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Structure of phytocenoses in beaver meadows in Lithuania

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The study presents data on the structure peculiarities of the beaver meadow phytocenoses. These meadows have been formed following the abandonment and consequent draining of beaver ponds approximately 10 years ago. Beaver meadow phytocenoses were compared with the plant communities of naturally flooded meadows in the Nemunas Delta and the Minija River valleys (West Lithuania).

Various phytocenoses are formed in beaver meadows, however, communities belonging to the *Poo palustris-Alopecuretum pratensis* association are the most frequent. Hygrophytes (*Carex* spp., *Equisetum* spp., *Poa palustris* and others) were dominating in the beaver meadows. In comparison with naturally flooded meadows, phytocenoses of beaver meadows are distinguished by the following peculiarities: 1) there are plenty of plant species tolerant to higher soil dampness, acidity and, slightly, to nutrition; 2) there are fewer plant species indifferent to the above soil features; 3) there are more dominant and subdominant species; 4) beaver meadows are distinguished by the richness of fewer plant species. Plant communities of beaver meadows have features characteristic of the early successive stages, and their features can be explained by specific habitat conditions, the most important of which seem to be the increased soil dampness, acidity and nutrition.

Key words: beaver meadows, naturally flooded meadows, phytocenoses structure, *Castor fiber*, Lithuania

INTRODUCTION

Beavers (*Castor fiber* and *C. canadensis*) are considered to be the keystone species in the shore ecosystems of the water bodies (Müller-Schwarze, Sun, 2003; Rosell et al., 2005). These mammals have a strong direct and indirect impact on plant communities (Barnes, Dribble, 1988; Bobrov, Chemeris, 2001; Ray et al., 2001). Firstly, beavers feed on grassy and woody vegetation. It is known that ca. 200 plant species form nutrition of the Eurasian beaver (Дъяков, 1975). Secondly, beavers' impact on phytocenoses is displayed indirectly when the environmental conditions are changed through the accumulation of biogenic substances in flood sediment, alteration in soil reaction and lighting (Wilde et al., 1950; Hodkinson, 1975; Naiman et al., 1988). These changes can improve growth conditions for some species, however, can worsen them for others.

Beaver impoundments are not a permanent phenomenon. Special habitats, the so-called "beaver meadows" (Ives, 1942), develop on the sites of floods when the beaver dams break down (or are artificially removed), and water drains out.

The present Eurasian beaver population in Lithuania started to develop around 50–60 years ago as a result of natural immigration and reintroduction (Prūsaitė, 1988). Beavers became especially abundant in Lithuania in the last decades. The average density of beaver population varied from 16.6 to 59.7 beaver settlements / 100 km^2 (Ulevičius, 1999). A big proportion of beaver ponds was found in small peripheral water bodies (Ulevičius, 1997), where beavers with their impoundments can especially strongly influence the structure of the adjacent phytocenoses.

Although beavers in Lithuania are widespread and densely inhabiting the landscape, their influence on plant communities in our country has never been studied. In other parts of the Eurasian beaver distribution range, exhaustive analyses of plant communities were done only in the European part of Russia (Evstigneev, Belyakov, 1997; Bobrov, Chemeris, 2001; Zavyalov et al., 2005). More of similar studies were carried out in North America (Ives, 1942; Donkor, Fryxell, 1999, 2000; Moore, 1999; McMaster, McMaster, 2000, 2001; Barnes, Malik, 2001; Ray et al., 2001; Wright et al., 2003), where Canadian beavers (*Castor canadensis*) are spread.

The aim of this work was to investigate the structure of the meadow phytocenoses which have developed instead of the former beaver impoundments and to compare them with structure of phytocenoses in the naturally flooded meadows.

MATERIALS AND METHODS

Investigations of meadow phytocenoses were carried out on the sites of abandoned beaver ponds in the Dvarupis River valley (56° 03' N, 21° 46' E) and in the Bartuva River valley (56° 06' N, 21° 49' E) in Plungė district (North-West Lithuania).

These research sites are located on the territory of the Žemaitija National Park or in its protection zone.

The highest precipitation (800 mm per year on average) is characteristic of this territory comparing to the rest of the country. Sometimes snow does not melt for a period exceeding a 100 days. The average temperature in January is −3 °C, and + 17 °C in July. The vegetation period in this area is shorter by 1–8 days than the average of Lithuania (Kulienė, Tomkus, 1990).

The hilly moraine landscape is characteristic of this territory. Soddy-podzolic soils dominate. The soils are strongly podzolic in the lower and damp parts of slopes. The soil temperature is low in wet dips because of big evaporation, the soil is usually badly aerated, has little microflora that mineralizes organic matter (Basalykas, 1977).

From the point of view of hydrology, the explored territory is a typical watershed territory, with high number of swampy plots and small streams. Most slopes of the river valleys are with springs (Mačiekus et al., 1999).

