# EFFECTS TO GRAZING ON PHOTOSYNTHETIC AND PRODUCTION CHARACTERISTICS C<sub>3</sub> AND C<sub>4</sub> OF STEPPE PLANTS IN SANDLAND OF THE BARGUZIN RIVER BASIN, BAIKAL REGION, RUSSIA

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Abstract Species composition, changes in the net photosynthetic rate, transpiration rate, water use efficiency and productivity of seven plant species (Artemisia frigida Willd., Cleistogenes squarrosa (Trin.) Keng, Carex duriuscula C.A. Mey., Kochia prostrata (L.) Schrad., Leymus chinensis (Trin.) Tzvelev, Potentilla acaulis L., Stipa krylovii Roshev.) in three grazing intensities: ungrazed plot, overgrazed plot and restored grazed plot were determined in the Sandland of the Barguzin river Basin, Baikal region, Russia. Our results indicate that, there are close coactions between the physiological properties of species and their competitive advantages in various types of land uses. Overgrazing and steppe restoration significantly effects on the physiological characteristics, including net photosynthetic rate, transpiration rate and water use efficiency. The changes in photosynthetic characteristics of plants can partly explained by their compensatory reactions.

**Key words:** net photosynthetic rate; overgrazing; restoration; species composition; transpiration; water use efficiency.

### INTRODUCTION

Intensively used ecosystems in livestock under the conditions of the Baikal region are the steppes. Ecosystems were provided for thousands of years with foods the local population. For last century has changed the system of management and methods of organization of pastoralism.

As a result of the strong damaging effect of herbivorous on herbages and ecosystems, generally, about 15% of steppe grassland in the region is classified as highly overgrazed. To restore them and to use rational it is necessary to develop the system of science-based measures. The study of the peculiarities of functioning of plant communities is a priority.

In this study, we surveyed species composition of ungrazed, overgrazed, and restored grazed plots and measured physiological properties (including photosynthesis, transpiration, water-use efficiency and etc.) of seven dominant species of plants. Our objectives were to determine effects of grazing and restoration on photosynthetic characteristics of dominant species of plants and to find physiological mechanisms of degradation of pastures.

## MATERIAL AND METHODS

This study was conducted in the Barguzin river Basin  $(53^{\circ}44' - 53^{\circ}55'N; 110^{\circ}07' - 110^{\circ}18' E)$ , which is located in the north-east of the Baikal region of the Russian Federation (fig 1.).

The study area covers an area of about  $21100 \text{ km}^2$  and includes the Barguzin valley, Barguzin and Ikat ridges. The climate in the Barguzin river Basin is of temperate semi-arid type. The annual mean temperature is negative. The period with negative temperatures lasts 7-8 months.

The period with a temperature  $>10^{\circ}$ C is 102-107 days. The annual precipitation ranges from 240- to 450-500 mm, with the average of 340 mm.

The amount of precipitation in winter and spring is low. The main mass (60-90%) falls during the period of the Pacific monsoons at the end of July – in early August. Therefore, the features of the growing season are a contrast type of moisture: very dry spring and early summer and wet-late summer.

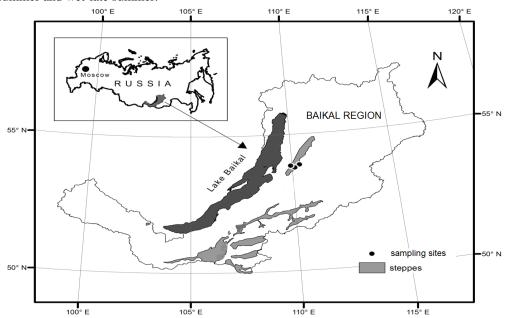


Figure.1 Study area and sampling sites.

Sometimes these regularities are violated, wet and dry periods during the vegetation change between each other (fig.2), which leads to transformative events in the ecosystems, observed in recent years.

Except for relief and the climate the important factor in the study area, which determine the existence of arid ecosystems are the sands. They are confined to the bottoms of rift depressions and to high terraces of the Barguzin River. Their thickness can reach 600 m. The strong wind flows carry the sands over considerable distances, which lead to the spread of deflationary phenomena. Thus, the altitude and exposure of the relief differentiation, low atmospheric moisture, predominance of sandy soils, enhancing the infiltration of atmospheric moisture, early thawing and warming of substrates led to the formation of a unique «island» of steppe among mountain taiga.

