$=$ Ecological Problems $=$

Comparative Productivity of Forest and Grass Ecosystems

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Abstract—Among the land-dominated natural formations, like forests and grasslands, the attention of humanity is drawn at present primarily to the former. It is the forests of temperate and tropical zones that are supposed to play an important role in the regulation of biosphere processes on Earth, including the current climate. This almost completely ignores the importance of herbaceous systems widely represented by steppes and meadows. The overwhelming superiority of forests over grass ecosystems in productivity and phytomass stock is recognized. A comparative analysis of production estimates (t/ha/year) and of organic material stocks (t/ha) in the underground and aboveground parts of herbaceous and forest ecosystems accumulated in the scientific literature has shown that meadows and steppes are not inferior (and often even superior) to forests both in the mass of accumulated organic matter and in annual growth of phytomass. The only difference is that organic production is localized in forest communities mainly in the aboveground part as considerable wood (trunk) mass while it is equally or more shifted underground in herbaceous communities in the form of soil organic matter. The leaf (photosynthesizing) masses of herbaceous and forest communities are close in quantity, respectively, and their synthesis of organic products and carbon exchange with the atmosphere are also similar. The author argues that the steppe and meadow ecosystems do not lag behind forests in organic mass and participation in biosphere processes, thus deserving no less effort for their preservation.

Keywords: forest and grass communities, steppe ecosystems, meadow ecosystems, annual production, aboveground phytomass, underground organic mass, soil organic material, biological productivity **DOI:** 10.1134/S1019331623010082

The current problems caused by climate warming have forced humanity to focus on the global role of forests. It is recognized that "forest ecosystems covering 33% of the Earth's surface are particularly important" [1, p. 44] in biosphere processes including climate dynamics. The Glasgow Climate Change Conference in November 2021 reiterated that forests were at the heart of national climate stabilization plans and that their preservation was one of the main ways to curb global warming. At the same time, it is evident that other seemingly no less important natural systems such as grasslands (including meadows and steppes) were almost completely ignored. Clearly, this neglect reflects the traditional attitude towards steppes and meadows as less productive natural formations than forests. Such notions are due to the overwhelming superiority of the wood mass accumulated over tens and even hundreds of years mainly in the form of woody material amounting to 150–500 t/ha in deciduous and broad-leaved forests and 10–37 t/ha in steppes [2]. According to experts, "the system of skel-

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etal transport organs enables forest phytocenoses … to maintain a leaf canopy during the growing season about double that of herbaceous phytocenoses in *LAI*¹ and primary productivity" [3, p. 126]. That is why there is a desire to replace steppe and meadow natural formations with richer and more productive forests the area of which is thought to be tangibly decreasing now due to human activities.

Meanwhile, it has long been noted that various plant communities should be similar in their productivity under similar growing conditions regardless of their species composition. In the opinion of A.A. Nichiporovich, "the plants use in cenoses with more or less efficiency the absorbed $PAR²$ energy. Accordingly, different phytocenoses form more or less the same yields in the case of optimum availability and in similar lighting conditions" [4, p. 36].

 $¹$ LAI is the leaf area index defined as the one-sided green leaf</sup> area per unit ground surface area $(m^2 m^{-2})$; ha ha⁻¹).

 $²$ PAR (Photosynthetically Active Radiation) designates the spec-</sup> tral range (wave band) of solar radiation that photosynthetic organisms are able to use in the process of photosynthesis.

In fact, it was found that in a forest–steppe natural zone (Central Black Earth Reserve) the annual production of organic matter was similar in the forests and in the meadow steppe (13.9 t/ha) under close growing conditions [5] and, according to other data, it was even markedly higher in the meadow steppe (20.9– 24.7 t/ha) $[6, 7]$. The production of forest ecosystems proved to be lower than that of meadow–steppe ecosystems in the Asian southern taiga under similar natural conditions, but in this case the authors believe that the lower forest performance may be due to underestimation of the underground root mass [1, p. 48]. It was also noted that the production of meadows in forest areas "usually lies within the same limits as the production of forests exceeding it only slightly" [8, p. 269]. Estimates have appeared recently according to which herbaceous communities in the steppes are two times more productive than forests [9], and the production of meadow steppes is more than three times higher than that of the adjacent broadleaf forests and southern taiga [10]. Similar relations were recorded when comparing forest and herbaceous ecosystems also in other regions of the Earth [11–13]. Nevertheless, these notions have not yet taken hold in the public consciousness although they emerged long ago [14, p. 11].