Phytocenoses of the abandoned beaver ponds were compared with phytocenoses of the naturally flooded meadows. These control investigations were carried out in the periodically flooded meadows of the Nemunas Delta (Šilutė district, West Lithuania; approximate coordinates: 55° 19' N, 21° 16' E; 55° 19' N, 21° 03' E; 55° 17' N, 21° 19' E), and the Minija River (Klaipėda district, West Lithuania; approximate coordinates: 55° 44' N, 21° 26' E; 55° 41' N, 21° 23' E; 55° 42' N, 21° 24' E). In the valleys of both rivers the main factor of soil pedogenesis is rich alluvial sediment settling following spring or summer floods. The meadows in the Nemunas Delta and the Minija River valleys are hayed and moderately pastured.

Phytocenoses in the abandoned beaver sites were investigated in June–July of 2005, while in the naturally flooded meadows, in June–July of 2002.

In the beaver meadows, 12 model plots were sampled (5 plots by the Dvarupis River and 7 by the Bartuva River). The size of the model plots was 15 × 15 m. The plots were chosen within a distance of 5–20 m from the main river watercourse (depending on the size of a former beaver impoundment). The distance between the model plots in the same river valley varied from 10 to 300 m. Beavers abandoned the investigated impoundments approximately 10 years ago.

In the naturally flooded meadows, 6 model plots (3 plots in the Nemunas Delta, 3 plots in the valley of Minija River) were sampled. These plots were chosen within 5–50 m from the main riverbed (depending on the size of the previously flooded area). Meadows were flooded in spring, ca. 3 months prior to the research.

The quantitative parameters of a species participation in a community were estimated using the De Vries method (Peeters, 1989; Skuodienė, 2004). 30 samples (handfuls of plants) were taken from every model plot and analysed. The location of samples in a model plot was chosen randomly.

The index of relative abundance was used in this work, where $P\%$ is relative abundance of species expressed in percent. The formula is as follows:

$$P\% = F\% / \Sigma F\% \times 100,$$

where $F\%$ is the frequency of occurrence of every species:

$$F\% = n/N \times 100,$$

where n is the number of handfuls, in which species were found; N is the total number of handfuls in a model plot; $\Sigma F\%$ is the sum of frequencies of occurrence of all the plant species in a model plot.

The data were analysed by using the prepared Microsoft Excel program package (Peeters, 1989). It gives indices that characterize the effect of environmental factors in a certain growing place (Peeters 1989; Skuodienė, Simonavičiūtė, 2004). Four of them are used in this work:

InH is the index of hydrotolerance, gained while counting the average hydrotolerance of all the plant species from a model plot. Hydrotolerance shows adaptation to damp conditions (the scale used ranges from 1 to 10, with 1 meaning species tolerating drought, and 10 expressing species that prefer dampness) (Ellenberg, 1992); InR is the index of plant adaptation to the acidity of soil, counted analogically (the scale used is from 1 to 5, with 1 meaning species that like acid soil, and 5 meaning species that prefer neutral soil reaction) (Ellenberg, 1992); InN is the index of plant adaptation to the nutrition of soil, first of all, to nitrogen (the scale used is from 1 to 5, with 1 meaning species that do not need nitrogen, and 5 representing species requiring a lot of nitrogen) (Ellenberg, 1992); CDD is the coefficient of dominance, counted while summing up the participation weight of all the species in handfuls from a model plot. CDD is higher if grassland has one or two dominating species (Skuodienė, 2004).

The names of plant species and higher taxones in Latin are presented using the Botanical Names Dictionary (Jankevičienė, 1998). Syntaxones have been described by applying blocks of diagnostic species (Балявичене, 1991; Rašomavičius, 1998). In phytocenoses, characteristic, differential, dominant ($36 < P\% \leq 64$) and subdominant ($16 < P\% \leq 36$) species were distinguished by their relative abundance using the Lubarski scale (Баканов, 1987). Similarity of phytocenoses was estimated using the Sörensen coefficient (Cs) (Мэгурран, 1992).

RESULTS

1. Syntaxonomical characteristics of phytocenoses

Various phytocenoses have developed in beaver meadows in the Dvarupis and Bartuva Rivers valleys (Table 1). Plant communities belonging to the *Poo palustris-Alopecuretum pratensis* association (4 beaver meadows) were identified most frequently. In comparison with other communities, the *Poo palustris-Alopecuretum pratensis* association is characterized by more damp habitats belonging to Cl. *Molinio-Arrhenatheretea elatioris*, which include mesophyte and wet meadow phytocenoses with the prevalence of hygrophytes.

Phytocenoses belonging to dryer habitat associations (*Festucetum pratensis, Festuco-Cynosuretum cristati, Caricetum distichae, Alopecuretum pratensis*) have formed in the Minija River valley and the Nemunas Delta flooded meadows.