Steppe communities (*Stipetum krylovii* MIRKIN *et al.*) are typical zonal type of vegetation of the region. Three steppe plots with different types of land uses were selected: ungrazed plot (UG) overgrazed plot (OG) and restored grazed plot (RG). The plots were located on a relatively small distance of each other, within 10 km; they supposedly were influenced by similar conditions. For more information about the plots see Table 1.

The sites were located in the places with the in detail studied type of soil in a relatively homogeneous vegetation cover. On the sampling site 10x0 m randomly were chosen 10 plots (1x1 m). The quantitative evaluation of productivity carried out in the period of maximum

accumulation of biomass. Above-ground biomass was determined by mowing. Dead grass and litter were selected by hand. Samples of each plant species were measured and counted. Above-ground part for each species was collected, packed in paper bags and taken to the laboratory for analysis. Fresh samples of each plant species were dried at 70° for about 48 hours and then weighed. Relative biomass of each species was obtained by calculating the ratio of the total biomass of each species to the sum of biomass in all quadrates. In each plot, species were grouped based on their duration of the life and life form. The relative biomass of a life form was determined based on the ratio of biomass of each life form to the total biomass of the community. The relative abundance of life forms was obtained by calculating the ratio of the number of species in each life form to the total number of species in the community.

Soil water content (SWC) of the surface layer (0-20 cm) was determined by the difference between moist and oven-dried ( $105^{\circ}$  C to constant mass) sample according to the following equation: SWC [%] = [(wet – dry soil mass) / dry soil mass]  $\times$  100.

The soil density (SD) of the surface layer (0-20 cm) was determined by calculating the drained soil mass to the volume of drill-cylinder.

Seven of the dominant species: Artemisia frigida, Cleistogenes squarrosa, Carex duriuscula, Kochia prostrata, Leymus chinensis, Potentilla acaulis, Stipa krylovii were subjected to physiological measurements. Net photosynthetic rate ( $P_N$ ), transpiration rate (E) were measured on the fully expanded leaves of each species from 08:00 to 11:00 only clear days in middle August, with the most commonly recorded photosynthetic photon flux density being from 1500 to 2000  $\mu$ molm<sup>-2</sup>s<sup>-1</sup> through LI-6400 portable gas exchange system (LI-COR, LINCOLN, NE, USA). Water use efficiency (WUE) was calculated as  $P_N$  / E (HAMID et al. 1990). For each species, five replicating samples were measured.

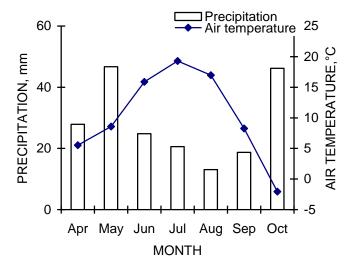


Figure 2 Monthly precipitation and mean air temperature in the Barguzin River Basin during growing season, 2014.

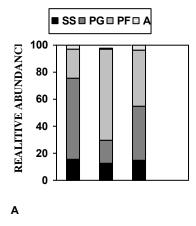
Meteorological data, including monthly precipitation and air temperature during vegetation period in 2014, were collected from the weather station Barguzin <a href="http://meteocenter.net/forecast/all.php">https://meteocenter.net/forecast/all.php</a>, <a href="https://www.meteoblue.com/ru/archive">https://www.meteoblue.com/ru/archive</a> (fig. 2). The nomenclature of plants: <a href="http://www.ipni.org">https://www.ipni.org</a>.

**STATISTICAL ANALYSIS** conducted using Excel. A comparison and calculation of data were made for above-ground biomass, soil water content (SWC) and soil density (SD) among different plots. The significant of differences was tested by t-test at p < 0.05 level. The same method was used to separate the significance of average means of  $P_N$ , E and WUE of different plant species in three plots.

