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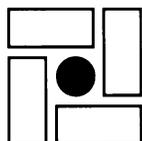
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Grazing Tolerance of the Vegetation of Dry Meadows

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Abstract—The transformation of plant communities of dry meadows under the influence of grazing was studied, as well as the resistance of some plant species to grazing and their ecological–biological features connected with grazing tolerance.

Since ancient times, herbivorous animals have had a substantial effect on meadow and steppe phytocenoses. Grazing was an indispensable condition for maintaining the equilibrium of grassland systems and their biological cycles. The amount of grazing animals was regulated by trophic relations and the capacity of pastures. However, when humans appeared on the earth and cattle breeding developed, human activity came to determine grazing loads. The overgrazing, exhaustion, and degradation of pastures became frequent and even common phenomena. Grazing ceased to be a factor maintaining the stability of grassland systems. In many cases, it turned into a destructive factor.

General estimations of the effect of cattle grazing on meadow ecosystems were given by Klapp (1961), Smelov (1966), Shennikov (1941), Rabotnov (1984), and others. They conclude that grazing results in soil compaction, decreased soil aeration, and the partial elimination of phytomass, especially in upper biogeocenotic horizons. Grazing also leads to increased soil heating and increased water evaporation from the soil surface. As a result, the total reconstruction of herbage takes place.

Despite the fact that the general laws of this process have largely been determined, some problems remain unsolved. In particular, little is known about the pasture degradation of meadow and separate stages of degradation in different botanical–geographical regions and different ecotopes. There is little information about the changes in the floristic composition, structure, and productivity of meadow plant communities under the conditions of degradation. The degree of tolerance of plant species and plant communities to grazing was not described in detail.

We studied dry meadows effected by grazing and situated on the western slope of the Middle Urals in the upper part of basin of the Sylva River. Several series of 100-m² sample plots were selected for the investigation. The plots represented different levels of grazing-induced transformation of meadow phytocenoses. On these plots, soil density was measured with the help of a Golubev densimeter. The composition of herbage, the ratio

of biormorphs, the aboveground and underground biomass, and the seed productivity of selected plant species were studied. Special attention was paid to the share of synanthropic plant species in the composition of herbage and the aboveground biomass. As a result, the stages of the transformation of meadow phytocenoses under the influence of grazing were determined, and the scale of the levels of the grazing tolerance of meadow vegetation was elaborated.

TRANSFORMATION OF DRY MEADOWS DUE TO GRAZING

The investigated meadows succeeded cut forests as a result of the gradual enlargement of meadow glades. At first, forest meadow glades were used as hay meadows. This resulted in an increased share of grasses in the herbage composition due to a decreased share of herbs and the exclusion of some forest species. The subsequent transition to grazing led to a higher share of synanthropic species (both apophytes and anthropophytes) in the herbage composition. Thus, to estimate the transformation of dry meadows due to grazing, it is possible to apply the index of synanthropization (Gorchakovskii and Abramchuk, 1983, 1993). This value represents the percentage of synanthropic species in the floristic composition of herbage and aboveground biomass (Table 1).

Considering the index of synanthropization and other values (soil density, composition and structure of herbage, ratio of dominant biormorphs), we determined four stages of the transformation of dry meadows due to grazing.

First stage. The first stage includes meadows used mainly as hay meadows with periodic grazing on the aftermath. The grazing load is low. The soil density corresponds to 6–10 kg/cm² on the densimeter. The herbage consists of high and semihigh grasses, such as *Phleum pratense*, *Festuca pratensis*, *Dactylis glomerata*, *Alopecurus pratensis*, and *Bromopsis inermis*, and relatively high herbs, including *Cirsium heterophyllum*, *Filipendula ulmaria*, *Trollius europaeus*, *Heracleum*

Table 1. The indices of synanthropization according to the percentage of synanthropic species, %

Percentage	Levels of synanthropization			
	I	II	III	IV
In the floristic composition	>15	16–25	26–60	61–100
In the aboveground biomass	>5	6–15	16–65	66–100

sibiricum, *Geranium sylvaticum*, *Aegopodium podagraria*, and others. We registered 53 species per 100 m², six of them synanthropic. The aboveground biomass was 400, and the underground biomass, 1800, for a total of 2200 g/m². The ratio of aboveground to underground biomass was 1 : 4.5. The index of synanthropization equaled 11% by the herbage species composition and 5% by the aboveground biomass.