More dominant and subdominant species were identified in the beaver meadows than in the flooded meadows (Table 1). The dominance coefficient in the beaver meadows varied from 0.94 in the *Junco-Molienetum caeruleae* association to 6.29 in the *Poo palustris-Alopecuretum pratensis* association. Dominant

Table 1. **Syntaxonomical description of phytocenoses in the beaver meadows and the naturally flooded meadows. P% is relative abundance; CDD is the coefficient of dominance**

Study site	Syntaxones	Characteristic (Ch), differential (Df), dominant (D), and subdominant (SD) species	P%	CDD
Dvarupis beaver meadows	Cl. *Phragmitetea australis* Klika 1941 O. *Magnocaricetalia elatae* Pignatti (1953) 1954 All. *Magnocaricion elatae* Koch 1926 Ass. *Caricetum rostratae* Osvald 1923	*Carex rostrata* Stokes – (Ch, SD) *Phalaroides arundinacea* L. Rauschert – (Ch)	23.7 1.0	1.49
	Cl. *Molinio-Arrhenatheretea elatioris* R. Tx. 1937 O. *Molinietalia caeruleae*.Koch 1926 All. *Molinion caeruleae* Koch 1926 Ass. *Junco-Molinietum caeruleae* Preising in R.Tx. et Preising 1951	*Juncus effusus* L. – (Df) *Juncus conlgomeratus* L. – (Df) *Equisetum palustre* L. – (SD)	9.8 8.2 18.0	0.94
	Cl. *Molinio-Arrhenatheretea elatioris* R. Tx. 1937 O. *Molinietalia caeruleae* Koch 1926 All. *Alopecurion pratensis* Passarge 1964 Ass. *Poo palustris-Alopecuretum pratensis* Shelyag-Sosonko et al. 1985	*Poa palustris* L. – (Ch) *Phalaroides arundinacea* L. Rauschert – (Df, D)	3.9 56.9	6.29
	Cl. *Molinio-Arrhenatheretea elatioris* R. Tx. 1937 O. *Molinietalia caeruleae* Koch 1926 All. *Calthion palustris* R. Tx. 1937 em. Lebrun et al. 1949 Ass. *Scirpetum sylvatici* Ralski 1931	*Scirpus sylvaticus* L. – (Ch, SD) *Lathyrus pratensis* L. – (SD)	22.7 17.3	2.57
	Cl. *Scheuchzerio-Caricetea nigrae* (Nordhagen 1936) R. Tx.1937 O. *Caricetalia nigrae* Koch 1926 All. *Caricion nigrae* Koch 1926 em. Klika 1934 Ass. *Caricetum nigrae* Br.-Bl.1915	*Agrostis canina* L. – (Ch) *Carex nigra* L. Reichard – (Ch) *Equisetum palustre* L. – (SD) *Equisetum fluviatile* L. – (SD)	1.0 11.2 19.4 16.3	1.51
Bartuva beaver meadows	Cl. *Molinio-Arrhenatheretea elatioris* R. Tx. 1937 O. *Molinietalia caeruleae* Koch 1926 All. *Alopecurion pratensis* Passarge 1964 Ass. *Poo palustris-Alopecuretum pratensis* Shelyag-Sosonko et al. 1985	*Poa palustris* L. – (Ch, SD) *Galium palustre* L. – (Df, SD) *Phalaroides arundinacea* L. Rauschert – (Df) *Stellaria palustris* Retz. – (Df) *Juncus effusus* L. – (SD)	35.0 31.7 3.3 13.3 17.9	4.63
	Cl. *Molinio-Arrhenatheretea elatioris* R. Tx. 1937 O. *Molinietalia caeruleae* Koch 1926 All. *Calthion palustris* R. Tx. 1937 em. Lebrun et al. 1949 Ass. *Deschampsietum cespitosae* Horvatic 1930	*Deschampsia cespitosa* (L.) P. Beauv. – (Ch, SD) *Poa pratensis* L. – (Ch) *Poa trivialis* L. – (Ch) *Ranunculus acris* L. – (Ch, SD)	21.7 5.0 5.0 28.3	2.81
	Cl. *Galio-Urticetea* Passarge ex Kopecký 1969 O. *Lamio-Chenopodietalia boni-henrici* Kopecký 1969 All. *Aegopodion podagrariae* R. Tx. 1967 Ass. *Urticetum dioicae* O.Bolòs 1959	*Anthriscus sylvestris* (L.) Hoffm. – (Ch, SD) *Urtica dioica* L. – (Ch, SD)	17.1 21.4	3.12
	Cl. *Phragmitetea australis* Klika 1941 O. *Magnocaricetalia elatae* Pignatti (1953) 1954 All. *Magnocaricion elatae* Koch 1926 Ass. *Caricetum rostratae* Osvald 1923	*Phalaroides arundinacea* L. Rauschert – (Ch) *Carex rostrata* Stokes – (Ch) *Equisetum palustre* L. – (SD)	1.0 10.7 25.2	1.29
Minija flooded meadows	Cl. *Molinio-Arrhenatheretea elatioris* R. Tx. 1937 O. *Arrhenatheretalia elatioris* Pawłowski 1928 All. *Arrhenatheretion elatioris* (Br.-Bl.1925) Koch 1926 Ass. *Festucetum pratensis* Soó 1938	*Festuca pratensis* Huds. – (Ch) *Poa pratensis* L. – (Ch) *Ranunculus acris* L. – (Ch) *Phleum pretense* L. – (Ch) *Trifolium pretense* L. – (Ch)	8.3 4.5 9.8 1.5 0.8	0.80
	Cl. *Molinio-Arrhenatheretea elatioris* R. Tx. 1937 O. *Arrhenatheretalia elatioris* (Br.-Bl.1925) Koch 1926 All. *Cynosurion cristati* R. Tx. 1947 Ass. *Festuco-Cynosuretum cristati* R.Tx. in Büker 1942	*Agrostis tenuis* Sibth. – (Ch) *Anthoxanthum odoratum* L. – (Ch) *Leontodon autumnalis* L. – (Ch) *Cynosurus cristatus* L. – (Ch) *Festuca pratensis* Huds. – (Ch)	7.7 5.8 1.0 1.0 7.7	1.29