The functional role of natural biological systems in biosphere and climate processes is not yet fully understood. Note that quite a few quantitative assessments of the role of forest and herbaceous systems have been accumulated by now. The trouble is, however, that these estimates have been made by experts separately or for forests or steppes and meadows without connection with each other and without comparing the results. Most public attention in the field of biological processes in natural ecosystems has been unreasonably focused on more attractive and outwardly conspicuous woodlands, which has led to the recognition of their key role.

We consider this issue by comparing directly the productivity and mass of accumulated organic matter in forest and herbaceous ecosystems in order to understand the comparative performance of each of them.

Artificial forest and natural herbaceous communities in the steppe ecosystem. As a result of the famous State (Stalin's) Plan for the Transformation of Nature adopted and approved in 1948, enormous efforts were made starting in 1950 to create artificial forest stands (public windbreaks) in the Russian steppe regions to combat dry hot winds and droughts and to increase the fertility of the land. Forests emerged in previously vacant steppe areas.

It is necessary to compare the productivity of natural steppe communities and of forest stands set up in their place. For this purpose, we use data of a longterm study of productivity of the natural steppe and of artificial forest vegetation, which was carried out by the Zhanybek Station of the Forest Institute, USSR

Academy of Sciences (now the Institute of Forest Science, Russian Academy of Sciences) in the Volgograd and West Kazakhstan regions. The area of the station is located in the arid steppe (desert steppe) climate zone with a complex soil-vegetation cover consisting of steppe mesophilic (meadow steppe) forb–bunchgrass–steppe communities on dark chestnut and chernozem-like soils in relief depressions, dry-steppe communities of halophilic semi-shrubs, and xerophilic graminoids and motley grasses on strongly saline solonetzic and light chestnut soils on microelevations and microslopes [15–18]. The experimental forest stands have grown by now with varying degrees of stability and preservation since the creation of public windbreaks in 1950 under these soil–vegetation conditions [19–21].

Forest and grass communities growing under conditions optimum for both with the same hydrothermal and soil parameters were selected for comparison including woodlands in large areas of closed steppe depressions, regularly flooded by meltwater on saltwashed dark (chernozem-like) soils with a fresh groundwater lens at about 7 m depth, and natural grasslands in steppe microdepressions, hollows flooded by meltwater and rainwater with meadow chestnut unsaline soils and a fresh groundwater lens at the same depth. Note that the herbs cover was absent in forest communities as a result of regular removal of herbs to eliminate its competition for scarce moisture.

To estimate the production (annual phytomass growth) of forest communities, we used published data on the productivity of a young (five-year) Siberian elm crop (*Ulmus pumila* L.) [22] and the results of measurements of the foliage mass, annual shoots, stem wood growth, and underground root mass of a 13-yearold mixed tree/shrub stand of the balsam poplar (*Populus balsamifera* L.), boxelder maple (*Acer negundo* L.), Siberian elm (*Ulmus pumila* L.), Russian olive (*Elaeagnus angustifolia* L.), and Tatarian honeysuckle (*Lonicera tatarica* L.) [23–25]. The annual phytomass growth of the young Siberian elm crop was estimated by annual weighing of the aboveground and underground dry weight of model trees for four years [22]. We converted the annual growth of trunk wood in the mixed tree/shrub crop initially expressed in volume units (cm³) into weight values based on the specific gravity (density) of the wood of each species. The underground mass was estimated in soil monoliths of $50 \times 25 \times 25$ cm from trenches down to 5 m deep separating large and small roots by diameter [24]. We limited our analysis of the underground phytomass of trees and grasses in all comparisons to the total underground root mass and separately to the mass of small roots less than 1 mm in diameter.

