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THE INFLUENCE OF PLANT DOMINANTS ON THE ASSOCIATED SPECIES ABUNDANCE IN WET TALL-HERB MEADOW PLANT COMMUNITIES

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Plant interactions in wet tall-herb meadow plant communities were described through dominant and edificator species identification. Five dominant species were identified: Alopecurus pratensis, Filipendula ulmaria, Deschampsia cespitosa, Anthriscus sylvestris*, and* Angelica sylvestris*. The effects of species were studied using ANOVA and correlation analyses. Not all dominants were recognised as edificators. Edificators (*Alopecurus pratensis, Filipendula ulmaria, Deschampsia cespitosa, Angelica sylvestris*) had a negative effect on the various abundance indicators of associated species: percent cover, number, phytomass, and height. The edificator effects differed significantly in their level and duration and depended on the biomorphs of dominants. The perennial species* Alopecurus pratensis, Filipendula ulmaria*, and* Deschampsia cespitosa *were strong constant edificators.* Angelica sylvestris*, a short-lived monocarpic from the* Apiaceae*, is a weak seasonal edificator, while* Anthriscus sylvestris *is not an edificator. Analysis of the life strategies of species showed that competitors are not always edificators (*Anthriscus sylvestris*), whereas stress-tolerant may show edificator properties (*Deschampsia cespitosa*). The associated plant species often show positive interactions. Most of the associated species are stress-tolerant and have not an edificator effect.*

Key words: *plant interactions, dominants, edificators, competitors, stress-tolerants.*

INTRODUCTION

Grassland (meadows) describe vegetation with dominance of perennial herbs, mostly grasses and sedges, which form a sod. This article discusses the problem of grasslands existing in the conditions of sufficient or excessive moisture that were actively exploited by man as hayfields and pastures. In the second half of the 20th century, reduction in the area occupied by grasslands occurred worldwide and especially in regions of active land use. In some regions of the UK the area of grassland decreased by six times (Treweek, 1996), in Eastern Europe and Russia by three times (Prach, 1993). This trend also continued in the 21st century (Prach, 2007). The grassland area reduction as a result of re-forestation (Woody encroachment) is associated with the termination of use of the land as agricultural and natural grazing land and associated with climate changes (Magee and Antos, 1992; Miller and Halpern, 1998; Griffiths *et al*., 2005; Devine *et al*., 2017). Grassland plays an important role in the maintenance of the biosphere, because it is a habitat and a forage base for more than half of the vertebrate species of the forest zone (Murphy *et al*., 2004; Ratajczak *et al*., 2012; Schirmel *et al*., 2017). In addition, meadows regulate the hydrological regime of the territories (Shennikov, 1941; Rabotnov, 1984; Loheide and Gorelick, 2006). A reduction of grassland area creates understanding of the need to examine mechanisms for sustainable development and the reasons of their degradation (Muller *et al*., 1998; McDonald, 2001; Middleton *et al*., 2006; Prach, 2007; Van Auken, 2009).

Among multiple elements of a particular plant community, dominant species have a key interest. Dominant species are defined here as most abundant, i.e. producing high cover and biomass, species that play a significant community role via strong influence, either positive or negative, on the state and abundance of the associated species (Hulbert, 1971; Grime, 1998). The mass ratio hypothesis (Grime, 1998) suggests that the traits and functional diversity of dominant species largely determines ecosystem function. These dominant species can constrain subordinate species success and diversity (Baer *et al*., 2004; McCain *et al*., 2010). Subordinate species are generally relatively smaller in stature, less abundant and occupy more restricted microhabitats (Grime, 1998), but can contribute most to floristic diversity, particularly in grassland (Gibson, 2009). Basing on identification of dominant species, spatial and functional aspects of plant community structure can be described (Ipatov *et al*., 2010).

In analysis of plant community structure, the main attention is usually paid to spatial aspects, while functional aspects remain poorly studied (Keddy *et al*., 2002; Grime, 2006). This is especially typical for wet meadow plant communities under homogeneous environmental conditions, where community heterogeneity can arise from local functional traits due to wide number of species, and multiplicity of dominant species (Keddy, 2010; Houseman and Gross, 2011).

