ecology* 39:593–603.
- Rosbakh, S., C. Römermann & P. Poschlod 2015. Specific leaf area correlates with temperature: new evidence of trait variation at the population, species and community levels. *Alpine Botany* 125:79–86.
- Schleuter, D., M. Daufresne, F. Massol & C. Argillier 2010. A user's guide to functional diversity indices. *Ecological Monographs* 80(3):469–484.
- Seregin, A.P. (ed.) 2022. *Moscow Digital Herbarium: Electronic resource*. Moscow State University, Moscow. Available from: https://plant.depo.msu.ru/ (last accessed 22.10.2022).
- Tilman, D., J. Knops, D. Wedin, P. Reich, M. Ritchie & E. Siemann 1997. The influence of functional diversity and composition on ecosystem processes. *Science* 277(5330): 1300–1302.
- Vandvik, V., A.H. Halbritter, Y. Yang, H. He, L. Zhang, A.B. Brummer, K. Klanderud, et al. 2020. Plant traits and

- vegetation data from climate warming experiments along an 1100 m elevation gradient in Gongga Mountains, China. *Scientific Data* 7:189.
- Wang, J., C. Zhang, H. Yang, C. Mou, L. Mo & P. Luo 2018. Plant community ecological strategy assembly response to yak grazing in an alpine meadow on the eastern Tibetan Plateau. Land Degradation and Development 29:2920–2931.
- Wang, Q. 2016. Seed plant handbook to the headwaters of Min River. Sichuan University Press, Chengdu (in Chinese).
- Wang, X., R. Michalet, L. Meng, X. Zhou, S. Chen, G. Du & S. Xiao 2021. Direct and indirect facilitation affect community productivity through changes in functional diversity in an alpine system. *Annals of Botany* 127:241–249.
- Wright, I.J. & M. Westoby 2001. Understanding seedling growth relationships through specific leaf area and leaf nitrogen concentration: generalizations across growth forms and growth irradiance. *Oecologia* 127:21–29.
- Yu, J., G. Hou, T. Zhou, P. Shi, N. Zong & J. Sun 2022. Variation of plant CSR strategies across a precipitation gradient in the alpine grasslands on the northern Tibet Plateau. Science of the Total Environment 838:156512.
- Zhou, Q. & Y. Gan 2016. The dominant wild plants Atlas in the Grassland of Northwest Sichnan province. Science Press, Beijing (in Chinese).
- Zhou, T., G. Hou, J. Sun, N. Zong & P. Shi 2021. Degradation shifts plant communities from S- to R-strategy in an alpine meadow, Tibetan Plateau. *Science of the Total Environment* 800:149572.