Table 1 (continued)

Nemunas Delta flooded meadows	Cl. *Phragmitetea australis* Klika 1941 O. *Magnocaricetalia elatae* Pignatti (1953) 1954 All. *Magnocaricion elatae* Koch 1926 Ass. *Caricetum distichae* Nowinski 1928	*Carex disticha* Huds – (Ch, SD) *Phalaroides arundinacea* L. Rauschert – (Ch, SD)	27.2 23.3	1.34
	Cl. *Molinio-Arrhenatheretae elatioris* R. Tx. 1937 O. *Molinietalia caeruleae* Koch 1926 All. *Alopecurion pratensis* Passarge 1964 Ass. *Alopecuretum pratensis* Regel 1925	*Veronica longifolia* L. – (Ch) *Alopecurus pratensis* L. – (Ch, SD) *Poa palustris* L. – (Ch) *Bromus inermis* Leyss. – (Ch) *Symphytum officinale* L. – (Ch)	0.7 18.2 3.4 3.2 0.8	3.59

or subdominant species were not found in the Minija River valley. In phytocenoses of the Nemunas Delta flooded meadows, three subdominant species were found. The dominance coefficient in the flooded meadows varied from 0.80 in the *Festucetum pratensis* association to 3.59 in the *Alopecuretum pratensis* association.

2. Structure of species and similarity of plant communities

There were fewer vascular plants species registered in the beaver meadow phytocenoses than in the Minija River flooded meadow phytocenoses, though the higher taxa number was only slightly different compared to all the studied sites. The number of plant species in the Nemunas Delta flooded meadows was similar to that in the beaver meadows (Table 2).

In the Dvarupis beaver meadows, 46 species of vascular plants were found. Here, the largest species number was characteristic of the *Poaceae* (9 species) and *Cyperaceae* (7 species) families. Among genera, *Carex* (5 species: *Carex rostrata, Carex acutiniformis, Carex nigra, Carex flava, Carex hirta*) and *Equisetum* (4 species: *Equisetum palustre, Equisetum fluviatile, Equisetum variegatum, Equisetum hyemale*) were distinguished by higher species diversity.

In the Bartuva beaver meadows, flora of vascular plants included 47 species. Similarly (like in the Dvarupis), families *Poaceae* (14 species) and *Cyperaceae* (8 species), genera *Carex* (6 species: *Carex cinerea, Carex rostrata, Carex acutiniformis, Carex acuta, Carex distans, Carex paniculata*), and *Poa* (4 species: *Poa palustris, Poa trivialis, Poa*

Table 2. **Presence (+) and the total number of plant species in the beaver meadows and the naturally flooded meadows**

Species	Dvarupis beaver meadows	Bartuva beaver meadows	Minija flooded meadows	Nemuno Delta flooded meadows
Family **Equisetaceae**				
Equisetum palustre	+	+	+	
Equisetum fluviatile	+	+		
Equisetum variegatum	+			
Equisetum hyemale	+			
Equisetum arvense			+	
Family **Ranunculaceae**				
Ranunculus acris		+	+	+
Ranunculus repens	+	+		+
Ranunculus flammula	+			
Family **Caryophyllaceae**				
Stellaria palustris	+	+	+	+
Stellaria graminea			+	
Lychnis flos-cuculi	+	+	+	+
Saponaria officinalis			+	
Family **Polygonaceae**				
Rumex aquaticus	+			
Rumex acetosa		+		+
Rumex acetosella			+	
Polygonum bistorta			+	+
Polygonum aviculare				+
Polygonum persicaria				+
Family **Primulaceae**				
Lysimachia vulgaris	+			
Lysimachia nummularia			+	+
Family **Brassicaceae**				
Cardamine pratensis				+
Erysimum cheiranthoides				+

Table 2 (continued)