The structure of grassland plant communities is usually an example of collective dominance. Their components can be the complexes of edificator sinusia, which become a single whole in the development, creating a special microenvironment. The concept of "edificators" as the creators or builders of plant communities was developed in the beginning of 20th century (Brawn-Blanquet and Pavillard, 1922). By the way, this term is widely distributed in the Russian-language literature. Later on, in the works of L. G. Ramensky (1935) and later J. P. Grime (1979), the concept of "strategy of life" based on biological abilities of species to occupy and hold a space was an important step in understanding the behaviour and interactions of species in plant communities. The strategy of dominant species can be described as violent (Ramensky, 1935) or competitive (Grime, 1979).

Fluctuating change of dominants in grassland plant communities is often observed (Rabotnov, 1967; 1996). This happens when the autecological optima of plant species are different and benefit is given to those or other species on the background of seasonal, inter-annual and multi-annual cyclical climatic changes. Thus, spatial and functional diversity of the dominants not only determines the heterogeneity of meadow vegetation but it is also very important for maintaining stability, resistance, and restoration of such ecosystems under external influence.

Generally, grassland edificators (or their sinusia), creating and defining the microenvironment conditions depend at the first on the mode of local environment (i.e. not dependent on plant communities) factors. In contrast to the edificators the development of the associated plant species (their abundance and composition) in the grasslands is controlled by the microenvironment that was generated by the edificators (Kurkin, 1976; 1998). Peach and Zedler (2006) in the study of wet flooded sedge grassland showed that tussocks of *Carex stricta* Lam. serve as microsites for grassland herbs. Edificators can contribute to the development of the associated species, creating conditions for their successful growth. The phenomenon of "hydraulic lift", improving the supply of moisture in the upper soil layers has been described for many plant species (Caldwell, 1990; Leffler *et al*., 2005; Liste and White, 2008). This is especially important for plants in dry environmental conditions. Edificators like grasses and large-leaved forbs affect the microenvironment and the surrounding vegetation (Mirkin *et al*., 1967; Zaugolnova and Mikhailova, 1978; Galanin, 1980; Ipatov *et al*., 2007; Lebedeva *et al*., 2009).

Study of functional structure employs different features that are often based on an experimental model of the environment and plant communities (Louault *et al*., 2005; Kraft *et al*., 2015). For example, the effect of dominants on species invasion was examined in experimental grass crops (Emery and Gross, 2006; Souza *et al*., 2011). However, the role of dominant species in communities, especially aspects of the exclusion of subordinate species, is not well understood yet (Gibson *et al*., 2012). Our research was conducted in a meadow without any anthropogenic activity for more than 50 years. It should be noted also that comparative analysis of all dominants within the same grassland has not previously been conducted. In our work we used three basic concepts: the dominant (the indicator of high abundance of the species), the edificator (the indicator of strong influence on the surrounding vegetation), and the competitor (the type of life strategy for Grime). Are these concepts identical? Are dominants or competitors always edificators, or not? The aim of this work was to determine the relationship of these characteristics in different meadow species. For this we defined the community role of all species, identification of dominants and their edificator strategy and features of their influence on vegetation. Our study of plant relationships was based on the use of abundance indicators like percent cover, species saturation (number of species per plot) and phytomass. The main indicator for assessing the edificator effect was the associated species abundance changes in a gradient of edificator abundance variation in plots 0.1 m^2, comparable to the edificator sizes. The composition of associated species was studied by analysis of morphological groups of species and types of life strategies for Grime. This study will be useful in studying the spatial and functional structure of the grassland community and to develop criteria of its sustainability.

MATERIALS AND METHODS

Study area. The present study was carried out in wet meadows of Nizhne-Svirsky Nature Reserve, Leningrad Region, Russia (border of southern and middle taiga). The investigated extensive meadow is located on the ancient lake-glacial terrace of Ladoga Lake. These meadows were initially formed at the expense of coniferous forests; before 1980, when the Reserve was established, they were used for hay collection and grazing. Since the protected regime, during the 50-year period, the meadow has not been subject to human impact and has retained its meadow physiognomy. Now, the studied meadow is surrounded by birch and aspen forests. The grasses (*Alopecurus pratensis* L., *Deschampsia cespitosa* (L.) P. Beauv., *Festuca rubra* L., *Phleum pratense* L.) and tall herbs (*Filipendula ulmaria*(L.) Maxim., *Anthriscus sylvestris* (L.) Hoffm., *Angelica sylvestris* L.) dominate and *Galium boreale* L., *G. uliginosum* L., *Geum rivale* L., *Carex nigra* (L.) Reichard, *Lysimachia vulgaris* L. are common. The designated syntaxon is *Angelico sylvestris-Filipendulion ulmariae* Passarge 1977 (MOL-08A *Filipendulo-Petasition* Br.-Bl. ex Duvigneaud 1949) (Mucina *et al*., 2016). The meadow has an aligned microrelief without pronounced depressions and increases, and thus we could carry out a comparative analysis of the impact of species in homogeneous environmental conditions. The soils are metamorphic sod-gley type on tape clays (AY-EL-BMg-Cg).

