The role of vertical structure in maintaining the stable functioning of meadow phytocenoses of the Middle Ob floodplain

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Abstract. The paper analyses the vertical structure of floodplain meadow communities of the Middle Ob and studies its association with yearly variations of weather conditions, soil regimes, and changes in the species composition of the grass stand. The vertical structure reflects the average annual conditions of floodplain ecotopes and is an adaptive mechanism for the stability of meadow phytocenoses during environmental dynamics.

1. Introduction
Sustainable functioning of biogeocenotic systems is complicated and comprises many aspects [1, 2, 3, 4]. Studying the regularities of the interaction between the vegetative community and its subsystems (species populations, ecological groups and life forms of plants) with environmental conditions and human impacts makes it possible to identify the mechanisms of sustainability and is necessary to solve the practical problems of protection, rational use, restoration of natural communities, and creation of artificial ones [5, 6, 7]. Herbal communities, and especially floodplain meadows, due to their ability to annually renew the above-ground organs [8], quickly respond to the change in various factors and are therefore convenient for studying adaptive mechanisms.

2. Material and methods
Stationary observations of meadow vegetation dynamics and alluvial-soil regimes were carried out in the Podobinsk key area of the Middle Ob floodplain (Tomsk Oblast) in 3 trial sites exhibiting various relief elements, altitude of floodplains, and types of alluvial soils. The mixed-fescue, sedge-bluegrass, soddy-sedge phytocenoses on the sod-meadow, meadow-marsh and marsh peat soils were studied. Synchronously, layer-by-layer temperature measurements and sampling of soils were done to determine the moisture content of nitrogen compounds available for plants, mobile phosphorus, and exchange potassium. The groundwater level was fixed. The flooding regime and weather conditions were taken into account using weather data and gauging stations. This allowed us to perform a complex analysis of the influence of flooding conditions, groundwater dynamics, and weather conditions on the hydration, food regimes of soils, and dynamics of grass stand [9]. The observation time was 7 years, which included extremely dry, extremely wet, and transitional years between them (table 1). The layered indices of soil regimes that were most contrasting years in terms of soil moisture (1983 and 1987), are given in table 2.
Analysis of fluctuations in phytocoenoses was done in accordance with herbage productivity indicators: the composition and ratio of the dominants; changes in the abundance and presence of other species; and the composition and relationship of ecological, biological, and biomorphological groups of species. The ecological groups were distinguished based on bioindication scales by L.G. Ramensky. The ecobiomorphs were characterized by the type of the morphostructure of their underground organs, vegetative mobility, life span, and life strategy. To determine the phytocoenotic indicators the method of accounting squares was used (accounting areas of 1 m$^2$ in a fivefold repetition). The selection of cuts was carried out during the flowering of most species.

Table 1. The alluvial soils’ regimes in the Podobinsk key area of the Middle Ob floodplain [10].