Rorippa palustris				+
Family **Urticaceae**				
Urtica dioica	+	+		
Family **Rosaceae**				
Potentilla palustris		+		
Potentilla erecta			+	+
Geum rivale	+	+		
Filipendula ulmaria	+			
Fragaria vesca			+	
Alchemilla xanthochlora			+	
Family **Lythraceae**				
Lythrum salicaria				+
Family **Fabaceae**				
Trifolium repens			+	+
Trifolium pratense			+	
Trifolium dubium			+	
Lathyrus pratensis	+	+	+	+
Vicia cracca	+		+	+
Vicia sepium			+	
Anthyllis vulneraria			+	
Medicago falcata			+	
Lotus corniculatus			+	
Family **Geraniaceae**				
Geranium palustre		+	+	
Family **Apiaceae**				
Anthriscus sylvestris	+	+	+	+
Aegopodium podagraria			+	+
Family **Dipsacaceae**				
Knautia arvensis			+	
Family **Rubiaceae**				
Galium palustre	+	+		+
Galium uliginosum	+	+		
Galium boreale	+			
Galium aparine			+	+
Galium album	+		+	
Galium elongatum	+			
Galium mollugo			+	
Galium verum				+
Family **Convolvulaceae**				
Convolvulus arvensis			+	
Calystegia sepium				+
Family **Boraginaceae**				
Myosostis scorpioides	+	+		
Myosostis caespitosa	+	+	+	
Myosostis palustris				+
Symphytum officinale				+
Family **Scrophulariaceae**				
Veronica longifolia			+	+
Veronica chamaedrys		+	+	+
Rhinanthus serotinus				+
Family **Plantaginaceae**				
Plantago major			+	
Plantago lanceaolata			+	+
Family **Lamiaceae**				
Scutellaria galericulata	+	+		
Mentha arvensis	+			

Table 2 (continued)

Prunella vulgaris			+	
Glechoma hederacea				+
Family **Asteraceae**				
Cirsium palustre	+	+		
Cirsium arvense			+	
Crepis paludosa		+		
Crepis mollis		+	+	
Achillea millefolium			+	
Achillea cartilaginea				+
Leucanthemum vulgare			+	
Taraxacum officinale			+	+
Leontodon autumnalis			+	+
Centaurea scabiosa			+	
Tanacetum vulgare			+	+
Family **Alismataceae**				
Alisma plantago-aquatica	+			
Family **Alliaceae**				
Allium vineale			+	
Family **Juncaceae**				
Juncus effusus	+	+	+	
Juncus conglomeratus	+	+		
Juncus articulatus	+		+	
Juncus-alpino-articulatus			+	
Luzula campestris		+		
Family **Cyperaceae**				
Carex cinerea		+		
Carex rostrata	+	+		
Carex disticha			+	+
Carex acutiformis	+	+		
Carex acuta		+		
Carex distans		+		
Carex nigra	+			
Carex hirta	+			
Carex flava	+			
Carex paniculata		+		
Scirpus sylvaticus	+	+	+	
Eriophorum angustifolium	+			
Eleocharis palustris		+		
Family **Poaceae**				
Elytrigia repens			+	+
Poa palustris	+	+		+
Poa trivialis		+	+	
Poa pratensis		+	+	+
Poa nemoralis		+		
Phalaroides arundinacea	+	+	+	+
Deschampsia cespitosa	+	+	+	+
Alopecurus pratensis		+	+	+
Bromopsis inermis		+	+	+
Festuca rubra	+	+		
Festuca pratensis		+	+	+
Helictotrichon pratense		+	+	
Helictotrichon pubescens			+	
Molinia caerulea		+		
Glyceria fluitans	+			
Glyceria maxima		+		
Calamagrostis epigeios	+			

Table 2 (continued)

Calamagrostis neglecta		+		
Agrostis stolonifera	+		+	+
Agrostis canina	+		+	
Agrostis tenuis			+	
Phleum pratense	+		+	+
Dactylis glomerata			+	
Holcus lanatus			+	
Anthoxanthum odoratum			+	
Cynosurus cristatus			+	
Briza media			+	
Total number of species	46	47	69	45

pratensis, Poa nemoralis) were distinguished by the highest species number.

The flora of vascular plants in the Minija River flooded meadow phytocenoses was represented by 69 species. The highest number of species was characteristic of genera *Agrostis* (3 species), *Juncus* (3 species), *Trifolium* (3 species) and *Galium* (3 species). Only 45 plant species were found in the Nemunas Delta flooded meadows, where genus *Galium* had the highest number of species (3 species).

When tested on the subject of phytocenoses similarity, the Dvarupis and Bartuva beaver meadows (coefficient of similarity, Cs = 0.52) formed one cluster, while the Minija River and the Nemunas Delta flooded meadows (Cs = 0.51) formed another one. Lower coefficients of phytocenoses similarity were estimated when the beaver meadows were compared with the flooded meadows (Cs = 0.26 to 0.35) (Table 3).