Plant community description. In the studied wet meadows, in July, 540 square plots of 0.1 m^2 were randomly located, in which the cover (%) of each species was estimated. The small plot size (33 × 33 cm) was chosen to match the area affected by dominant plants. Analysis of species saturation was carried out by using the average number of species per plot, and for comparison of effect of various species. Specific phenological studies were not conducted. However, the phenological state of the species was recorded at the time of the vegetation description, and also data from the literature were used (Anonymous, 2006). The plots embraced all of the variability of vegetation in the wet meadows. To determine the patterns of vertical distribution of species phytomass, plants in the 0.1 m^2 plots were harvested by taking 22 cuts: in patches of the four dominants and in the area around them. The plant material was separated by species, cut into fragments of 10 cm and weighed in raw form.

Statistical analysis. Statistical data processing was carried out using STATISTICA 10 Enterprise 10.0.1011.6 with ANOVA (Analysis of Variance) and correlation analysis. Maximal and mean values with standard errors of cover and frequency were calculated for each plant species. The summed cover of the associated species and the number of associated species per plot were calculated. We classified the plant species as grasses and forbs, and further by plant size, in the following morphological groups: tall grasses (*Phleum pratense*, *Festuca pratensis* Huds.), small grasses (*Poa pratensis* L., *Agrostis tenuis* Sibth.), tall forbs (*Centaurea jacea* L., *Ranunculus acris* L.), and small forbs (*Stellaria graminea* L., *Veronica chamaedrys* L.). Data on species strategy (Grime, 1979) are taken from the Internet resource (Anonymous, 2018).

The Kolmogorov-Smirnov Criterion showed that the summed cover of the associated species had a normal distribution, and ANOVA was used to test for significant differences. Cover of individual species and summed cover for species among morphological groups and the number of species per plot did not have a normal distribution, and the Kruskal–Wallis criterion was used to test for significant differences. Spearman Rank Order Correlation coefficients were calculated.

Analysis of variance was used to determine the effect of dominant species on the summed cover of the associated species. So, for each dominant species, square correlation ratios (η^2) reflecting the power of its influence on the sum cover of the associated species were calculated. The sample was divided into groups according to the four gradations of cover for each species (0–5, 10–20, 25–65, 70–100%) to assess the strength of their influence. The average values of the summed projective cover were calculated for the whole sample (y) and within groups ($\bar{y}$). Then the total (C_y) and factorial (under the influence of dominant species) (C_x) variation was calculated:

$$C_y = \sum y_i^2 - \frac{(\sum y_i)^2}{n}, \; C_x = \sum \frac{(\sum y_{\text{int}.gr.})^2}{n_{gr.}} - \frac{(\sum y_i)^2}{n},$$

y_i – individual parameter value, $\bar{y}$ – overall mean, $\bar{y}_{gr.}$– group mean, $y_{\text{int.gr.}}$ – separate parameter values in this group, n – total sample, $n_{gr.}$ – number of values in the group. The part of factorial variation (C_x) in the total variation (C_y) – the value of the Square Correlation Ratio (η^2) – showed the strength of the species effect:

$$\eta^2 = \frac{C_x}{C_y}$$

Values of η^2 vary from 0 to 1: the larger the value, the stronger the effect. The direction of the effect was identified basing on the sign of the Spearman Rank Order Correlation Indicators (R) and supported by character of the slope of the empiric regression line ("+" – positive influence, "-" – negative influence). Positive effects were considered as stimulating, while negative were regarded as eliminating or limiting.

