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内蒙古羊草草原植物种能量含量及其在群落中的作用

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摘要：根据 11a 的野外实验对内蒙古羊草草原群落 42 种植物的能量含量（含灰分）及其在群落中的相对生物量进行了研究。不同植物种地上部分的能量含量在（3156 ± 1141）J/g 和（8141 ± 527）J/g 之间变动，所有物种的平均能量含量为（6899 ± 840）J/g，种间变异系数 4.9%。小叶锦鸡儿具有最高的能量含量。禾草的平均能量含量高于杂草。根据生活型和生长型，草本物种被进一步分组，能量含量从高到低的排列顺序为：高禾草（7717 ± 92）J/g ＞豆科植物（7228 ± 433）J/g ＞矮禾草（7250 ± 218）J/g ＞其余杂草（6784 ± 529）J/g ＞半灌木（6719 ± 69）J/g ＞1、2 年生植物（5911 ± 1759）J/g。42 种植物的能量含量和它们在群落中的相对生物量存在显著正相关关系。根据它们在群落中的构成比例进行分组，以物种在群落中的相对生物量为权重，各组能量含量依次为：优势种（7740 J/g）＞伴生种（7244 J/g^{-1}）＞偶见种（6653 J/g）。高能量含量的植物更具竞争力，在群落中通常占据优势地位，而低能量含量的植物竞争力通常较弱，构成草原群落的伴生种或偶见种。

关键词：羊草草原；植物的能量含量；群落作用

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The caloric content of plant species and its role in a *Leymus chinensis* steppe community of Inner Mongolia, China

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Abstract: The caloric contents of 42 species and their composition in a *Leymus chinensis* steppe community of Inner Mongolia in China were determined and analyzed for 11 years. The caloric content ($\bar{x} \pm 1SD$) of aboveground parts for plant species varied from (3156 ± 1141) J/g ash-contained to (8141 ± 527) J/g. The average caloric content of all species was (6899 ± 840) J/g and their inter-specific CV was 4.9%. Of all the species, *Caragana microphylla* had the highest caloric content (8142 J/g). Grasses had a higher ($P < 0.05$) average caloric content (7425 ± 291) J/g than forbs (6734 ± 844) J/g. When the herbaceous species were classified into subgroups according to life form and growth form,

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the order of average caloric contents, from high to low, were: tall grasses (7717 ± 92) J/g > Legume (7228 ± 433) J/g > short grasses (7250 ± 218) J/g > remaining forbs (6784 ± 529) J/g > subshrubs (6719 ± 69) J/g > annuals and biennials (5911 ± 1759) J/g.

There was a positive correlation ($P < 0.05$) between the caloric contents of 42 species and their relative biomass in the community. When all species were classified into three groups according to their composition in the community, the averaged caloric contents, weighted by the species relative biomass, followed the order: Dominant (7740 J/g) > companion (7244 J/g) > incidental (6653 J/g). The plants with high caloric contents were more competitive, which allows them to gain a dominant status, while the competitive abilities of plants with low caloric contents were generally weak. The latter made up the companion or incidental species in a steppe community.

Key Words: *Leymus chinensis* steppe; caloric contents of plant; community role

Introduction

The study of caloric content is the basis for assessing energy fixation, transformation and utilization efficiency and nutrient value of the plants. It is often necessary to convert biomass to energy by using caloric equivalents in the studies of energy flow through the ecosystem. This requires caloric determinations of either principal species comprising the community or composite community samples [1]. The oxygen bomb calorimeter was first used by Long [2] to determine the caloric contents of different parts of the sunflower plant and since then has been applied in many ecosystem studies [2,3–8]. A number of studies indicated that caloric contents varied with the plant part, exposure to light, nutrient status, season and soil types for the same species. It also varied between various phyletic or ecological categories [2,9–11]. Many authors have suggested that the energy content of ecological materials should be determined for specific environmental situations. Despite intraspecific variability, caloric content is still a relatively stable parameter for the same species; the range of intraspecific variation was not enough to conceal the differences among species [2]. In studies where broadly based temporal or spatial averages are most appropriate.

Caloric content is a function of the plants' genetic constitution, nutritive status, and life history [9]. Long [2] expected the two processes of fundamental importance in plant life, competition in the community and adaptation in the individual, can be evaluated more accurately and objectively by means of caloric contents.