3. Variety of ecological groups of plant species

By the ecological spectrum, the majority of flora growing in the Dvarupis and Bartuva beaver meadows belong to plants of moistened or damp ecotops. Hygrophytes (such as *Equisetum fluviatile, Glyceria fluitans, Carex nigra, Glyceria maxima, Poa palustris* etc.) and hygromesophytes (such as *Equisetum palustre, Phalaroides arundinacea, Deschampsia cespitosa, Geum rivale, Filipendula ulmaria*) were prevailing in the beaver meadows studied while mesophytes (such as *Poa trivialis, Agrostis stolonifera, Phleum pratense, Plantago major, Alchemilla xanthochlora*) were dominating in the naturally flooded meadow phytocenoses (Table 4). The index of hydrotolerance was higher in the beaver meadows (mean InH = 8.22, and 7.86 in the Dvarupis and Bartuva, respectively), than in the Nemunas Delta (mean InH = 7.09) and the Minija River (mean InH = 2.76) flooded meadows. In the beaver meadows, there

Table 3. **Similarity (by Sörensen's Cs) of plant communities in the studied meadows**

Studied meadows	Bartuva beaver meadows	Minija flooded meadows	Nemunas Delta flooded meadows
Dvarupis beaver meadows	0.52	0.26	0.26
Bartuva beaver meadows	–	0.33	0.35
Minija flooded meadows	–	–	0.51

Table 4. **Distribution of plant species (in % of relative abundance) by ecological groups according to adaptation to soil dampness and the index of species hydrotolerance (InH) in the beaver meadows and the flooded meadows**

Study site	No. of model plots	Ecological groups according to adaptation to soil dampness					Mean InH (min-max)
		Xeromesophytes	Mesophytes	Hygromesophytes	Hygrophytes	Indifferent species	
Dvarupis beaver meadows	5	–	19.5	41.3	37.0	2.2	8.22 (7.32–8.84)
Bartuva beaver meadows	7	6.4	25.5	34.0	32.0	2.1	7.86 (6.66–8.74)
Minija flooded meadows	3	23.2	39.1	17.4	7.3	13.0	5.08 (4.32–6.17)
Nemunas Delta flooded meadows	3	9.1	45.5	25.0	9.1	11.3	7.09 (6.52–8.17)

Table 5. **Distribution of plant species (in % of relative abundance) by ecological groups from the viewpoint of soil reaction and the index of soil acidity (InR) in the beaver meadows and the flooded meadows**

Study site	No. of model plots	Ecological groups according to adaptation to soil reaction						Mean InR (min-max)
		Highly acid	Acid	Moderately acid	Slightly acid	Neutral	Indifferent species	
Dvarupis beaver meadows	5	–	23.9	4.4	26.1	–	45.6	1.77 (0.74–2.88)
Bartuva beaver meadows	7	–	21.3	12.8	23.3	–	42.6	1.80 (1.18–2.80)
Minija flooded meadows	3	1.5	8.7	11.6	26.1	1.5	66.7	1.61 (1.42–1.85)
Nemunas Delta flooded meadows	3	–	2.2	11.4	29.6	–	66.8	2.45 (2.22–2.85)

Table 6. **Distribution of plant species (in % of relative abundance) by ecological groups from the viewpoint of soil nutrition and the index of soil nutrition (InN) in the beaver meadows and the flooded meadows**

Research site	No. of model plots	Ecological groups according to adaptation to soil nutrition						Mean InN (min–max)
		Oligotrophic plants	Oligomesotrophic plants	Mesotrophic plants	Eutromesotrophic plants	Eutrophic plants	Indifferent species	
Dvarupis beaver meadows	5	21.7	19.6	26.1	19.6	2.2	10.8	2.91 (2.28–3.75)
Bartuva beaver meadows	7	14.9	25.5	25.5	17.0	4.3	12.8	3.10 (2.37–3.60)
Minija flooded meadows	3	13.0	21.7	30.5	17.4	–	17.4	2.76 (2.75–2.77)
Nemunas Delta flooded meadows	3	6.8	6.8	34.1	29.5	2.3	20.5	3.14 (3.07–3.19)

were fewer species indifferent to dampness found than in the flooded meadows.

In the Dvarupis and Bartuva beaver meadows, there mostly grew plants that were adapted to slightly acid (*Poa palustris, Phalaroides arundinacea, Festuca rubra, Vicia cracca, Bromopsis inermis*) and acid (*Deschampsia cespitosa, Carex nigra, Stellaria palustris, Luzula campestris*) soil reaction. Much fewer plants adapted to grow in acid soil (*Deschampsia cespitosa, Agrostis tenuis, Briza media, Galium aparine, Potentilla erecta*) were found in the flooded meadows. In the beaver meadows there were fewer plants that were indifferent to soil reaction than in the flooded meadows. There were no considerable differences between the beaver meadows and the flooded meadows when comparing the index of soil reaction (InR) (Table 5).