The study of herbaceous vegetation and its productivity began in the first year of operation of the station (1950) and has continued intermittently up to the present. The aboveground phytomass production was

Phytocenosis. age and test year	Precipitation, mm/year	Annual growth of aboveground phytomass, t/ha/year			Underground phytomass, t/ha		Total mass of thin roots and	
		Trunks and large branches	Leaves and annual shoots	Total	Total	Thin roots \leq 1 mm	aboveground products, t/ha	Source
Siberian elm, 5 years, 1963	225	20.3	8 $6.4*$	28.3	8.7	$2.3**$	$30.6***$	$[22]$
Tree/shrub, 13 years, 1952	371	10	$6.5*$	16.5	23.8	12.6	29.1	[23, 24]
Meadow-steppe forb-grass grassland, 1950	167		2.8	2.8	36.8	25	27.7	$[15]$
Meadow-steppe forb-grass grassland, 1952	371		4.2	4.2	31.5	29.9	34.1	$[28]$
Meadow-steppe forb-grass grassland, 1960	305		3.2	3.2	17.5	15.7	18.9	$[29]$

Table 1. The phytomass and annual production in steppe (grass) communities and forest crops at the Dzhanybek Station under optimal and similar growing conditions, t/ha (dry weight)

Note: *leaf mass, **annual growth of root mass, ***annual stand production.

determined by standard cut-sample methods throughout the growing season with subsequent recalculation [26] by the sum of masses of dominant species at the time of maximum growth of each (i.e., by summing up the peaks [27]). The underground grass mass was measured with standard methods in soil monoliths at the root layer depth (1 or 2 m) separating large and small roots by diameter [15, 28, 29].

The annual growth of model trees in the Siberian elm crop determined by the difference between tree masses of the current and previous years in a closed five-year-old stand about 5.5 m tall with a trunk diameter of 10 cm and LAI of 7 has reached its maximum value by this age (Table 1). The annual production of the aboveground mass was quite high (28.3 t/ha) and many times greater than the underground mass (2.3 t/ha). Characteristically, the above-ground production is represented mainly by growth of trunk wood (20.3 t/ha). The leaf mass was 6.4 and 8 t/ha together with the annual shoots. The total aboveground and underground annual production in the elm crop was 30.6 t/ha. 3

The production and phytomass of the thirteenyear-old mixed tree/shrub community are somewhat different in structure. The annual growth of the aboveground phytomass (16.5 t/ha) is lower there than in the Siberian elm stand, and it is also formed mainly by growth of trunks and large branches (10 t/ha). However, the underground mass is much higher. It is 23.8 t/ha, of which 12.6 t/ha falls on thin roots of less than 1 mm. The leaf mass $(6.5 t/ha)$ is almost the same

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as in the elm stand. The total production of the aboveground phytomass and of the underground mass of thin roots is 29.1 t/ha, which is similar to that of the elm. The lower productivity of the aboveground phytomass of the tree-shrub community as compared to the Siberian elm stand (16.5 and 28.3 t/ha) may be because of the participation in this community of shrubs much of the mass of which is localized in the underground part like it is in grasses.

In the compared natural herbaceous grass–forb community, the total underground phytomass varied from 17.5 to 36.8 t/ha between 1950 and 1960 with its overwhelming part (15.7 to 29.9 t/ha) being thin roots (Table 1). The aboveground mass $(2.8 \text{ to } 4.2 \text{ t/ha})$ was many times inferior to the underground mass; their ratio varying between 1 : 6 and 1 : 13. The total aboveground production and underground mass of thin roots in the grass–forb community was 18.9 to 34.1 t/ha in different years.

The same amounts of production and phytomass in a similar steppe community were independently obtained in the neighboring Northern Caspian region located in the same climate and geomorphological conditions [30]. The aboveground mass of the meadow–steppe community varied there over 14 years of observations from 5.8 to 8.9 t/ha in dry and wet years and the underground mass was between 13.9 and 18.0 t/ha totaling 19.7 to 26.9 t/ha; i.e., it practically coincided with the above values at the Zhanybek Station. Likewise, the primary production in different herbaceous phytocenoses varied from 31.5 to 38.9 t/ha under similar conditions of the Azov steppes, the aboveground part producing 1.8 to 9.3 t/ha and the underground part 29–30.1 t/ha [31].

³ We made an updated calculation of the aboveground production values [26] based on the author's initial data $[22]$, so the value of annual production in our calculation (30.6 t/ha) differs from the original value in the source (22.8 t/ha).