However little has been published concerning the relationship between the caloric content of plants or animals and its role in the community. Wang and Liu [7] and Guo *et al* [1] reported higher caloric contents in dominant than in secondary species in steppe communities. The typical steppe dominated by *Leymus chinensis* is the zonal community that occurs extensively in temperate region of China and eastern Eurasian. The total area is about 420000 km^2 and more than half is in China. It is important for hay production and grazing. In this paper, we focus on the caloric contents of different plant species and their competitive ability in a *L. chinensis* steppe of Inner Mongolia.

1 Materials and Methods

1.1 Study site and climate:

Studies were conducted on a site in the *L. chinensis* steppe at the Grassland Ecosystem Station of Academia Sinica in the Xilin Gol League, Inner Mongolia (43°33′N, 116°40′E, ca. 1225m elevation). The site was representative of the temperate steppe region of China and dominated by *L. chinensis*. It was located on a flat sloping field (a slope of 2 — 4 degrees) on secondary basalt beside the Xilin River. The soil is a Dark Chestnut with a humus layer that is 20 — 30cm thick and a calcic layer below 50 — 60cm.

The climate of the area is temperate semiarid steppe with cold and dry winters and warm and relatively humid summers. Average annual precipitation was 351 mm over 18 years from 1982 — 1998 with a standard deviation of

69.3 mm and a range from 283.2 to 507 mm. Average annual temperature was 0.53 C with a standard deviation of 0.72 C over the same time period. Maxima in precipitation and temperature occur in May to September and minima occur in December, January and February. The annual potential Evapotranspiration ranges from 1600 — 1800 mm, which is 4 — 5 times of precipitation. The combination of high temperature with high humidity in summer provides suitable condition for the growth of steppe plants. The frost-free period is 91 days and the growing season for steppe plants is about 150 days.

1.2 Vegetation

L. chinensis, a eurytopic xerophyte rhizomotous grass, accounts for approximately 50% of the biomass in this community. The secondary species are densely tufted xerophytes such as *Stipa grandis*, *Achnatherum sibiricum*, *Koeloria cristata*, and *Agropyron michnoi*and. Grasses constitute about 70% of the biomass while forbs make up the balance. There are about 75 forb species with taproots or bulbs, which account for 87% of all plant species in the community. The site had been subject to grazing by sheep and cattle until 1978 when grazing was excluded with a fenced exclosure [3]. The community is now representative of a late seral stage.

The height of flowering tillers is about 50 — 60 cm and the leaf layer is about 30 cm. Vegetative ground cover is about 30% — 40% and can reach 70% in a year with high precipitation. Average aboveground biomass was 199 $g \cdot m^{-2}$ with a deviation of 52 $g \cdot m^{-2}$ over 17 years from 1982 — 1998.

1.3 Sampling Methods:

In *L chinensis* steppe site, a permanent mowing succession experiment plot was established since 1982 in order to explore the appropriate mowing date and frequency, the plot includes 9 mowing treatments, among them 5 treatments of different date mowing were set, the treatments was mown once in each year, time of sampling is respectively at Jun. 23, Jul. 8, Aug. 2, Aug. 16 and Sep. 12, at the same time 6 replicated 1 m^2 quadrats were sampled stochastic in adjacent unmown control plot in above date from 1991 — 2001, All living and recent dead herbaceous biomass was clipped at 6cm to ground level and separated by species. The number of plants and height of each species present were recorded in each quadrate. At the same time, all samples of each species were collected and then dried to constant weight at 55 ℃ and weighted, the biomass of each species were recorded in each quadrate, and are expressed as $g \cdot m^{-2}$ by oven-dry wt.

Then the samples in each time were mixed by species and ground in a Wiley mill (20 mesh screen) and compressed into pellets in preparation for caloric determinations. Triplicate caloric determinations were made of each sample using a Parr 1281 oxygen bomb calorimeter. In this paper caloric contents were not corrected for ash content, and are expressed as J/g oven-dry wt.

1.4 Data analysis

In this paper, the samples were pooled for statistical analyses are from the control plot, total 5 times in each year × 11 year × 6 quadrats in each times, *i. e.* 330 quadrats were pooled for calculating relative biomass of each species. Due to not all species were collected in each time, so total 348 samples of 42 species were pooled for determining caloric contents.