| Soil* | Flooding regime** | GWL, cm | RPM, mm | Soil temperature, °C | NH$^4$ | NO$^3$ | P$^{5}$O$^5$ | K$^0$ | mg/kg of soil | mg/100 g of soil |
|-------|-------------------|---------|---------|----------------------|--------|--------|-----------|-------|---------------|-----------------|
| ABP   | 1978-79-AH        | 40      | 78.4    | 12.9                 | 110.8  | 5.8    | 8.0       | 10.9  |
|       | 1980-83-PI        | 60      | 70.5    | 14.7                 | 52.3   | 4.7    | 6.2       | 13.1  |
|       | 1984-85-HH        | 25      | 99.5    | 16.8                 | 88.6   | 5.5    | 8.6       | 13.9  |
|       | 1986-88-HH        | 20      | 126.8   | 13.6                 | 112.2  | 1.2    | 8.4       | 14.5  |
|       | 1989-90-AH        | 65      | 91.2    | 15.5                 | 23     | 4.6    | 38        | 10.6  |
|       | 1991-HH           | 30      | 207.9   | 13.8                 | 97.8   | 2.2    | 9.7       | 7.7   |
|       | 1992-94-AH        | 20      | 77.8    | 15                   | 54.9   | 4.3    | 8         | 9.1   |
| AMB   | 1978-79-AH        | 60      | 49      | 15.6                 | 51.7   | 3.2    | 13.1      | 12.9  |
|       | 1980-83-PI        | 65      | 45      | 13                   | 14.5   | 7.6    | 6.7       | 9.7   |
|       | 1984-85-HH        | 50      | 88      | 15.8                 | 39.4   | 5.4    | 7.2       | 10.5  |
|       | 1986-88-HH        | 45      | 113.3   | 13.6                 | 40.3   | 4.2    | 8.1       | 10.8  |
|       | 1989-90-AH        | 90      | 47.5    | 14.9                 | 13     | 6.3    | 18.5      | 8.7   |
|       | 1991-92-AH        | 70      | 43.8    | 16.4                 | 48.7   | 2.9    | 12.6      | 11.2  |
|       | 1993-94-AH        | 75      | 34      | 17.9                 | 59     | 5.4    | 7.5       | 9.6   |
| ATM   | 1978-79-AH        | 120     | 37.3    | 15.8                 | 21.1   | 8      | 13.6      | 6.7   |
|       | 1980-83-PI        | 140     | 12.2    | 14.8                 | 12.3   | 2.1    | 10.7      | 7.2   |
|       | 1984-85-HH        | 120     | 52.4    | 14.6                 | 30.3   | 5.9    | 7.4       | 11.4  |
|       | 1986-88-HH        | 110     | 58.8    | 13.6                 | 28.1   | 4.7    | 8.4       | 12.2  |
|       | 1989-90-AH        | 140     | 15.2    | 15.8                 | 21.5   | 1.5    | 19.5      | 7.2   |
|       | 1991-92-AH        | 100     | 24.7    | 17.2                 | 9.5    | 1.2    | 11        | 5     |
|       | 1993-94-PI        | 100     | 11.7    | 17.3                 | 8.2    | 0.9    | 8.2       | 5.7   |

*ABP–alluvial bogpeat soil, AMB – alluvial meadow-bog soil, ATM – alluvial turf-meadow soil, GWL – ground water level, RPM – reserves of productive soil moisture

**PI – period of inundation, AH – average humidification period, HH – period of high humidity.

To study the vertical structure of the meadows excavations of the soil profile were done to the depth of propagation of the plants’ root systems, the roots and rhizomes were cleared from the soil so that their spatial disposition was not disturbed, then the structure of the root systems was fixed on millimeter paper.
Figure 1. The vertical structure of the meadow communities in the Podobinsk area of the Middle Ob floodplain:
A) mixed-fescue phytocenosis on alluvial turf-meadow soil
I, II, III – phytocoenogens; A.m. – Achillea millefolium, P.m. – Plantago media, T.o. – Taraxacum officinale, A.p. – Alopecurus pratensis, F.p. – Festuca pratensis, T.l. – Trifolium lupinaster, C.p. – Carex praeox, G.v. – Galium verum
B) soddy-sedge phytocenosis on alluvial bog peat soil
I, II–phytocoenogens; C.c. – Carex cespitosa, C.d. – Cnidium dubium, E.f. – Equisetum fluviatile, P.p. – Poa pratensis, T.o. – Taraxacum officinale
C) sedge-bluegrass phytocenosis on alluvial meadow-bog soil
I, II – phytocoenogens; C.c. – Carex cespitosa, Poa pratensis, A.g. – Agrostis gigantea, R.a. – Ranunculus acris, L.p. – Lathyrus palustris

Soil profile stratification was carried out on the root systems of plants, soil phytoocoenogens (rhizohorizons) were distinguished - layers of soil, characterized by the specificity of the roots of certain plant species – figure 1A, B, C.
Table 2. Thermal and water availability in the soil profile of the Podobinsky section of the Middle Ob floodplain in 1983 and 1987 [10].