Second stage. Meadows at this stage are primarily used for grazing, and the load is moderate. The soil density corresponds to 11–18 g/cm² on the densimeter. The herbage mainly consists of short grasses (*Poa pratensis*, *Festuca rubra*, and *Anthoxanthum odoratum*) and lower herbs (*Solidago virgaurea*, *Carum carvi*, *Leucanthemum vulgare*, *Pimpinella saxifraga*, *Prunella vulgaris*, and *Galeopsis ladanum*). We found 32 species per 100 m², seven of them synanthropic. The aboveground biomass was 200, and the underground biomass, 1400, for a total of 1600 g/m². The ratio of aboveground to underground biomass was 1 : 7. The index of synanthropization was 21.9% according to the floristic composition and 14% by the aboveground biomass.

Third stage. Here, the grazing load is high. The soil density corresponds to 19–25 kg/cm². Short grasses such as *Poa pratensis* and *P. annua* dominate in the herbage, as well as middle and low herbs (*Alchemilla tubulosa*, *Achillea millefolium*, *Trifolium repens*, *Plantago major*, *P. media*, *Lathyrus pratensis*, *Taraxacum officinale*, *Leontodon autumnalis*, *Matricaria perforata*, and *Potentilla anserina*). Per 100 m², 25 species were found, 17 of them synanthropic. The aboveground biomass was 90, and the underground biomass, 720, for a total of 810 g/m². The ratio between aboveground and underground biomass was 1 : 8. The index of synanthropization was 68% by the floristic composition and 58% by the aboveground biomass.

Fourth stage. Here, the grazing load is extreme. The soil density corresponds to 26–30 g/cm². The herbage is low and consists mainly of *Polygonum aviculare* with small admixture of *Capsella bursa-pastoris*, *Berteroa incana*, *Poa annua*, and others. Per 100 m², 11 species were registered, all of them synanthropic. The aboveground biomass was 30, and the underground biomass, 270, for a total of 300 g/m². The ratio between aboveground and underground biomass was 1 : 9. The index of synanthropization was 100% by both the floristic species composition and the aboveground biomass.

During the transformation of meadows by grazing, their floristic composition is impoverished, while the

role of synanthropic species in the herbage composition increases. Plant communities dominated by grasses are replaced by communities dominated by herbs. Polydominant communities are changed to oligo- and monodominant ones. The share of synanthropic plants (both by the number of species and biomass) increases and then completely dominates. Plants with high competitive capacity are replaced by plants with low competitive capacity and large ecological amplitude providing for their existence on dense soils with low fertility. The productivity of meadow communities diminishes. The amount of aboveground biomass decreases relative to underground biomass.

The composition of prevailing biormorphs changes as well. As the intensity of grazing increases, high grasses are replaced by semihigh and then short grasses. Among herbs, more or less high dicotyledonous perennial plants with fragile erect stems unable to rise after being trampled are replaced by plants with elastic stems that are able to erect themselves after trampling. Later, the primary positions are occupied by perennial rosette plants and vegetatively mobile plants with creeping aboveground rooting shoots.

At advanced stages of the degradation of meadows by grazing, annual and biennial plants replace perennial ones among both grasses and herbs. Dominant positions pass to *Poa annua*, *Polygonum aviculare*, *Capsella bursa-pastoris*, *Galeopsis ladanum*, and *Matricaria perforata*.

Our previous studies (Gorchakovskii and Abramchuk, 1983, 1993) indicated the convergence of meadow phytocenoses during degradation by grazing. Instead of the relatively significant variability of initial plant communities, only a small number of homogeneous communities are formed at advanced successional stages.

SEED PRODUCTIVITY OF SOME PLANTS THAT ARE THE MOST RESISTANT TO GRAZING

The ability of plants to quickly occupy trampled areas on pastures and remain there at intensive grazing loads depends to a great extent on the peculiarities of their reproduction by seeds. To examine this phenomenon, studies of the seed productivity of *Plantago major*, *Taraxacum officinale*, *Leontodon autumnalis* and *Capsella bursa-pastoris* were conducted over two summer seasons. Phytocenoses at advanced stages of degradation were investigated. The following values were determined: the amount of fruits and seeds per plant, the mass of one thousand seeds, germinating ability, and seed vigor.