In the beaver meadows, the most abundant species preferring soils of moderate nutrition, mesotrophic plants (*Equisetum fluviatile, Deschampsia cespitosa, Glyceria fluitans, Juncus effuses, Galium palustre*), were dominant. The situation in this respect was similar to the one in the flooded meadows, however, dominance of mesotrophic plants here was more conspicuous than in the beaver meadows where the ecological groups were distributed more evenly. Despite low proportion of eutrophic plants in all the studied sites, they were comparatively more abundant in the beaver meadows (*Urtica dioica, Poa trivialis, Glyceria maxima*). The index of soil nutrition (InN) was more variable, and the upper limits of this index were higher in the beaver meadows, especially when comparing with the one in the Minija River flooded meadows. In the beaver meadows, there were relatively fewer abundant plants indifferent to soil nutrition (Table 6).

DISCUSSION

The beaver meadows differed from the flooded meadows by most of the parameters studied. Uneven environmental conditions and succession levels could predetermine these differences. One of the main factors can be the fact that beaver meadows are not affected by the periodical seasonal floods which are very common in the valleys of large rivers, especially in the Nemunas Delta flooded meadows.

Floods are usually short in time in the Minija River valley and they form very favourable conditions for meadow plants after the floods subside. Thus, the flooded meadow phytocenoses were adapted to such conditions during a long time. Floods of moderate frequency increase the diversity of meadow species while very frequent and rarely repeating but long lasting floods diminish the diversity (Pollock et al., 1998; Gipiškis, unpubl.). A relatively low diversity of plant species in the Nemunas Delta flooded meadows might be determined by long lasting floods that act depressively on certain species of grassy vegetation (Gipiškis, unpubl.). Probably because of that, the Nemunas Delta flooded meadows are closer to beaver meadows by the majority of parameters studied. The highest richness of plant species (30–40 species) was detected in the Minija flooded meadows where floods last considerably shorter than in the Nemunas Delta.

The beaver meadows started to develop when beaver impoundments were drained out, in our case, approximately 10 years ago. According to some authors (Evstigneev, Belyakov, 1997), the beaver impact on phytocenoses is divided into the three temporal stages: 1) a stage of active beaver pond with high water level and dominance of hydrophytes lasting approximately up to 10 years; 2) a stage of abandoned beaver pond and formation of beaver meadow in loco of former pond (from 10 to 30 years); 3) a forest stage in loco of former pond (30 and more years). Our data represent the second (the beaver meadow) stage. In this stage edaphic factors, such as soil dampness, reaction, nutrition and others, are probably very important to meadow phytocenoses succession. It is characteristic of the beaver meadow soils to have higher soil dampness and thicker upper O and A horizons, where large amounts of organic substances are accumulated (Johnston et al., 1995).

A relatively small number of species in the beaver meadows can be conditioned by great dampness that the majority of the meadow plant species cannot tolerate. In the beaver meadows studied, species that are well adapted to high dampness of soil were prevailing. This is shown by a higher index of hydrotolerance than in the flooded meadows (except the Nemunas Delta, where the flooding conditions are especial as discussed above), and in addition, by the domination of hygromesophytes and hygrophytes in the beaver meadow phytocenoses. In this respect, the ecological structure of flora of the beaver meadows seems to be similar, at least across Central and Eastern Europe, because the domination of hygrophytes and hygromesophytes in the beaver meadow phytocenoses was identified in the Darwin Reserve in Russia (Zavyalov et al., 2005). Soil dampness was one of the basic factors that determined the number of species and the structure of communities in the beaver meadows in some sites in North America: in more drained meadows the diversity of plant species was usually higher than that in the less drained meadows (McMaster, McMaster, 2001; Wright et al., 2003).

The beaver impoundment is considered to be an open ecosystem in which energy and substances metabolism balance is positive because energy and nutrients here are more accumulated than the utilized or exported ones (Hodkinson, 1975; Naiman, Melillo, 1984; Meentemeyer, Butler, 1999; Correll et al., 2000). More appropriate conditions for mineralization of the accumulated organic substances establish when the beaver impoundments are drained out, thus, soils of the beaver meadows should be rich in nutrients, including nitrogen. Moreover, nitrogen is fixed by bacteria living in the impoundment sediments, consequently, some sites, inhabited by beavers, can accumulate a 100 times more nitrogen than the same sites prior to beavers' settling (Naiman, Melillo, 1984). However, mineralization might be slow in the beaver meadows because of high dampness of soil, which is also enhanced by high capacity of organic substances to hold water.

Our research did not reveal any distinct differences between the beaver meadows and the flooded meadows while analysing the ecological structure of communities with respect to soil nutrition. However, eutrophic species were found to be slightly more abundant in the beaver meadows, the variation range of the index of soil nutrition was also higher compared to the flooded meadows (InN = 2.28–3.75 and InN = 2.75–3.19, respectively). This shows that species of wide ecological spectrum, i.e. preferring both poor soil and rich soil, can grow in the beaver meadows. A research carried out in North America showed that the number of plant species in the beaver meadows can negatively correlate with the amount of soil nitrogen (Wright et al., 2003), but, in our case, this factor could hardly influence the smaller amount of species in the beaver meadows (e. g., more than soil dampness) than in the Minija flooded meadows.