| Layer, cm | Soil | Duration of the temperature period | Sum of temperatures | RPM, mm | AMR |
|-----------|------|-----------------------------------|---------------------|--------|-----|
|           |      | 10°C | 15°C | 10°C | 15°C |
| 0-10      | ABP  | 100  | 80   | 1,503 | 1,248 | 36.9 | 0.8  |
|           | AMB  | 92   | 67   | 1,527 | 1,050 | 25.6 | 0.7  |
|           | ATM  | 100  | 74   | 1,591 | 1,267 | 16.4 | 0.5  |
| 0-20      | ABP  | 94   | 74   | 1,532 | 1,201 | 83.9 | 1.0  |
|           | AMB  | 96   | 58   | 1,422 | 857   | 54.0 | 0.6  |
|           | ATM  | 92   | 73   | 1,490 | 1,105 | 27.5 | 0.5  |
| 0-30      | ABP  | 101  | 76   | 1,495 | 1,193 | 129.7| 0.5  |
|           | AMB  | 93   | 21   | 1,326 | 340   | 80.0 | 1.2  |
|           | ATM  | 97   | 52   | 1,431 | 826   | 41.5 |       |
| 0-60      | ABP  |      |      | 272.6 |       |      |      |
|           | AMB  |      |      | 185.2 |       |      |      |
|           | ATM  |      |      | 112.6 |       |      |      |
|           |      |      |      |       |       |      |      |
| 0-10      | ABP  | 105  | 55   | 1,745 | 1,095 | 58.4 | 1.3  |
|           | AMB  | 103  | 58   | 1,577 | 1,018 | 110.1| 2.0  |
|           | ATM  | 94   | 60   | 1,449 | 1,002 | 33.3 |       |
| 0-20      | ABP  | 106  | 53   | 1,570 | 902   | 119.3| 1.5  |
|           | AMB  | 103  | 52   | 1,521 | 896   | 158.7| 2.4  |
|           | ATM  | 90   | 40   | 1,346 | 650   | 54.7 | 1.1  |
| 0-30      | ABP  | 103  | 51   | 1,533 | 857   | 187.1|       |
|           | AMB  | 101  | 53   | 1,444 | 846   | 222.4|       |
|           | ATM  | 95   | 32   | 1,406 | 563   | 94.9 |       |
| 0-60      | ABP  |      |      | 297.5 |       |      |      |
|           | AMB  |      |      | 484.1 |       |      |      |
|           | ATM  |      |      | 162.5 |       |      |      |

Note. ABP – alluvial bogpeat soil, AMB – alluvial meadow-bog soil, ATM – alluvial turf-meadow soil, RPM – reserves of productive soil moisture, AMR – active moisture range.

3. Result and discussions

It was found that in different types of floodplain soils the active layer occupied by plant roots ranges from 80 cm in soddy-meadow light loamy soils to 30-40 cm in marsh peat and meadow-bog soils of heavy loamy soils. The number of rhizohorizons is also different: in the underground part of the herb-fescue community, three rhizohorizons are distinguished, and in the subterranean part of the sedge-bluegrass and soddy-sedge community there are two of them (figure 1A, B, C). The vertical profile of the soddy-sedge cenosis is characterized by mosaicism, due to the dominance of Carex cespitosa.

The vertical underground and above-ground layerage of the mixed herb-fescue phytocenosis on ATM is clearly seen. In the underground part the following rhizohorizons are distinguished: 1 – Achillea millefolium L. (0-5 cm), 2 – Festuca pratensis Huds.(5-20 cm), and 3 – Galium verum L. (20-80 cm). It is typical that the root systems of all phytocenosis cereals are confined to the upper rhizohorizons (figure 1A).

Sod-meadow soil in mixed dynamics is characterized by optimal and insufficient moistening, respectively, in communities of in which mesophytes and xeromesophytes predominate. With changes in the weather and flood conditions over the years, the moisture, temperature, and amount of plant nutrients in all soil horizons varies, particularly sharply in the surface ones (table 1, 2). The community's adaptability to these fluctuations is expressed by the fact that in all the rhizogrizones
there are the roots of ecologically different plants. Horizon *F. pratensis* (5-20 cm) has the regime of optimal moisture more often than the upper and lower parts of the root-inhabited stratum and is mainly formed by the mesophytes’ roots.