RESULTS

In the studied wet meadow communities, five plant species, including *Alopecurus pratensis*, *Filipendula ulmaria*, *Deschampsia cespitosa*, *Anthriscus sylvestris,* and *Angelica sylvestris*, were very abundant, with high average (10–23%) and, most importantly, maximum (85–100%) values of cover, and formed dominance patches, and thus we refer them to dominants (Table 1).

To estimate their edificator roles, we identified the plots with domination by a certain plant species (more than 50% cover, with less than 50% cover of any other species), and background control plots (no species with cover > 50%) (Table 2). Compared to background plots, plots with domination of *Alopecurus pratensis*, *Filipendula ulmaria*, *Deschampsia cespitosa, Angelica sylvestris* had a lower number and summed cover of associated species, and particularly for *Deschampsia cespitosa* (Table 2). However, domination of *Anthriscus sylvestris* had the opposite effect: higher cover of many associated species like *Phleum pratense*, *Agrostis tenuis*, *Galium boreale* L. and *Veronica chamaedrys*, and higher summed cover than in background plots. Some species, for example *Vicia sepium* L. and *Lathyrus pratensis* L. did not show significant differences in cover between dominant and background plots.

Results of ANOVA and correlation analysis revealed that *Alopecurus pratensis*, *Filipendula ulmaria, Deschampsia cespitosa,* and *Angelica sylvestris* had a significant negative effect on the associated species (Table 3). *Alopecurus pratensis* significantly affected both the cover of associated species and their number. *Filipendula ulmaria* and

Table 1

COVER AND FREQUENCY OF THE MOST ABUNDANT SPECIES IN THE MEADOWS

Plant species	Cover, %		Frequency, %
	mean ± SE	maximal	
Alopecurus pratensis	22.7 ± 1.1	100	77
Filipendula ulmaria	19.7 ± 1.2	100	57
Anthriscus sylvestris	15.4 ± 0.7	70	88
Angelica sylvestris	11.0 ± 0.9	85	58
Deschampsia cespitosa	10.4 ± 1.0	95	31
Festuca rubra	7.0 ± 0.4	60	68
Phleum pratense	5.8 ± 0.4	60	43
Melampyrum nemorosum	5.8 ± 0.4	50	56
Vicia sepium	4.2 ± 0.3	50	54
Centaurea jacea	3.8 ± 0.3	50	14
Lathyrus pratensis	3.5 ± 0.3	50	40
Veronica chamaedrys	3.2 ± 0.2	50	54
Poa pratensis	2.2 ± 0.2	60	30
Festuca pratensis	2.0 ± 0.3	50	22
Galium boreale	1.4 ± 0.3	60	8
Geum rivale	1.3 ± 0.3	60	5
Agrostis tenuis	1.0 ± 0.1	30	13
Galium uliginosum	0.8 ± 0.1	20	21
Carex nigra	0.8 ± 0.1	20	14
Ranunculus acris	0.8 ± 0.1	20	17
Stellaria graminea	0.8 ± 0.1	15	21
Achillea millefolium	0.7 ± 0.1	25	14
Lysimachia vulgaris	0.3 ± 0.1	25	4

Deschampsia cespitosa caused a significant decrease in the cover of the associated species, but no significant effect on the number of species. The effect of *Angelica sylvestris* was negative on the cover of associated species and positive on their number. *Anthriscus sylvestris* had a positive effect on both summed cover and number of species. The empirical regression lines confirm the observed effects of dominant species (Fig. 1). Increase in the abundance of dominants *Alopecurus pratensis*, *Filipendula ulmaria*, *Deschampsia cespitosa*, and *Angelica sylvestris* significantly lowered summed cover of the associated species (particularly for the dominant *Deschampsia cespitosa*), while *Anthriscus sylvestris* did not show this effect.

Most of other meadow plant species demonstrated positive relations. Unlike dominants, presence of most of other common species was significantly positively related to the number of associated species, but not for the summed cover of associated species (Table 3).

Alopecurus pratensis, Filipendula ulmaria, Angelica sylvestris, and *Anthriscus sylvestris* have a competitor strategy, whereas most of other species are stress-tolerant plants (*Festuca pratensis, Phleum pratense*, *Melampyrum nemorosum, Poa pratensis*, *Agrostis tenuis, Stellaria graminea*, *Veronica chamaedrys*) (Table 3). *Alopecurus pratensis*, *Filipendula ulmaria*, *Deschampsia cespitosa*, and *Angelica sylvestris* were the only species with edificator properties (Table 3).