Relative biomass of species was served as indicating the function and dominant degree of species in the community:

$$\text{Relative biomass } (\%) = \text{the biomass of one species / community biomass} \times 100$$

In order to explore variability of caloric content of plants, three classification means were adopted (Table 1).

Classification-1: all species were sorted into shrubs, Graminoids (grasses, *Carex* spp.) and forbs based on life forms.

Classification-2: in the base of classification1, the Graminoids were subdivided into tall grasses and short grasses; the forbs were subdivided into legumes, annuals and biennials, subshrubs and remaining forbs based on their life form and growth form.

Classification-3: based on their relative biomass in the community, all species were classified into one of three groups: Dominant (> 6% relative biomass), companion (1 to 6% relative biomass) and incidental (< 1% relative biomass). The dominant group consisted of *L. chinensis*, *S. grandis*, and *A. sibiricum*, which accounted for more than 50% of community biomass. The companion group contained 15 species that comprised about 40% of community biomass while the incidental group contributed less than 10% of relative biomass.

Comparisons between groups in each classification were analyzed by the *t*-test and ANOVA. The data analyses and charts were produced with Microsoft Excel 2000, SigmaPlot 2000 and SPSS 8.0.

2 Results

2.1 Caloric content of main species in a *Leymus chinensis* steppe community.

During our 12-year study, 42 species were determined for caloric content out of a total of 65 that were recorded (Table 1). Their caloric content, averaged over all collection periods ranged from (3157 ± 1141) J/g ash-contained oven-dry weight for *Salsola collina* to (8142 ± 528) J/g for *Caragana microphylla*, which was the only shrub in the site (Table 1). The mean caloric content of all species was (6899 ± 840) with a CV of 4.9 %. Species that ranked 2^{nd}, 3^{rd} and 4^{th} in caloric contents were *S. grandis*, *Thermopsis lanceolata*, and *Adenophora stenanthina*. *L. chinensis*, the most dominant species in this community, had a caloric content that averaged (7671 ± 375) J/g. All the graminoid species had caloric contents that exceeded the mean content (Table 1). The average caloric content of 8 grass species was (7425 ± 291) J/g, ranging from (7010 ± 374) J/g for *C. korshinskyi* to (7973 ± 492) J/g for *S. grandis*. The content of 33 forbs species averaged (6734 ± 844) J/g, ranging from (3157 ± 1141) J/g for *Salsola collina* to 17908 J/g for *Thermopsis lanceolata* (Table 1). The mean caloric content of grasses was higher (P = 0.032) than that of forbs. Variability of caloric content was greater among forbs species than grass species (CV = 5.0 % for forbs, 1.7 % for grasses, Fig. 1-A).

Table 1 Caloric content and relative biomass of plant populations in *Leymus chinensis* steppe and their functional classification SpeciesRelative biomass

Species	Relative biomass (%)	Average caloric content (J/g)	Classification-1 (Based on life forms)	Classification-2 (Based on life forms and growth forms)	Classification-3 (Based on relative biomass)	Sampling number
Leymus chinensis	26.97	17671 ± 375	G	TG	D	41
Stipa grandis	16.44	17973 ± 492	G	TG	D	37
Achnatherum sibiricum	8.36	17509 ± 539	G	TG	D	34
Agropyron cristatum	5.94	17230 ± 528	G	SG	C	19
Carex korshinskyi	5.46	17010 ± 374	G	SG	C	14
Caragana microphylla	5.29	18142 ± 528	SH	SH	C	18
Allium senescens	3.77	17505 ± 239	F	RF	C	14
Artemisia commutata	3.51	17093 ± 664	F	RF	C	22
Serratula centauroides	3.15	16549 ± 450	F	RF	C	13
Koeleria cristata	2.45	17178 ± 605	G	SG	C	30
Kochia prostrata	1.93	16788 ± 438	F	SSH	C	12
Cleistogenes squarrosa	1.46	17169 ± 672	G	SG	C	4
Oxytropis myriophylla	1.42	16827	F	L	C	1
Anemarrhena asphodeloides	1.35	17294	F	RF	C	1
Artemisia scoparia	1.25	17729 ± 478	F	A	C	14
Artemisia frigida	1.2	16651 ± 602	F	SSH	C	2
Poa attenuata	1.14	17661 ± 566	G	SG	C	4