In community dynamics, the significance of biological groups of species (cereals, legumes, herbage) is clearly seen, which, in our opinion, contributes to the stability of the biogeochemical exchange of biogeocoenosis. The determining biogeochemical role of cereals is obvious, since this group dominates in the herbal phytocenoses, creating the main part of the above ground and underground phytomass. The herbage yields the maximum phytomass in the arid years, while a group of legumes does so in the transitional periods, when the content of nitrates increases in soils (table 1). Therefore, the plants from groups of herbs and legumes are the important components of the meadow community, as they contribute to its stability.

Smaller differences in species at the ecobiomorph level are also significant. During dry years, xeromesophyll herbs predominate in the grass stand, either with both superficial and deep rooting or only with deep rooting. The reason is that in different years the conditions optimal for absorbing moisture and nutrient elements are formed at particular depths. In this case there is no increase in the mass of more hygrophilous species, the roots of which are developed in the same horizon. This fact shows the reality of the physiological differences between the species belonging to one biome but to different ecological groups [11, 12].

The underground structure of the soddy-sedge phytocenosis on ABP is represented by rhizohorizons: bluegrass and sedge soddy (figure 1B). In the horizon of bluegrass (0-10 cm), the roots of mesophilous plants are predominantly distributed, but there are also rhizomes and roots of hygrophilous species (*Lisimachia vulgaris* L., *Caltha palustris* L., *Alisma plantago-aquatica* L.), which do not grow annually in the herbage. In the soddy sedge horizon (10-30 cm) the roots of other dominants of the community, *Agrostis gigantea* Roth., *Poa palustris* L., *Equisetum fluviatile* L., are located.

When the observations began the soil was moist and cold (table 1), and *C. cespitosa*, *A. gigantea*, and *E. fluviatile* dominated. Without flooding (1981–1983) the upper horizon was well heated, and its moisture content was low (table 2). Flooding years (1984–1985) provided an excess of moisture in all horizons. In subsequent years, the soil profile was excessively moistened, and there was a decrease in the mass of all species, which led to a decrease in the total grass mass.

In this dynamic, the most stable species was *C. cespitosa*, whose roots developed in all horizons, and the rhizomes form tufts on the soil surface. The mesophilous species, whose roots are distributed in the 0-10 cm layer, reached a high abundance in the years without flooding under optimal moisture conditions. The hydrophilic species, whose roots developed in the same horizon, were either not present in the herbage in those years, or had sharply reduced phytomass. They developed in the inundation years with excessive moisture. For the deep-rooted *E. fluviatile*, the years with optimum moisture in the lower soil layers were favorable.

If we consider the structure of the underground part of the soddy-sedge community to indicate the hydrothermal regimes of soils, we can note the following: 1. The confinement of the root systems of mesophilous plants exclusively to the 0-10 cm layer indicates that in ABP the optimum conditions for moistening, aeration and heat supply are possible only in the upper horizon, and possibly include its considerable desiccation. 2. The penetration of the roots of the more moisture-loving mesophytes into the 0-20-cm layer reflects a different hydrothermal situation, when the oscillation of conditions is less significant and the regime of mean, suboptimal moistening prevails. 3. The lower rhizohorizon is constantly excessively moistened and characterized by low heat supply; here the roots of hydrophilic species with a universal type of root system penetrate several horizons. 4. The maximum contrast of regimes is characteristic of an upper rhizohorizon, a high contrast – of a layer of 10-20 cm, the regime stability – of a layer of 20-40 cm.

The vertical structure of the sedge-bluegrass phytocenosis on AMB (figure 1C) is more uniform, since *C. cespitosa* here forms not tussocks, but tufts, 5-10 cm high and about 25 cm in diameter. Soddy sedge and bluegrass dominate, but in some years *Poa palustris* L., *Alopecurus pratensis* L. and
Carex acuta L. dominate. The root systems of mesophiulous species are concentrated in the soil layer of 0-15 cm (figure 1C); other plants’ roots penetrate into deep soil layers (up to 40 cm), but the main mass of the roots are in the layer up to 25 cm deep.