The analysis of aboveground phytomass distribution by height showed that *Deschampsia cespitosa* and *Filipendula ulmaria* had a stronger negative effect on phytomass and the height of associated species, compared with effect of *Alopecurus pratensis* and *Angelica sylvestris* (Fig. 2).

Analysis of the effect of dominants on the morphological groups of plants showed that *Alopecurus pratensis, Filipendula ulmaria*, and *Deschampsia cespitosa* had a strong negative effect on both tall grasses and tall forbs, but small grasses and small forbs were less sensitive to this effect (Table 4).

DISCUSSION

The analysis showed that the strongest effect is exerted by *Alopecurus pratensis*, *Filipendula ulmaria* and *Deschampsia cespitosa.* These species are perennials, and over years accumulate a large underground phytomass. They were shown to have a significant negative effect on the associated species and thereby functioned edificators (Table 3). Their edificator features were quite distinct. *Alopecurus pratensis* is a "collective edificator ": its patches are represented by multiple plants with high shoot density. According to the values of η^2 and R, its negative impact on the abundance of associated species was the strongest. *Filipendula ulmaria* and *Deschampsia cespitosa* are generally "individual edificators", which affect the associated species by individual intensively developed plants. Obviously, because of this, their effect on abundance and especially on the number of species is somewhat weaker, as there is more space for associated species. Perhaps species saturation is a less sensitive indicator compared to cover in meadow communities (meadow plant species can occur sporadically in sites of dominants). Other authors (Schirmel *et al.,* 2017) observed that increased grazing by large herbivores led to a decrease in vegetation biomass, but not species diversity.

The effects of *Angelica sylvestris* and *Anthriscus sylvestris* differed from that of the other dominants. These species belong to the *Apiaceae* and are short-lived monocarpics with compact root systems. The effect of *Angelica sylvestris* was relatively weaker due to different directions of effect on the abundance of associated species (Table 3). Thus, the effect of *Angelica sylvestris* is less powerful and evidently time-dependent. This species can be considered as a weak "seasonal dominant and edificator": it plays a significant community role in the studied wet meadows in July when this species flowers and reaches maximum height and phytomass (Anonymous, 2006). *Anthriscus sylvestris* does not show any negative effect, and it had positive effect on both parameters of species abundance. Thus, this species is dominant but likely not an edificator. It weakly affects the surrounding vegetation, because it bears fruit already in July,

Table 2

COVER (%) OF PLANT SPECIES AND THEIR NUMBER (MEAN ± SE, %) IN PLOTS WITH DOMINANTS (> 50% PROJECTIVE COVER) AND BACKGROUND CONTROL PLOTS (NO. SPECIES > 50%)