Plantago major is a perennial polycarpic racemose-root plant with a short rhizome. The mass of 1000 seeds is reported to be 0.25–0.35 g (Fisyunov, 1984). Data on its seed productivity are quite contradictory: up to 2000 (Mal'tsev, 1932), 61 000 (Shlyakova, 1982), or 320 000

seeds per plant (Fisyunov, 1984). Forty percent of seeds germinate at a soil depth of 1 cm; and only 5–6%, at a depth of 3 cm. Seeds remain viable for seven years (Shlyakova, 1982).

Our observations demonstrated that the seed productivity of *Plantago major* decreased upon the degradation of meadow phytocenoses. This value was equal to 33000 seeds per plant at the second stage of degradation, 19000 seeds at the third stage, and 7500 seeds at the fourth stage. Respectively, the number of fruits per generative shoot decreased from 250 to 170, as well as the number of seeds in one fruit (from ten to six). The mass of 1000 seeds was 0.19–0.22 g, the germinating ability was 86–90%, and seed vigor was 76.7–89%.

Taraxacum officinale is a perennial taprooted polycarpic plant with facultative root suckers and a sympodial system of vegetative rosette, semirosette, and rosetteless generative shoots. It develops quickly on unsodded soils and flowers and fructifies in the second year of life. In undisturbed communities, it flowers only in the fourth year. When the roots are damaged, regenerative buds are formed, and aboveground shoots develop (Dmitriev *et al.*, 1982). The mass of 1000 seeds is reported to be 0.5–0.75 g (Fisyunov, 1984) or 0.2–0.7 g (Kott, 1955). Seed productivity can be up to 7000 (Kott, 1955) or 12200 achenes per plant (Fisyunov, 1984). Seeds germinate at a depth less than 4–5 cm.

According to our data, the seed productivity of *Taraxacum officinale* decreases from 1400 seeds per plant at the second stage of meadow degradation to 390 seeds at the fourth stage. However, data from a single sampling are listed here. In fact, a single plant forms generative shoots several times per season and thus produces more seeds. The amount of generative shoots per plant insignificantly varies at different degradation stages (from six to four). The mass of 1000 seeds was 0.42–0.47 g, the germinating ability was 79.4–86%, and the seed vigor was 48–49%.

Leontodon autumnalis is a perennial racemose-root plant with a shortened rhizome and abundant secondary roots. The mass of 1000 seeds is reported to be 0.7 g (*Kormovye rasteniya ...*, 1951) or 0.9–1.0 g (Fisyunov, 1984). Seed productivity is either 1200 (*Kormovye rasteniya ...*, 1951) or 4900 seeds per plant (Fisyunov, 1984).

Our data demonstrate that the seed productivity of *Leontodon autumnalis* decreases upon meadow degradation from the second to the fourth stage. The number of achenes per plant diminishes from 4600 to 480; the number of achenes in an inflorescence, from 82 to 48; the number of generative shoots per plant, from 14 to 5; and the number of inflorescences per generative shoot, from four to two. Like *Taraxacum officinale*, this plant can produce more seeds during a season due to the formation of new generative shoots. The mass of 1000 seeds was 0.48–0.49 g, the germinating ability was 71–80%, and seed vigor was 62–67%.

The fruits of *Taraxacum officinale* and *Leontodon autumnalis* are achenes with pilose appendages providing for high “sailing” capacity. Seeds can thus be transported long distances. The most active fructification of *Taraxacum* takes place in May and June, while that of *Leontodon* occurs from late July to late autumn. These two species complement each other by their dissemination periods. Their seeds have no dormant period and can germinate immediately after dissemination (Kott, 1955). As a result, they can populate trampled areas during the entire growth season. Remaining in soil, seeds are able to germinate for 2–3 years or more (*Kormovye rasteniya ...*, 1951).

Capsella bursa-pastoris is an annual or biennial plant with a taproot system and produces compressed siliques. The seeds are small and spread when the siliques crack. The mass of 1000 seeds is 0.1–0.2 g (Fisyunov, 1984). According to different references, one plant produces up to 12000 (Simonov, 1987), 50000–70000 (Mal'tsev, 1932), 70000 (*Kormovye rasteniya ...*, 1951), 60000–80000 (Sokolov and Chesalin, 1952), or 237000 seeds (Fisyunov, 1984). Seeds germinate at a depth of less than 2–3 cm and remain viable for 3–5 years (Fisyunov, 1984).