# RESULTS AND DISCUSSIONS

The steppe vegetation of studied areas belongs to the class *Cleistogenetea squarrosae* Mirkin *et al.* 1992. The total number species identified in the class is 417. The herbage is thinned; the projective cover degree is 20-60 %. The saturation of species is low – 25-30/100m². The maximum height of herb layer is 40-50 cm. It is relatively homogeneous, multispecies. The layer structure is presented by 3 levels. The first level with a height 30-50 cm and the projective cover degree of 5-12% forms *Stipa krylovii*. In the second level with a height 15-20 cm is dominated by *Artemisia frigida*, which with the other plant species covers a surface area of 15–25%. The third one, with a height 5-10 cm and the projective cover of 10-30% is mainly composed of *Cleistogenes squarrosa*, *Potentilla acaulis*, *Thymus baicalensis* and vegetative part of grasses and forbs.

In the studied plots: OG, UG and RG were found 8, 15, 22 plant species (fig. 3). Species compositions were different between the three plots. In OG dominated perennial forbs with *Carex duriuscula* and *Potentilla acaulis*, accounting for more than 50% of abundance. UG were abundant perennial grasses - *Stipa krylovii*, *Cleistogenes squarrosa*. RG values of perennial grasses and forbs was almost equal and were to 40% and 41.3 respectively. In all plots there is a low abundance of annuals. UG and RG abundance of sub-shrubs was almost equal and slightly decreased in OG.



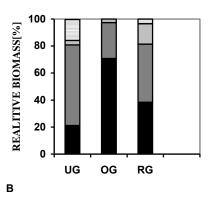


Figure 3. Relative abundance (*A*) and relative biomass (*B*) of different life forms in three plots. A: annuals, PG: perennial grasses, PF: perennial forbs, SS: sub-shrubs.

The differentiation of the abundance of life forms in three plots correlated with the number of plant species (Table. 2). However, the relative biomass of different life forms is showed other values. In UG dominated the biomass of perennial grasses (53.47%), the loss of biomass of perennial forbs compensated by annuals. OG of more than 70 % of the biomass was

sub-shrubs - *Artemisia frigida*, *Artemisia obtusiloba*. RG noted recorded the equal contribution to the production of plant community of sub-shrubs and perennial grasses.

 $P_N$  Carex duriuscula, Potentilla acaulis, Stipa krylovii increased from UG to RG and reached the highest mean in OG (Table. 3).  $P_N$  Cleistogenes squarrosa decreased in RG and increased in OG plots.  $P_N$  Kochia prostrata OG was higher, than RG. At Artemisia frigida was no significant differences  $P_N$  in UG and OG, in RG plots slightly increased.  $P_N$  Leymus chinensis showed significant differences between OG and RG plots.

Table
Name, photosynthetic pathway, life form, and relative biomass of plant species of three plots in the
Barguzin River Basin, Baikal region, Russia.

Smaaina	Photosynth.	Life form	Relative biomass [%]		
Species			UG	OG	RG
Agropyron cristatum	$C_3$	PG	_	_	7.66±1.24
Cleistogenes squarrosa	$\mathbb{C}_4$	PG	$1.74\pm0.15$	_	$1.09\pm0.10$
Koeleria cristata	$C_3$	PG	$1.27\pm0.62$	_	1.77±0.61
Leymus chinensis	$C_3$	PG	_	$7.44\pm0.98$	$0.59\pm0.21$
Stipa krylovii	$C_3$	PG	$6.83\pm0.48$	$3.61\pm0.52$	$7.37\pm0.11$
Artemisia scoparia	$C_3$	A	$1.14\pm0.46$	_	3.05±0.69
Chenopodium aristatum	$C_3$	Α	$0.07\pm0.04$	$0.01\pm0.01$	_
Heteropappus biennis	$C_3$	Α	14.28±2.23	_	$0.41\pm0.13$
Lappula squarrosa	$C_3$	Α	_	_	_
Artemisia frigida	$C_3$	SS	21.18±1.91	35.91±13.15	6.91±0.91
Artemisia obtusiloba	$C_3$	SS	_	34.94±10.40	_
Kochia prostrata	$C_4$	SS	$0.02\pm0.02$	_	31.53±10.16
Allium anisopodium	$C_3$	PF	_	_	$2.44\pm0.65$
Allium bidentatum	$C_3$	PF	$0.02\pm0.02$	_	$0.83\pm0.70$
Allium ramosum	$C_3$	PF	$0.02\pm0.02$	_	2.21±1.20
Allium tenuissium	$C_3$	PF	$0.06\pm0.03$	_	$0.84\pm0.40$
Astragalus adsurgens	$C_3$	PF	33.05±11.46	15.45±1.56	_
Carex duriuscula	$C_3$	PF	_	_	18.6±1.91
Cymbaria dahurica	$C_3$	PF	$0.21\pm0.14$	_	$0.18\pm0.18$
Galium verum	$C_3$	PF	14.47±3.64	$0.12\pm0.08$	_
Iris humilis	$C_3$	PF	_	_	$0.11\pm0.10$
Limonium flexsuosum	$C_3$	PF	_	_	5.08±1.19
Oxytropis bargusinensis	$C_3$	PF	$2.30\pm0.61$	$2.52\pm0.19$	2.27±0.17
Potentilla acaulis	$C_3$	PF	$3.34\pm0.31$	_	$2.28\pm0.22$
Potentilla bifurca	$C_3$	PF	_	_	$1.06\pm0.12$
Silene jeniseensis	$C_3$	PF	_	_	3.71±0.33
Saussurea amara	C <sub>3</sub>	PF	_	_	$0.01\pm0.01$
Sum of species			15	8	22