续表

Species	Relative biomass (%)	Average caloric content (J/g)	Classification-1 (Based on life forms)	Classification-2 (Based on life forms and growth forms)	Classification-3 (Based on relative biomass)	Sampling number
Pocokia ruthenica	1.06	16930 ± 591	F	L	C	4
Allium anisopodium	0.77	16602	F	RF	I	1
Cymbaria dahurica	0.72	16541	F	RF	I	2
Potentilla acaulis	0.71	16157 ± 615	F	RF	I	8
Gentiana squarrosa	0.68	–	F	A	I	–
Heteropappus altaicus	0.6	16323	F	RF	I	1
Potentilla tanacetifolia	0.48	16417 ± 212	F	RF	I	3
Pedicularis atriata	0.48	–	F	RF	I	–
Orostachys malacophyllus	0.46	–	F	A	I	–
Potentilla bifurca	0.45	17091 ± 722	F	RF	I	6
Allium tenuissimum	0.37	16203	F	RF	I	1
Allium condensatum	0.33	16050	F	RF	I	1
Saposhnikovia divaricata	0.31	16972 ± 673	F	RF	I	3
Qrostachys fimbriatus	0.26	–	F	A	I	–
Thalictrum petaloideum	0.2	16830 ± 607	F	RF	I	3
Melandrium apricum	0.18	–	F	A	I	–
Saussurea japonica	0.16	17103	F	A	I	1
Allium bidentatum	0.09	–	F	RF	I	–
Iris tenuifolia	0.08	16710 ± 708	F	RF	I	3
Dontostemon micranthus	0.05	–	F	A	I	–
Haplophyllum dauricum	0.05	–	F	RF	I	–
Bupleurum scorzonerifolium	0.04	17824	F	RF	I	1
Allium ramosum	0.04	16903	F	RF	I	1
Asparagus dauricus	0.03	17218	F	RF	I	1
Astragalus adsurgens	0.03	–	F	RF	I	–
Chenopodium album	0.03	–	F	A	I	–
Schizonepeta tenuifolia	0.03	–	F	A	I	–
Limonium bicolor	0.02	–	F	RF	I	–
Gentianopsis barbata	0.02	–	F	A	I	–
Salsola collina	0.02	13157 ± 1141	F	A	I	9
Thalictrum squarrosum	0.02	–	F	RF	I	–
Adenophora crispata	0.02	–	F	RF	I	–
Sibbaldia adpressa	0.02	15751	F	RF	I	1
Sedum aizoon	0.02	–	F	RF	I	–
Pulsatilla turczaninovii	0.02	16495 ± 1381	F	RF	I	3
Thermopsis lanceolata	0.01	17908	F	L	I	1
Potentilla virticillaris	0.01	16713	F	RF	I	1
Chenopodium aristatum	0.01	15657 ± 510	F	A	I	6
Adenophora stenanthina	0.01	17880 ± 236	F	RF	I	2
Gueldenstaedtia verna	0.01	–	F	A	I	–
Potentilla sericea	0.01	–	F	RF	I	–
Festuca ovina	<0.01	–	G	SG	I	–
Linum stelleroides	<0.01	–	F	A	I	–
Axyris amaranthoides	<0.01	–	F	A	I	–
Astragalus galactites	<0.01	17448 ± 1476	F	L	I	2
Hedysarum gmelinii	<0.01	–	F	L	I	–
Silene jenisseensis	<0.01	16903 ± 217	F	RF	I	3

Note: F-forbs, G-grasses, SH-shrubs, TG-tall grasses, SG-short grasses, L-Legume plant, SSH-subshrubs, A- annuals and biennials, RF-Remaining forbs, D-dominant, C-companion, I-incidental

From Fig. 1-B, we can find the order of average caloric contents from high to low is *C. microphylla* > tall grasses > Legumes > short grasses > remaining forbs > subshrubs > annuals and biennials. Generally, the caloric content of *C. microphylla* was greater than the average content of species in each of the other groups. However, it was not