The difference between the environmental regimes of AMB and ABP soil consists, first, in the absence of clearly pronounced stratification of temperature and moisture changes. Changes in the hydrothermal parameters of the soil, connected with the dynamics of flooding and weather conditions, usually covers the entire profile, although at a depth of about 20 cm there is a limit to the change in regimes. Above this level, a sharp fluctuation of moisture can occur – from excessively humid to arid conditions. In the underlying horizon, the range of changes in the humidification state is from excess to optimum. Lack of moisture is observed in the absence of soil flooding for several years.

This may be the reason why the structure of the rhizohorizons of the sedge-bluegrass community is not clearly expressed; only the roots of mesophytes and poorly-established species from the group of xeromesophytes are definitely confined to the upper soil layer. The more moisture-loving eumesophytes and hydromesophytes in the cenosis maximally spread their underground organs in the upper rhizohorizon; however, their root systems happen to penetrate deeper. The inactive stems-root and short-stemmed herbs are not numerous in the community. Long-stemmed vegetatively mobile cereals and sedges of the most diverse ecological requirements (from xeromesophytes to aerohydrophytes) dominate.

Regimes of meadow-bog soils vary greatly from year to year, which probably determines the spread of plant species with different ecological and biological properties. Thus, in one rhizohorizon, the roots of P. pratensis and A. pratensis develop, but if the former predominates in dry years, when optimal and insufficient moisture are observed in the surface layer of soils, then the second one occurs during flooding, when the high humidity conditions in this horizon are combined with high temperatures. The abundance of A. gigantea decreases with lack of moisture, both in the upper and lower horizons. To develop sedges, excessive moisture and lower temperatures are necessary.

Since ammonification and nitrification processes intensify in the years without flooding, various mesophilic, nitratephylic grasses are widely spread in the herbage – Cirsium setosum Bess., Ranunculus acris L., Taraxacum officinale Wigg. Deterioration of soil aeration, with prolonged flooding of the cenosis for several consecutive years, leads to a high (toxic) ammonia nitrogen concentration (table 1). The hydrophilic sedges and marsh herbs become dominant, which confirms the idea of better adaptive ability of swamp sedges to use ammonium nitrogen for their development [13, 14].

Thus, the nature of constitutional and spatial (vertical) structure helps to understand the mechanisms of adaptation of plant communities to unfavorable environmental conditions. The composition and underground vertical layers of the meadow community are determined by the mean annual fluctuations of the hydrothermal and food conditions in certain soil layers and represent an adaptation to the range of their variation. The soil horizons are heterogeneous in their physical and biological properties. The phytocenosis responds to these conditions by selecting ecologically and biologically different plant species, as well as by the natural placement of their root systems in space. Vertical distribution of root systems along the soil profile carries the information about soil regimes and can be used for indication purposes.

The structural differences between the meadow phytocoenosis cover the functional differences. Morphologically distinct are the swamp and meadow-bog types of communities according to the presence of a coarse and turf form of sedge soddy, which reacts to excessive moistening and weak aeration of bog soils. From the meadow type of phytocoenosis, the absence of a longline of stem-root and short-stemmed herbage and the relatively small thickness of the root layer are no less distinct. The basic similarity between the dynamic processes of the swamp and meadow-bog types is reflected in the structure of soil phytocoenogens, when the root systems of mesophytes and aerohydrophytes are combined in the upper soil layer, but these groups of species develop in different years. Increased dynamics of the meadow-bog community compared to the marsh phytocoenosis is expressed in the predominance of vegetatively mobile forms.
The meadow type of phytocenosis differs more significantly. The communities of this type are characterized by a considerable thickness of the root-inhabited soil stratum and the presence of 3 or more rhizohorizons in the underground part. The maximum occupancy by the root systems and rhizomes of the upper rhizohorizons indicates the prevailing source of moisture and nutrients with precipitation.

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