Means  $\pm$  SE. Different letters indicate the significant difference in value among three plots (t-test, p<0.05). SS, PG, PF, and A represent sub-shrubs, perennial grasses, perennial forbs, and annuals, respectively.

**E** Cleistogenes squarrosa, Potentilla acaulis, Stipa krylovii increased with the intensity of grazing and the highest rates of transpiration were found in OG plots (Table. 2). Carex duriuscula showed similar changes in E, but the differences were lessened. There were significant differences in E of Kochia prostrata in UG, RG plots. The exceptions are Artemisia frigida and Leymus chinensis, whose indicators of transpiration are not so much changed.

**WUE** of 7 plant species have identified multi-directional changes with the intensity of grazing (Table 2). *Leymus chinensis*, *Stipa krylovii*, *Potentilla acaulis* significantly decreased

WUE with the intensity of grazing. The other species - Carex duriuscula, Cleistogenes squarrosa increased the means of WUE with the intensity of grazing. An exception is the Artemisia frigida, which decreased WUE from UG to RG and increased WUE with the increasing of grazing pasture. Kochia prostrata showed different means in UG and RG.

Table
Photosynthetic characteristics of seven dominant species of three plots in the Barguzin River Basin,
Baikal region, Russia

		Baikal region, Ri				
D1-4-	C	Parameters Par E WIJE				
Plots	Species	P <sub>N</sub>		WUE		
		(µmol CO <sub>2</sub> m <sup>-2</sup> s <sup>-1</sup> )	(mmol H <sub>2</sub> O m <sup>-2</sup> s- <sup>1</sup> )	(µmol CO <sub>2</sub> mmol H <sub>2</sub> O)		
	Artemisia frigida	$12.54\pm0.28$	$4.88\pm0.50$	2.57±0.56		
	Carex duriuscula	$4.83\pm0.41$	$3.39\pm0.60$	$1.42\pm0.25$		
UG	Cleistogenes squarrosa	6.76±0.47	$5.24\pm0.74$	$1.29\pm0.63$		
	Kochia prostrata	$14.94\pm0.94$	$3.86\pm0.87$	$3.87 \pm 1.08$		
	Leymus chinensis	-	-	$3.04\pm0.47$		
	Potentilla acaulis	$8.78\pm0.19$	$4.01\pm0.70$	$2.19\pm0.28$		
	Stipa krylovii	$8.98 \pm 0.28$	$3.34\pm0.50$	$2.69\pm0.55$		
	Artemisia frigida	12.54±0.20	5.78±0.76	2.17±0.26		
	Carex duriuscula	$14.90\pm0.77$	9.87±1.54	1.51±0.37		
OG	Cleistogenes squarrosa	25.97±0.46	11.29±1.51	2.30±0.31		
	Kochia prostrate	-	-	-		
	Leymus chinensis	$7.03\pm0.44$	$3.86\pm0.67$	1.82±0.65		
	Potentilla acaulis	23.11±0.68	14.39±2.67	$2.05\pm0.45$		
	Stipa krylovii	19.12±0.29	11.18±1.44	1.71±0.19		
	Artemisia frigida	$13.24\pm0.40$	6.93±0.87	1.91±0.46		
RG	Carex duriuscula	$7.55\pm4.06$	5.07±0.56	$1.49\pm0.23$		
	Cleistogenes squarrosa	5.96±0.13	3.97±0.61	1.50±0.21		
	Leymus chinensis	21.26±0.11	5.73±0.32	$3.71\pm0.33$		
	Potentilla acaulis	21.03±0.38	7.45±0.50	$2.94\pm0.75$		
	Stipa krylovii	13.89±0.29	$5.40\pm0.87$	2.57±0.33		