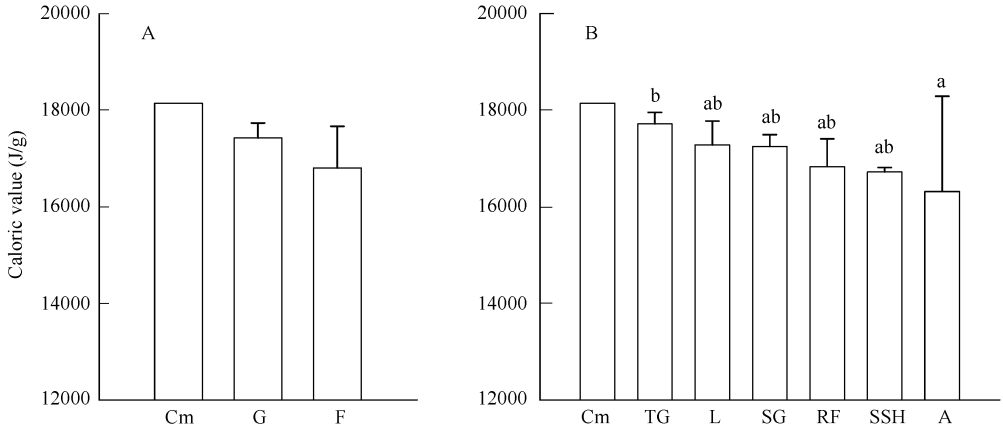

Fig. 1 Comparison of caloric contents (mean ± SD) of selected plant groups in a *Leymus chinensis* steppe community

(A: Classification-1, B: Classification-2. F-forbs, G-grasses, Cm-*Caragana microphylla*, TG-tall grasses, SG-short grasses, L-Legume plants, SSH-subshrubs, A- annuals and biennials, RF-Remaining forbs) Means with the same small letter do not differ ($P>0.05$) according to Duncan's Multiple Range test

much greater than the caloric content of *S. grandis*, *L. chinensis*, and *A. sibiricum* that were all dominant (Table 1). The 4 annual species yielded the lowest average caloric content of all growth forms (5911J/g ± 1759 J/g). The caloric contents of five short grasses, four legumes, two subshrubs, remaining forbs averaged 17249J/g ± 218J/g, 17228J/g ± 433J/g, 16719J/g ± 69J/g, and 16784J/g ± 529J/g respectively (Table 1). On average, the caloric contents of tall grasses, legumes, short grasses and forbs had no differences ($P>0.05$).

Caloric contents varied considerably from one species to another within each group. Annuals and biennial species exhibited the greatest variability (CV = 11.1%) while those of other groups were relative small, (2.5% for Legumes, 3.2% for remaining forbs, 1.3 % for short grasses, 0.4 % for subshrubs, 1.1% for tall grasses).

2.2 The relationship between caloric content of plant species and its role in the community

The caloric content of species was related to their relative biomass in the community (Fig. 2).

The caloric content of each group was weighted according to the relative biomass of their species. The caloric content of the dominant group was the greatest followed by the companion and incidental groups (Fig. 3).

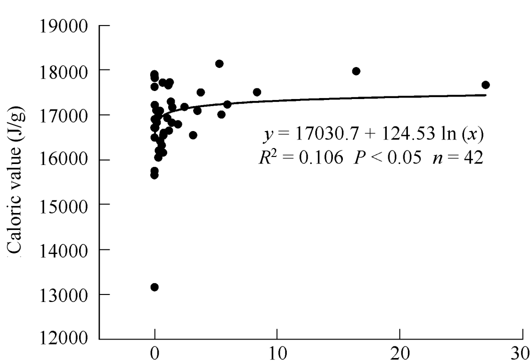

Fig. 2 Regression analysis between relative biomass and caloric contents for different species in a *Leymus chinensis* steppe community

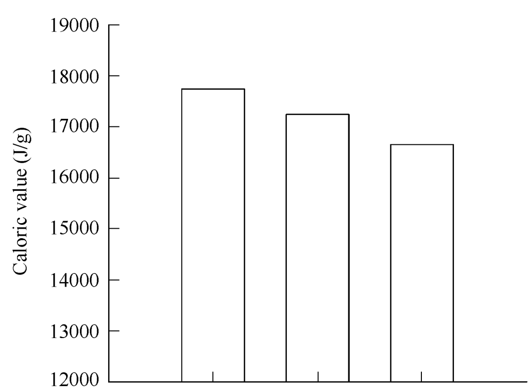

Fig. 3 Averaged caloric contents of different groups in a *Leymus chinensis* steppe community weighted by the relative biomass of their representative species

3 Discussion

Caloric content is a useful parameter in assessing the photosynthetic efficiency of plants but it is affected by species, growing conditions, morphological structure, age, period of sampling, and other factors. The higher caloric content of a shrub, represented by *C. microphylla*, is higher than the herbaceous species. Similar results have been reported for tundra plants [,10,14,15], for alpine meadows plants [6], for rain forest plants [7] and for steppe plants in China [7,18]. Our results showed significant higher caloric contents of grasses than forbs, which is similar to that of Smith [9].