Plant species	Plots with domination of					Background plots
	Alopecurus pratensis	*Filipendula ulmaria*	*Deschampsia cespitosa*	*Angelica sylvestris*	*Anthriscus sylvestris*	
*Alopecurus pratensis**	70 ± 1.4	13 ± 1.4	4 ± 1.4	14 ± 2.4	15 ± 4.7	12 ± 0.9
*Filipendula ulmaria**	12 ± 1.5	75 ± 1.9	6 ± 1.6	2 ± 1.1	11 ± 3.7	9 ± 0.8
*Deschampsia cespitosa**	2 ± 1.8	2 ± 0.7	76 ± 1.5	3 ± 1.0	4 ± 2.3	5 ± 0.7
*Angelica sylvestris**	4 ± 1.0	4 ± 0.9	3 ± 0.7	73 ± 1.0	3 ± 2.2	8 ± 0.8
*Anthriscus sylvestris**	15 ± 1.3	12 ± 1.3	9 ± 1.5	10 ± 1.7	63 ± 1.3	13 ± 0.8
*Festuca rubra**	7 ± 0.9	6 ± 0.7	11 ± 1.5	4 ± 1.0	6 ± 2.4	6 ± 0.7
*F. pratensis**	1 ± 0.4	2 ± 0.4	0.5 ± 0.3	2 ± 0.7	4 ± 1.7	31 ± 0.5
*Phleum pratense**	2 ± 0.6	7 ± 1.2	5 ± 1.1	2 ± 0.9	20 ± 5.1	6 ± 0.7
*Melampyrum nemorosum**	7 ± 1.0	9 ± 1.2	1 ± 0.3	4 ± 1.2	7 ± 1.9	5 ± 0.5
Vicia sepium	4 ± 0.6	4 ± 0.8	3 ± 0.8	6 ± 1.3	8 ± 2.3	4 ± 0.4
*Centaurea jacea**	3 ± 0.9	2 ± 0.5	0.2 ± 0.2	5 ± 1.5	0.1 ± 0.1	5 ± 0.6
Lathyrus pratensis	4 ± 0.7	2 ± 0.5	2 ± 0.7	4 ± 1.2	5 ± 2.0	4 ± 0.5
*Veronica chamaedrys**	2 ± 0.3	2 ± 0.6	4 ± 1.0	4 ± 0.9	8 ± 2.3	4 ± 0.4
*Poa pratensis**	1 ± 0.5	3 ± 0.5	2 ± 0.8	3 ± 1.7	6 ± 1.9	20 ± 0.3
*Galium boreale**	2 ± 0.7	1 ± 0.6	0.5 ± 0.4	0	8 ± 4.0	1 ± 0.4
*Agrostis tenuis**	1 ± 0.3	1 ± 0.3	0.5 ± 0.2	1 ± 0.5	4 ± 1.3	1 ± 03
Carex nigra	1 ± 0.4	1 ± 0.4	0.5 ± 0.2	0.1 ± 0.1	2 ± 1.2	1 ± 0.1
*Ranunculus acris**	0.3 ± 0.1	0.2 ± 0.1	1 ± 0.5	0.3 ± 0.1	2 ± 1.5	1 ± 0.2
*Achillea millefolium**	0.3 ± 0.1	1 ± 0.4	0.4 ± 0.2	2 ± 0.4	3 ± 2.0	1 ± 0.2
Summed cover of associated species*	78 ± 3.3	78 ± 4.9	59 ± 4.8	76 ± 5.6	117 ± 6.6	93 ± 3.5
Species number / 0.1 m²*	8.5 ± 0.2	9.0 ± 0.3	8.1 ± 0.3	9.6 ± 0.3	9.9 ± 0.6	10.3 ± 0.1

* denotes species and indicators whose values significantly differs in six types of plots according to the Kruskal–Wallis Criterion (p <0.05).

when it ends its development. Thus, the power of effect of dominants depends on its biomorph.

The competitor life strategies of the dominants *Alopecurus pratensis*, *Filipendula ulmaria*, and *Angelica sylvestris* were associated with the role as edificators (Table 3). *Anthriscus sylvestris,* which has features of a competitor, is not an edificator, perhaps due to features of its seasonal development. In open meadow landscapes, *Deschampsia cespitosa* forms a dense tussock and it is an edificator, despite its stress-tolerant strategy. Some species with features of competitors (for example *Festuca rubra*) are not edificators, obviously, due to low abundance. Thus, the realisation of the potential life strategy depends on the environmental conditions and abundance of species.

The analysis of vertical stratigraphy of foliage showed that all dominants reduce phytomass and height of associated species (Fig. 2). *Deschampsia cespitosa* and *Filipendula ulmaria* had a strong influence. The effect of *Alopecurus pratensis* and *Angelica sylvestris* was weaker, evidently due to their relatively smaller effect on competitively strong tall forbs with high phytomass (Table 4).

Previously it was also shown that some grasses like *Stipa pennata* L., *Festuca beckeri* (Hack.) Trautv. (Uranov and Mikhailova, 1974; Zaugolnova and Mikhailova, 1978) and large-leaved forbs like *Filipendula ulmaria*, *Trifolium montanum* L., *Cirsium arvense* (L.) Scop., *C. setosum* (Willd.) Besser, *Geranium sylvaticum* L. (Mirkin *et al.*, 1967; Galanin, 1980; Ipatov *et al.*, 2007, Lebedeva *et al.*, 2009) can prevent the growth of neighbouring species due to spatial exclusion and local changes of environmental drivers.