Means  $\pm$  SE. Capital letters indicate the difference in mean value of each species among different plots, whereas small letters represent the difference in mean values among species in the same plot. Significant difference among variables was determined by t-test (p<0.05).

The steppes of the Barguzin River Basin in Baikal region are a model area of semi-arid ecosystems in the Siberian-Central Asian sector of Palearctic (LAVRENKO *et al.* 1991) and belong to the communities of the class *Cleistogenetea squarrosae* Mirkin *et al.* 1992.

Herbivore grazing is an important factor, determining the condition of grassland ecosystems and their components. It strongly influences on the dynamics of plant communities, the change of primary production, decomposition of organic matter and cycling and distribution of nutrient matters, competitive coactions among plant species (McNaughton 1985, Fahnestock & Detling 1999, Klanderud *et al.* 2005, Niu, 2008). Moreover, the increase of grazing pressure leads to disturbance and soil compaction, the decrease of water infiltration and soil erosion (Ubugunov *et al.* 2014).

The important factor, which contribute to the stable functioning of steppe ecosystems, ensuring the normal growth and development of plants in arid and semi-arid areas is water. Our results showed significant differences in water supply and soil density between monitoring plots. The water content decreased with the increasing of grazing intensity. Soil moisture was as follows: UG> RG> OG. (Table 1). Gradual reduction in soil moisture content with the increasing grazing pasture has influenced on the decrease of productivity and change in structure and composition of phytocenoses.

The severe climatic conditions have developed various adaptive mechanisms, among which particularly important for the existence of steppe plants are photosynthetic types. In all communities in the overwhelming majority dominate  $C_3$  species, and only two species were with  $C_4$  by photosynthetic pathway. These results are consistent with the results of other studies, conducted in China (NI, 2003, Su *et al.* 2000, TIESZEN and SONG, 1990, CHEN, 2007) and Mongolia (PYANKOV *et al.* 2000).

The observed ratio of  $C_3/C_4$  plants is relatively low (Table 2.) and are found in the steppes of Asia, North and South America (SUYKER and VERMA, 2001).

The significant role of  $C_3$  plants is largely determined by the productivity, and together with the dynamics of composition and structure provides the stability of communities (Vermeire *et al.* 2008).  $C_3$   $\mu$   $C_4$  sub-shrubs represent more than 1/3 of the biomass of pasture. The reduction of the grazing intensity has lud to the decrease of biomass  $C_3$  and the increase of the biomass  $C_4$  of sub-shrubs. In the conditions of the reserved status the value of sub-shrubs markedly reduced (fig 2).

The grazing intensity has found a significant influence on  $P_N$ , E and WUE of the dominant plant species with different photosynthetic pathways.

In general,  $P_N$  Carex duriuscula, Cleistogenes squarrosa, Stipa krylovii has increased from UG to OG plots where it reached a maximum. The increase of  $P_N$  may be due to mechanical damage of plants as a result of overgrazing, grazing livestock and the need of greater energy for regrowth and development (DORMAAR and WILLMS, 1998, HOU, 2001), therefore, compensatory growth (NOWAK and CALDWELL, 1984).