Thus, the annual production of meadow–steppe grasslands (18.9 to 34.1 t/ha) in the above steppe region under optimum and identical growing conditions of trees and grasses differed little from the performance of trees and tree/shrub communities (29.1 to 30.6 t/ha). Thus, the annual production of meadow– steppe grasslands (18.9 to 34.1 t/ha) in the above steppe region under optimum and identical growing conditions of trees and grasses differed little from the performance of trees and tree/shrub communities (29.1 to 30.6 t/ha). Clearly, artificial forest and forest/shrub communities and natural herbaceous communities under the conditions most favorable for growth and in similar hydrothermal conditions produce a similar quantity of phytomass. It is noteworthy that the aboveground production values of the forest tree community (Siberian elm) and averaged values of the underground mass (thin roots) of the grass community are almost the same (28.3 and 23.5 t/ha). The underground mass of thin roots of the forest (elm) community and aboveground production of herbaceous communities (2.3 and 3.4 t/ha) were also low and relatively close. Thus, it turns out that the only difference is that organic production is localized in forest communities with considerable trunk mass mainly aboveground, while the production is shifted underground in grass communities as was pointed out above [32]. These data are consistent with the above-mentioned notions of more or less equal productivity of phytocenoses different in composition and structure but growing under the same conditions.

However, the estimate of the equal productivity of the compared communities in this case was obtained in arid climate conditions uncharacteristic of forests, which may have adversely affected their productivity and the comparison results. Now consider the productivity of both communities under natural growing conditions.

The productivity of natural forest and herbaceous communities. Widespread research in the second half of the 20th century into the biological productivity of natural systems under the International Biological Program (IBP) and the active study by soil scientists of the biological cycle in the soil–plant system, which was started at the same time, resulted in the active accumulation of quantitative productivity estimates $[1-3, 8, 33-35]$. Their sampling analysis has shown that the annual production in the zonal series of European forests different in composition (from forest– steppe oak woods to coniferous–broadleaf forests) varies from 4.4 to 24.9 t/ha (Table 2). The aboveground phytomass accounts for most of the annual growth $(2.1-18.3 \text{ t/ha})$, while the phytomass of roots is much less $(0.6–6.7 t/ha)$.

Annual production with the same range of fluctuations is noticeably higher than that of forests (8.3– 38.9 t/ha) in steppe and meadow–steppe phytocenoses located at the same geographic latitudes with similar natural conditions, the main part accounting for the underground mass (6.0 to 30.8 t/ha) and a smaller part (1.2 to 11.2 t/ha), for the aboveground mass (Table 3). Note that the large range of fluctuations in annual production was due to the heterogeneity of plant growth conditions in each geographical location. For example, low-productive forest stands on poor solonetzic soils (4.4 t/ha) and more productive upland oak woods (11.2 t/ha) on fertile dark-gray soils were in the same line (see Table 2) in the Tellerman Forest (Voronezh region) with overmature oak woods. The heterogeneity of production of forb–grass meadow–steppe vegetation in the Northern Caspian region (19.7 to 26.9 t/ha) with a soil moisture deficit characteristic of steppes was caused by variability of the atmospheric precipitation over the years; i.e., it related to the dynamics of moisture availability of plants (see Table 3).

This superiority of grass communities over forest communities is characteristic not only of temperate regions, but also of the boreal climate belt to the north with zonal taiga forests and dry meadows (Karelia, Leningrad oblast). The annual production of dry and floodplain meadows was 18.1 t/ha and did not drop below 10.7 t/ha there (see Table 3), while it did not exceed 9.1 t/ha in forest communities decreasing sometimes to 4.7 t/ha (see Table 2). Obviously, the productivity of natural forest ecosystems in all compared cases not only did not exceed the productivity of grass ecosystems, but was noticeably lower.