Our studies demonstrate that the production of seeds per plant decreased from 18400 at the third stage of degradation to 7200 at the fourth stage (in the sample plot at second stage, this species was not found). The number of fruits in an inflorescence decreased from 310 to 140, while the number of seeds in a fruit remained approximately the same. The mass of 1000 seeds was 0.11–0.12 g, the germinating ability was 75–78%, and seed vigor was 74–88%.

The life cycle of *Capsella bursa-pastoris* is very short. This plant is able to produce two or three generations per summer (Mal'tsev, 1932), and the seeds germinate quickly. This species has three forms: spring, hibernating, and winter (Kott, 1955). Plants with flowers and fruits can be found during the whole growth season.

For comparison, let us consider *Polygonum aviculare*. This is an annual plant widespread on trampled sites. The stems exhibit profuse branching or, under conditions of grazing, are prostrate. It flowers from June to late autumn. The fruit is of a nutlet type. One plant produces up to 5400 nutlets (Fisyunov, 1984). Seeds ripen in September and mostly germinate in spring. Remaining in soil, they retain their germinating ability for five years. The seeds are able to germinate at depths of less than 8–10 cm (Fisyunov, 1984). According to our observations, *Polygonum aviculare* regenerates well on dense trampled soils, and its seeds can germinate near the soil surface and even at the surface. This plant regenerates after grazing and even after multiple mowings.

The most favorable conditions for the germination of annual and biennial plants (*Capsella bursa-pastoris* and *Polygonum aviculare*) in the pastures are in spring after the snow melts and in early summer after strong

Table 2. Levels of grazing tolerance of meadow plants

Level	Adaptive features, plant response to grazing and trampling	Dominant biormorphs, morphobiological peculiarities of plants	Typical species
1	Aboveground shoots do not rise after trampling; most of the aboveground biomass is consumed by grazing cattle. The regeneration of vegetative shoots is poor. Most of the aboveground biomass is located in the middle and upper sublayers	High rhizomatous and loose-caespitose grasses; elongated vegetative shoots prevail. Dicotyledonous perennial herbs with erect stems and large succulent leaves	<i>Bromopsis inermis</i> , <i>Phleum pratense</i> <i>Trollius europaeus</i> , <i>Cirsium heterophyllum</i> , <i>Filipendula ulmaria</i>
2	Aboveground shoots partly rise after trampling. Shoot regeneration is poor. Most of the aboveground biomass is located in the middle and lower sublayers	Semihigh rhizomatous-loose-caespitose and loose-caespitose grasses	<i>Festuca pratensis</i> , <i>Dactylis glomerata</i> , <i>Alopecurus pratensis</i>
3	Aboveground shoots are able to rise after trampling. Shoot regeneration is well pronounced. Most of the aboveground biomass is located in a lower sublayer	Short rhizomatous-loose-caespitose and loose-caespitose grasses; shortened vegetative shoots dominate. Dicotyledonous perennial plants with erect elastic stems	<i>Poa pratensis</i> , <i>Festuca rubra</i> , <i>Anthoxanthum odoratum</i> <i>Achillea millefolium</i>
4	Shoot regeneration is intensive. Most of the aboveground biomass is situated in a lower horizon. Plants quickly inhabit trampled areas with the help of seed and sometimes vegetative regeneration	Rosette dicotyledonous perennial plants. Fructification is abundant; fruits and seeds are small; some species have air-borne seeds Dicotyledonous perennial plants with elongated creeping rooting shoots capable of transforming into new individuals when they are torn away by animal hooves.	<i>Taraxacum officinale</i> , <i>Leontodon autumnalis</i> , <i>Plantago major</i> <i>Trifolium repens</i>
5	Low height; vegetative mobility, i.e., the ability to quick inhabit trampled areas with the help of vegetative reproduction	Dicotyledonous perennial plants with elongated creeping rooting runners	<i>Potentilla anserina</i>
6	Low height; the ability to quickly populate trampled sites with the help of seed reproduction, quick seed germination, and the quick formation and rooting of shoots and young plants (when the soil is sufficiently moist)	Annual or biennial herbs. Fructification is very abundant, and the seeds are very small	<i>Polygonum aviculare</i> , <i>Capsella bursa-pastoris</i>

rains. At these times, the soil surface is well moistened. In the dry summer period, the soil surface of trampled areas is covered with a dense cracked crust preventing seed germination. Animal hooves seem to enhance the successful germination of these plants by helping seeds penetrate the soil.