Apparently, not always high mean  $P_N$  provided by the disturbance of plant integrity. So, *Potentilla. acaulis* was not damaged, but had the highest rates  $P_N$  in OG plots. A gradual decrease in the intensity of its photosynthesis in RG and UG plots, probably, was connected with ineffective light interception due to the change in layer structures of plant communities and with reduced photosynthetic activity of the leaf surface. Significant rates of photosynthesis in the absence of grazing we observed in *Leymus chinensis*. Later, with the increasing of grazing intensity prior indicators reduced. An exception is *Artemisia frigida*, which practically did not change the value of photosynthesis under various conditions of land uses, that provided by different adaptive peculiarities of a plant (LI, 1993, GAO *et al.* 2007). The reactions of plants on different conditions of pasturing are evident not only on the parameters of the intensity of photosynthesis, but and transpiration. The minimum water use on the transpiration is marked in UG plots, with the increase in grazing intensity is gradually increased and reached the maximum in OG plots.

Our results largely are consistent with the statements (Cox et al. 1988), that high or low grazing intensity may change E plants. The reason may be connected with the different water content in the soil, where plants grew or plant abundance to help the creation of the mutual shading, which can influence the rate of transpiration. At the same time we can not exclude the adaptation of the plants, with which they regulate water exchange.

It is quite natural, that the WUF of plants, which is defined by  $P_{\rm N}$  / E, depended on different conditions of pasturing. It did not almost change in all plots in *Carex duriuscula*, which is probably related with compensatory reactions of species. Significantly it reduced under overgrazing in *Stipa krylovii*, *Potentilla acaulis*, indicating their adaptation to stressful conditions (Sun *et al.* 2011 High and stable WUE *Artemisia frigida* to different regimes of pasturing enabled it to sustain a high photosynthetic activity in low water availability conditions of and produce more saccharides using limiting water resources (CHEN *et al.* 2005). *Cleistogenes squarrosa* with increasing of grazing pasture increased the WUE, which is

consistent with the results of other studies (WANG and WANG 2001, LIANG, MICHALK, MILLAR, 2002, GAO et al. 2007).

#### **CONCLUSIONS**

Thus, on the basis of the received data, it was determined, that there are close coactions between the physiological properties of species and their competitive advantages in different types of land uses. Overgrazing and steppe restoration significantly influence on physiological characteristics, including PN, E µ WUE.

The changes in photosynthetic characteristics of plants can be partly explained by their compensatory reactions. Identified characteristics largely determine the structural-production reactions of plant species of main photosynthetic types and life forms on different conditions of pasturing. The growth of biomass of sub-shrubs with the increase of grazing intensity compensates for the decrease of biomass of individual plant species and life forms in the total biomass of phytocenoses. The increase of productivity in the group of sub-shrubs and obvious trends to further significant reduction in the overall productivity of the herbage indicate a greater influence of overgrazing, which can lead to major shifts in the harvest and composition of herbage. By lasting impact of herbivores on the vegetation cover in overgrazed plots, preserved plants and their forage productivity were more responsive to changes under different conditions of pasturing and precipitation. The stability of communities is provided by an important role of plants with  $C_3$  type of photosynthesis.

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# **BIBLIOGRAPHY**

- CHEN S., BAI Y., LIN G., LIANG Y., HAN X.: Effects of grazing on photosynthetic characteristics of major steppe species in the Xilin River Basin, Inner Mongolia, China. Photosynthetica. 43 (4): 559-565, 2005.
- CHEN S., BAI Y., LIN G., HUANG J., HAN X.: Isotopic carbon composition and related characters of dominant species along an environmental gradient in Inner Mongolia, China. J. Arid Environ. 71: 12–28, 2007.
- Cox R., PARR T.W., PLANT R.A.: Water use and water-use-efficiency of perennial ryograss swards as affected by height and frequency of cutting and seed rate. Grass Forage Sci. 44: 97–
- DORMAAR J.F., WILLMS W.D.: Effect of forty-four years of grazing on fescue grassland soils. J. Range Manage. 51 (1): 122–126, 1998.
- FAHNESTOCK J.T., DETLING J.K.: The influence of herbivory on plant cover and species composition in the Pryor Mountain Wild Horse Range, USA. Plant Ecol. 144: 145-157, 1999.
- GAO Y.Z., WANG S.P., HAN X.G., CHEN Q.S., ZHOU Z.Y.: Defoliation, nitrogen and competition: effects on plant growth and biomass allocation of *Cleistogenes squarrosa* and *Artemisia frigida*. J. Plant Nutr. Soil Sc. 170: 115–122, 2007.
- HAMID A., AGATA W., KAWAMITSU Y.: Photosynthesis, transpiration and water use efficiency in four cultivars of mungbean, *Vigna radiata* (L.) Wilczek. Photosynthetica. 24: 96–101, 1990
- Hou F.J.: Effects of grazing on photosynthesis and respiration of herbage and on its absorption and transpiration of nitrogen and carbon. Chinese Journal of Applied Ecology. 12: 938–942, 2001.
- Li Y.H.: [Grazing dynamics of the species diversity in *Aneurolepidium chinense* steppe and *Stipa grandis* steppe.] Acta Bot. Sin. 35: 877-884, 1993. [In Chin.]