What were the reasons for these clear differences under an equal or close radiation regime and similar availability of moisture? The experts explain the lower production of the forest ecosystem compared to the meadow–steppe ecosystem in the Central Siberian Transect by possible underestimation of the share of the underground phytomass in the forests [1]. Indeed, it is usually recorded down to no more than 2 m. However, a significant proportion of roots (19.1 to 29.3%) was located deeper than 2 m in two soil trenches dug in the steppe climatic zone (Zhanybek Station) to a depth of 5 to 5.5 m in tree plantations [24]. Apparently, up to one-third of the root mass in tree (forest) plantations may be disregarded in conventional studies (to a depth of less than 2 m).

There must be another explanation for the lower potential production in the forests compared to steppes and meadows. It is the difference between organic mass consumption for the respiration of wood and herbaceous plant life-forms. According to calculations, the total consumption of organic carbon for respiration of goutweed–sedge oak forests of different ages (20 to 200 years) is 16 to 20 t/ha per year, which corresponds to 75% of the annual gross production of photosynthesis with 61% to 67% of this consumption accounting for the respiration of trunks [3, 42]. The respiration consumption is assumed to be under 50% in herbaceous cenoses, including steppe ecosystems,

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Table 2. The annual production of aboveground, underground, and total phytomass of forest communities under conditions of temperate and boreal latitudes of European Russia and neighboring regions (t/ha/year, dry weight)

Note: *foliage mass, **mass of sucking roots.

despite the increased underground organic mass. They varied between 39 and 60% [41] in the forb–grass meadow and dry steppes of Transbaikalia; i.e., they were noticeably lower than in the forests. It would seem that it is the large size of the skeletal (trunk) part in the aboveground mass of forest phytocenoses with their high respiration consumption that explains the lower potential production in forests. According to the latest data, however, up to 70–78% of the phytocenosis production is mineralized and is released into the atmosphere in the form of $CO₂$ [10] in the ecosystems of meadow and dry steppes, respectively, the consumption of organic matter for respiration in this case not being inferior to that of the forests.

The comparative data set out above are consistent with the assertions made at the beginning of this paper about the more or less equal productivity of plant communities different in their species composition but growing under the same conditions. In any case, grass communities, including steppe ones, are not only as productive as forest communities, but often surpass them. The variability of primary productivity is determined by hydrothermal characteristics of ecosystems and depends largely on two factors: moisture availability for plants and the radiation regime of the environment. That is why when moisture is sufficient an increase in productivity can be traced from the northern tundra ecosystems to the southern steppe ecosystems in line with the growth of the radiation regime. In this case, the same plant communities in different climatic belts differ from each other; in particular, the production of broadleaved forests in the subtropical belt is almost twice as high as in the subboreal belt [43]. At the same time, communities within the same climatic belt, different in composition and life-forms (grasslands and forests), are similar or tend towards some superiority of herbaceous productivity as can be seen from our comparison.

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Plant community and geographic coordinates	Total production, t/ha/year	Aboveground production, t/ha/year	Underground production, t/ha/year	Source
	Temperate Belt			
Khomutovskaya Steppe Reserve, meadow and steppe communities $(47^{\circ}17' \text{ N}, 38^{\circ}11' \text{ E})$	$31.5 - 38.9$	$1.8 - 9.3$	$29 - 30.1$	$[31]$
Meadow and steppe, Central Chernozem Reserve $(51°40' N, 36°20' E)$	20.9	6.5	14.4	[6]
Mikhailovskaya Virgin Land meadow-steppe $(50^{\circ}45' N, 34^{\circ}12' E)$	$9.8 - 12.8$	$3.8 - 4.8$	$6 - 8$	$[39]$
Grass-forb meadow-steppe, Northern Caspian region $(50^{\circ} N, 51^{\circ} E)$	$19.7 - 26.9$	$5.8 - 8.9$	$13.9 - 18$	$[30]$
Meadow-steppe (Central Chernozem Zone), 1972-1981 (51°40' N, 36°20' E)	$15.5 - 37.8$	$4.2 - 11.2$	$11.3 - 26.4$	$[7]$
Steppe-meadow of Ob oblast, 1982-1984. (54°38' N, 83°18' E)	$23.2 - 25.2$	$4.8 - 6.7$	$17.2 - 19.6$	$[7]$
Tyva Republic, meadow, true, dry, deserted steppes $(50^{\circ} N, 95^{\circ} E)$	$8.3 - 34.4$	$1.2 - 3.6$	$7.1 - 30.8$	$[40]$
Steppe-meadow of Transbaikalia $(51^{\circ}18' - 52^{\circ}71' N, 106^{\circ}29' - 111^{\circ}56' E)$	$14.1 - 24$	$1.2 - 5$	$12.2 - 19$	$[41]$
	Boreal Belt			
Floodplain meadows, Karelian Isthmus (61°07' N, 29°55' E)	18.1	11.8	6.4	$[34]$
Dry meadows, Onega Lake basin $(61^{\circ} N, 34^{\circ} E)$	10.7	4.2	6.5	$[1]$
Dry meadows, Leningrad oblast (60° N, 34° E)	14.1	3.7	10.4	$[1]$