The energy content of plant material is determined by the chemical composition of the organic substances. All organisms can be thought of as being composed of lipid, protein, carbohydrate, water, and ash fractions. An overview of the energy content of substances, which are important in plant structure, is provided by Pain [20], Lieth [21], and Neitzke [8]. Of the organic compounds contained in plants, lipids contain the highest caloric values (38.9 kJ/g) while carbohydrates have the lowest values (5.7 — 17.6 kJ/g). Lignin (26.4 kJ/g) and protein (23 kJ/g) have relatively high caloric values. In consequence, when determinations show high caloric contents it is usually an indication that the material contains an unusual amount of lipid, protein or lignin.

Bliss [] suggested that shrubs had a higher lipid content than herbs. Wang and Liu [7] presumed that the larger caloric contents for shrub and tall herbaceous plants might result from a relatively large concentration of lignin or lignin – like substances. However, a causal interpretation of the variations in the caloric contents for different groups is extremely difficult to achieve in the absence of an exact quantitative and qualitative analysis of the substances present, as has been shown by the author's data and the data of other authors.

The caloric contents have relation to accumulation, transportation, allocation of contain-energy material in plant body, and are restricted by genetic characteristic and growing status of plant further again. In the community the plants those grow better, have stronger photosynthesis, and can complete life history usually have higher caloric contents. So the caloric content is contacted with the bio-ecology characteristic of plant, and can be looked upon as a complex index reflecting variety of life activity in the organization and grow status of plant.

In this study, the three dominants with a high caloric content, late seral species (*L. chinensis*, *S. grandis* and *A. sibiricum*), have may be due to that they occupied the favorable upper vegetation stratum and captured more light. We speculate that plants with a relatively high caloric content are strong competitors and generally occupy a dominant status in the community while plants with a relatively low caloric content are weak competitors. These plants make up the companion or incidental species in the steppe community.

Caloric content of species is an ecological attribute, and varies with environment and plant community. However, many aspects of plant differentiation with respect to their caloric content remain unclear. Special studies are necessary to elucidate the relationships between the caloric content of plants and the multiple environmental factors, the intensity of physiological processes, and the biochemical composition of organic matter synthesized and accumulated by plants.

Our results showed there are certain relationships between the caloric contents of the species and their function in the community. The order of caloric content shows dominant > companion > incidental. Other scholars also mentioned a little in their article [7, 11], but not revealed and verified this kind of relationship with experimental data, we verified primary the relationship by analyzing many years of experimental data.

Though the experiment condition is limited, experiment design and sampling measures are still not perfect, we believe the relationship between caloric values of plant and its role in the community will provide some new ideas for the energy ecology research, contributing to reveal competition mechanism of plant in the community from the aspect of energy ecology.

4 Conclusion

The caloric content of aboveground parts varied from (3156 ± 1141) J/g ash-contained to (8141 ± 527) J/g for 42 plant species in a *Leymus chinensis* steppe community of Inner Mongolia in China. The average caloric content of all species was (6899 ± 840) J/g and their inter-specific CV was 4.9%. Of all the species, *Caragana microphylla* had the highest caloric content. Grasses had a higher average caloric content than forbs. When the herbaceous species were classified into subgroups according to life form and growth form, the order of average caloric contents, from high to low, were: tall grasses > Legume > short grasses > remaining forbs > subshrubs > annuals and biennials.

There was a positive correlation between the caloric contents of 42 species and their relative biomass in the community. When all species were classified into three groups according to their composition in the community, the averaged caloric contents, weighted by the species relative biomass, followed the order: Dominant > companion > incidental. The plants with high caloric contents were more competitive, which allows them to gain a dominant status, while the competitive abilities of plants with low caloric contents were generally weak. The latter made up the companion or incidental species in a steppe community.

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