- LIANG C., MICHALK D.L., MILLAR G.D.: The ecology and growth patterns of *Cleistogenes* species in degraded grasslands of eastern Inner Mongolia, China. J. Appl. Ecol. 39:584–594, 2002
- LAVRENKO E.M, KARAMYSHEVA Z.V., NIKULINA R.I.: [The steppes of Eurasia]. Nauka, Leningrad 1991. [In Russian]
- McNaughton S.J.: Ecology of a grazing ecosystem: the Serengeti. Ecol. Monogr. 55:259-294, 1985.
- KLANDERUD K. & TOTLAND Ø.: The relative importance of neighbors and abiotic environmental conditions for population dynamic parameters of two alpine plant species. J. Ecol. 93:493–501, 2005.
- NI J.: Plant functional types and climate along a precipitation gradient in temperate grasslands, north-east China and south-east Mongolia. J. Arid Environ. 53: 501–516, 2003.
- NIU S.L., WANG S.Q.: Warming changes plant competitive hierarchy in a temperate steppe in Northern China. J. Plant Ecol.-UK. 1:103-110, 2008.
- Nowak R.S., Caldwell M.M.: A test of compensatory photosynthesis in the field: implications for herbivory tolerance. Oecologia. 62:322–329, 1984.
- Su B., Han X.G., Lin L.H., Huang J.H., Bai Y.F., Qu C.M.: Responses of  $\delta^{13}$ C value and water use efficiency of plant species to environmental gradients along the grassland zone of Northeast China Transect Acta Phytoecologica Sinica. 24: 648–655, 2000.
- Sun J., Liu M., Li S. et al.: Survival strategy of *Stipa krylovii* and *Agropyron cristatum* in typical steppe of Inner Mongolia. Acta Ecologica Sinica. 31(8):2148-2159, 2011.
- PYANKOV V.I., GUNIN P.D., TSOOG S., BLACK C.C.: C<sub>4</sub> plants in the vegetation of Mongolia: their natural occurrence and geographical distribution in relation to climate. Oecologia. 123: 15-31, 2000.
- SUYKER, A.E., VERMA, S.B.: Year-round observations of the net ecosystem exchange of carbon dioxide in a native tallgrass prairie. Glob. Change Biol. 7: 279-289, 2001.
- TIESZEN L.L., SONG B.Y.: [Stable carbon isotopic variation among plants of the Inner Mongolian grasslands]. In: Jiang Shu, Chen Zuozhong and Xiao Xiangming, eds. Reports from the Inner Mongolia Grassland Ecosystem Research Station of Academia Sinica (1979-1988). Pp. 273-287. Science Press, Beijing 1990.
- UBUGUNOV L., RUPYSHEV Y., UBUGUNOV V., HOU X., VISHNYAKOVA O., LAVRENTIEVA I., UBUGUNOVA V., REN W., DING Y.: Impact of Climate and Grazing on Biomass Components of Eastern Russia Typical Steppe. Journal of Integrative Agriculture. 13(6):1183-1192, 2014
- WANG S.P., WANG Y.F.: Study on over-compensation growth of *Cleistogenes squarrosa* population in Inner Mongolia steppe. Acta Bot. Sin. 43: 413–418, 2001.