The impact of soil nutrition on species diversity could be diminished by higher acidity of wet soils in the beaver meadows. In such conditions, consumption of biogenic substances by plants of the most species is limited. The majority of meadow plants can grow normally in soils of different pH, but the maximum biomass of a species in a phytocenose can be realized only in the soil with optimal pH (Rimkus, 2003). Our results reveal conditions of relatively high soil acidity in the beaver meadows. Higher proportion (than in the flooded meadows) of plants in the beaver meadows were adapted to grow in acid soil, and the minimal index of soil acidity in the beaver meadows (InR_{min} = 0.74) was as much as twice lower than that in the flooded meadows (InR_{min} = 1.42). This indicates high tolerance of plants, growing in the beaver meadows, to acid soils.

Dominant and subdominant species that were more characteristic of the beaver meadows than of the flooded ones also demonstrate specific conditions of the phytocenoses studied. The beaver meadow subdominants *Carex rostrata*, *Scirpus* *sylvaticus*, *Equisetum palustre* are indicators of standing surface water and a high level of ground water. Very little air gets to such a wet soil. In these conditions, plants can grow because there are air pathways in their stems and roots, through which the air-born oxygen can get to the soil and provide appropriate conditions around the plant roots for the decomposition of aerobic bacteria. This is the way in which biogenic substance preserved in organic compounds becomes available for these plants, and they can grow in sites where other plants can not (Petkevičius, 1993). Another subdominant species of the beaver meadows – *Poa palustris* – is good at competing because this species is highly resistant to dampness, it grows well in acid (pH = 5) soils (Petkevičius, 1993). *Deschampsia caespitosa* is a tall, long living grass which forms mycorrhize in its thick roots. Plants that form mycorrhize can grow in wetter and more acid soils. Fungi settled in their roots help decompose organic substances (Petkevičius, Stanevičius, 1982).

Specific habitat conditions in the beaver meadows are also characterized by some other indices. In comparison with the flooded meadows, there were fewer abundant species indifferent to soil dampness, reaction and nutrition in the beaver meadows. Although the fact that there were phytocenoses identified in the beaver meadows belonging to different associations, the coefficient of similarity among them was defined to be higher than comparing the beaver meadows with the flooded ones. This shows that both beaver and flooded meadows have specific flora.

A relatively small diversity of plant species in the beaver meadows should not form a wrong opinion about the negative impact of beavers to plant diversity on the landscape scale. Our study was conducted just on a local scale, i.e. it was limited by separate spots on the landscape. Within these spots, phytocenoses are influenced by specific factors that might be considerably less important in other places (Wright et al., 2002). Beavers create higher biotope diversity by their activity, thus, it is logical to expect flora diversity growth on the landscape scale (Evstigneev, Belyakov, 1997; Wright et al., 2002, 2003; Rosell et al., 2005). A relatively small diversity of plant species in the beaver meadows could be predetermined by temporal limitation of our research, which actually represents beaver ponds abandoned ca.10 years ago. There are data to the effect that the duration of existence of beaver sites is an important factor in the diversity of plants (McMaster, McMaster, 2000, 2001; Wright et al., 2003).

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FITOCENOZIŲ STRUKTŪRA BEBRŲ PIEVOSE LIETUVOJE

Santrauka
Straipsnyje pateikiama duomenų apie bebrų pievų, kurios pradėjo formuotis maždaug prieš 10 metų nuleistų bebrų patvankų vietose, fitocenozių struktūros ypatybes. Bebrų pievų fitocenozės buvo lyginamos su Nemuno deltos ir Minijos upės slėnių natūralių užliejamų pievų augalų bendrijomis.

Bebrų pievose formuojasi įvairios fitocenozės, tačiau dažniausios buvo *Poo palustris–Alopecuretum pratensis* asociacijai priklausančios bendrijos. Bebrų pievose vyravo higrofitai (*Carex* spp., *Equisetum* spp., *Poa palustris* ir kt.). Lyginant su natūraliomis užliejamomis pievomis, bebrų pievos išsiskyrė: 1) didesniam dirvos drėgnumui, rūgštumui ir nežymiai eutrofiškumui tolerantiškų rūšių gausumu, 2) mažesniu rūšių, kurios indiferentiškos išvardytų dirvos parametrų požiūriu, skaičiumi, 3) didesniu dominantinių ir s ubdominantinių rūšių skaičiumi, 4) mažesniu bendruoju rūšių skaičiumi. Bebrų pievų augalų bendrijos pasižymi ankstyvoms pievų sukcesijos stadijoms būdingais bruožais, kuriuos galima paaiškinti savitomis augimviečių ypatybėmis. Svarbiausios iš jų – padidėjęs dirvos drėgnumas, rūgštumas ir trofiškumas.

Raktažodžiai: bebrų pievos, natūralios užliejamos pievos, fitocenozių struktūra, *Castor fiber*, Lietuva