Table 3. The annual production of aboveground, underground, and total phytomass of steppe and meadow communities in temperate and boreal latitudes of European Russia and neighboring regions (t/ha/year, dry weight)

Organic mass of forest and herbaceous ecosystems. The currently widespread view of forests as key regulators of biosphere (including climate) processes on land is based on their obvious superiority over meadows and steppes in plant mass accumulated in the aboveground part for many tens and hundreds of years in the form of trunk wood. Indeed, according to existing estimates, the plant biomass stocks in forest ecosystems of the European and Asian part of Russia from the northern taiga to the subtropical zones range from 100 to 400 t/ha while they are 10 to 20 t/ha in meadow and steppe ecosystems [8]. However, this comparative estimate does not take into account the important part of the organic material created and accumulated by grasses in the form of soil organic matter over many years too. Grass phytocenoses are not inferior to forests with their wood mass if we consider the soil organic mass created by grasses.

The organic mass formed by forests and grasslands, including soil organic matter, is practically the same. Organic carbon stocks in the taiga climate belt (Kostroma oblast) are actually estimated for meadow (grassland) and forest (spruce) ecosystems to vary (by maximum values) from 127 to 195 t/ha [44]. Likewise, in the forest–steppe climatic zone (Kursk oblast), these values in forest (broad-leaved) and meadow chernozem ecosystems vary just between 404 and 440 t/ha [44]. Thus, the grass and forest ecosystems are almost equal in terms of the organic matter created and accumulated there. The only difference is that most organic biomass in forest ecosystems is localized in the aboveground sphere (wood), while it is underground in meadow and steppe ecosystems.

Subsurface organic material of the soil is hidden from view and is not perceived as a substrate of biological (plant) origin, but it is owing to this material that the steppe ecosystems equal in the organic matter stocks the forest ecosystems together with their huge wood mass. Add to this the fact that steppe land enriched with soil organic matter is the most fertile earth and serves as an important breadbasket for the population together with farm crops grown thereon.

* * *

Going back to comparisons of the role of forest and grass ecosystems in climate change, the material thus presented confirms that the herbaceous ecosystems

are not inferior to forests in productivity and organic matter stocks and, consequently, in the activity of organic carbon fluxes between them and the atmosphere. Carbon sequestration by an ecosystem impacts the atmospheric $CO₂$ concentrations and is thought to affect the greenhouse effect and global climate processes. The synthesis of organic matter in grass and forest ecosystems (t/ha per year) is almost identical. Accordingly, the uptakes of $CO₂$ by the ecosystems are almost the same. The differences are only in the localization of organic production, being in the soil in one case and in the trunk mass in the other. As for $CO₂$ emissions from soils (carbon release to the atmosphere) as a result of root respiration and microbial decomposition of soil organic matter, the meadow ecosystem has recently been estimated to exceed noticeably those of the forest ecosystem [45]. However, in this particular case, the performance of the forest ecosystem must have been clearly greatly underestimated. This calculation did not take into account the respiration of the trunk mass in the forest stand. If we estimate carbon emissions from the entire ecosystem including not only soil respiration, but also the aboveground plant biomass (including trunks), these values are likely to become equal.

Thus, forests are far from being the only or even the main element responsible for biosphere processes on land. Grass ecosystems are no less and perhaps even more efficient in regulating the biosphere and climate processes. They are not inferior to forests and in many cases surpass them in their biomass and functional role. Certainly, grass ecosystems and steppes in particular deserve no less attention, protection, and maintenance of natural forms for their functioning.

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