In interpreting the data above, note that the decrease in seed productivity per individual plant during meadow degradation is compensated by an increased number of individuals. Therefore, the output of viable seeds from synanthropic plants per unit area is higher at the most advanced degradation stages than at earlier ones. No decrease in germinating ability and seed vigor with meadow degradation was found.

ADAPTIVE CAPACITY OF MEADOW PLANTS PROVIDING FOR THEIR GRAZING TOLERANCE: TOLERANCE LEVELS

The grazing tolerance of meadow plants is determined to a large extent by their ability to grow under conditions of intensive pasturing and strong soil

compression. For many plant species, this ability is expressed in different ways. In connection with this, it is possible to identify six levels of the tolerance of meadow plants (Table 2).

Tolerance is connected to a range of morphobiological features of plants and their reproductive strategy. There are several specific features determining plant survival (both grasses and herbs) under conditions of relatively intensive grazing, specifically, the position of the major part of stems and leaves near the soil surface (up to 10 cm) and the elasticity of stems capable of resisting mechanical damage and restoring their upright position after the load is removed. Moreover, the quick regeneration of aboveground shoots after grazing, low palatability, low forage quality, and the presence of prickles, rough stems, etc. are also very important.

Grass survival under conditions of intensive grazing is enhanced by the surface location of the tillering node allowing the plants to grow on condensed soils, the presence of sod, and domination by short vegetative shoots.

For herbs, the low damage to stems and leaves by grazing is due to the domination of rosette plants and plants creeping on the soil surface. An important property is the ability of plants to actively populate areas with damaged sod and bare soil surfaces resulting from disturbance by animal hooves, water erosion, etc. Vegetatively mobile plants possess this ability due to the formation of elongated creeping rooting shoots. Shoot fragments cut by animal hooves give life to new individuals. In the case of reproduction by seeds, the most important role is played by a long period of fructification (due to the separate development of different plants and different flowers of the same plant from one phenophase to another). Other important features are high seed productivity; seed capacity for air-borne dissemination; high germinative capacity and seed vigor; the preservation of seed germinating ability for a long period until favorable conditions for germination occur; and the ability of seeds to germinate on the soil surface after having passed through the gut of animals.

In addition, the following features are significant: the quick formation and rooting of seedlings, quick growth, the ability of young plants to completely use the period when the soil is moist, and an early generative phase (the second year of life for perennial plants). Annual and biennial cycles of development open additional possibilities for the quick population of trampled areas. In this case, seeds are produced in the first year of life. Sometimes, this happens several times in a summer season if such plants give rise to two or three generations per year.

Among meadow plants inhabiting strongly trampled pastures, there are some species that combine intensive vegetative reproduction with intensive reproduction by seeds. For example, *Potentilla anserina* not only quickly populates bare areas with runners, but also, according to Fisyunov (1984), produces up to 300000 seeds per plant.

CONCLUSION

Meadow phytocenoses are transformed under the influence of grazing and a gradual increase in grazing loads. Part of the herbage is eliminated, aboveground organs and regenerative buds of plants are damaged, and the vertical structure of the meadow community is altered. The herbage becomes lower, and most of the aboveground phytomass is found in the lowest layer. Herbage productivity decreases, while the ratio between aboveground and underground biomass changes in favor of underground biomass. The sod area and total projective coverage decrease, and the herbage becomes more heterogeneous. Vegetatively mobile plants increase the fragmentation of clones, leading to enhanced shoot formation. Aboveground shoots are situated close to the soil; as a result, rooting becomes easier. The floristic composition is impoverished, and the

ratio of biormorphs changes. There is a transition from domination by perennial plants to domination by annual and biennial plants, and the percentage of synanthropic species increases. As a result, plant communities with a very poor floristic composition are formed. They consist of only or almost only synanthropic species.

During the transformation of meadows due to grazing, less tolerant plants are replaced by species that are more tolerant to grazing. The criteria of the presence of plant species associated with different tolerance levels and the ratio of species belonging to various levels can be used to estimate the status of meadow phytocenoses within the framework of the ecological monitoring of natural grasslands.

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