Analysis of the influence of dominants on species of different morphological groups showed that *Alopecurus pratensis* had stronger effect on grasses in comparison with forbs, whereas *Filipendula ulmaria, Deschampsia cespitosa, Angelica sylvestris* and *Anthriscus sylvestris* had the opposite effect. Obviously, species of similar biomorphs are more competitive with each other. *Alopecurus pratensis, Filipendula ulmaria, Deschampsia cespitosa* have strong negative effect on tall grasses and on tall forbs, whereas their effect on small grasses and small forbs is weaker (Table 4). Perhaps, tall associated plant species are under intensive competition with dominants, while small individuals are less dependent on dominants. In a previous study focused on *Geranium sylvaticum* L. (Lebedeva *et al.*, 2009) similar results were obtained. It was observed also that species with clinging stems (*Vicia sepium, Lathyrus pratensis*) did not show significant differences in their cover in patches of dominants and in the background; their raised shoot make them independent of the supporting species.

Table 3

TYPE OF STRATEGY FOR GRIME, RELATIONSHIPS BETWEEN PLANT SPECIES COVER AND THE SUMMED COVER AND SPECIES NUMBER PER PLOT OF THEIR ASSOCIATED SPECIES, AND EDIFICATOR PROPERTIES OF SPECIES

Plant species	Type of strategy for Grime	Parameters			Edificator properties
		Summed cover of associated species		Species number / 0.1 m2	
		η²	R	R	
Alopecurus pratensis	C-CS	**0.29**	**– 0.52**	**– 0.09**	+
Filipendula ulmaria	C-SC	**0.25**	**– 0.43**	– 0.04	+
Deschampsia cespitosa	SC-CS	**0.27**	**– 0.39**	– 0.07	+
Angelica sylvestris	C-CR	**0.26**	**– 0.46**	**0.16**	+
Anthriscus sylvestris	CR	**0.02**	**0.13**	**0.20**	-
Festuca rubra	CR	**0.24**	**0.40**	**0.12**	-
F. pratensis	CS	0.02	0.02	**0.18**	-
Phleum pratense	CS	**0.11**	– 0.07	**0.26**	-
Melampyrum nemorosum	SR	**0.15**	**0.11**	**0.23**	-
Vicia sepium	CS	**0.12**	0.05	**0.20**	-
Centaurea jacea	-	**0.15**	**– 0.20**	**0.36**	-
Lathyrus pratensis	CS	**0.13**	0.04	**0.18**	-
Veronica chamaedrys	S-CS	**0.09**	– 0.06	**0.13**	-
Poa pratensis	CS	**0.08**	**0.23**	**0.39**	-
Agrostis tenuis	CS	**0.07**	**0.29**	**0.35**	-
Stellaria graminea	CS	**0.04**	0.01	**0.38**	-
Achillea millefolium	CR-CS	**0.09**	– 0.08	**0.21**	-

η², Square Correlation Ratios; in the dispersion complex an influencing factor – plant species; *R*, Spearman Rank Order Correlations; values significant at $p < 0.05$ are marked in bold.

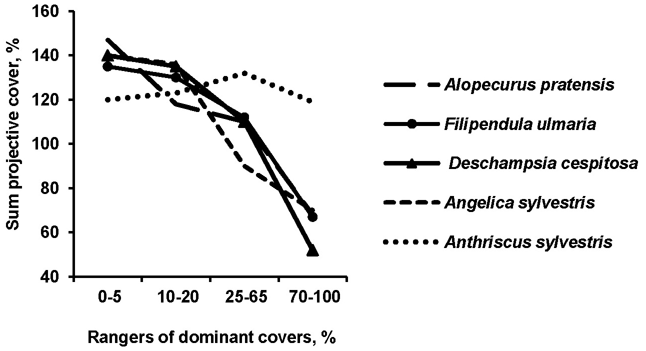

Fig. 1. Relationship of associated species summed cover in range classes replaced by dominant species cover.

Most meadow plant species are not dominant species and are not edificators: they do not have negative impact on each other and demonstrate positive relations. This is especially evident for the number of species (Table 3). The relationships of particular species with summed covers shows less reliable positive connections, and also reveals potential dominants (*Centaurea jacea*). Clear positive effects are produced by the host-dependent semi-parasitic species (*Melampyrum nemorosum* L.). Perhaps, the stress-tolerance strategy of many meadow species (*Festuca pratensis, Phleum pratense*, *Melampyrum nemorosum, Lathyrus pratensis, Poa pratensis*, *Agrostis tenuis, Stellaria graminea*, *Veronica chamaedrys* and other), which form multi-species communities, is affected (Table 3).

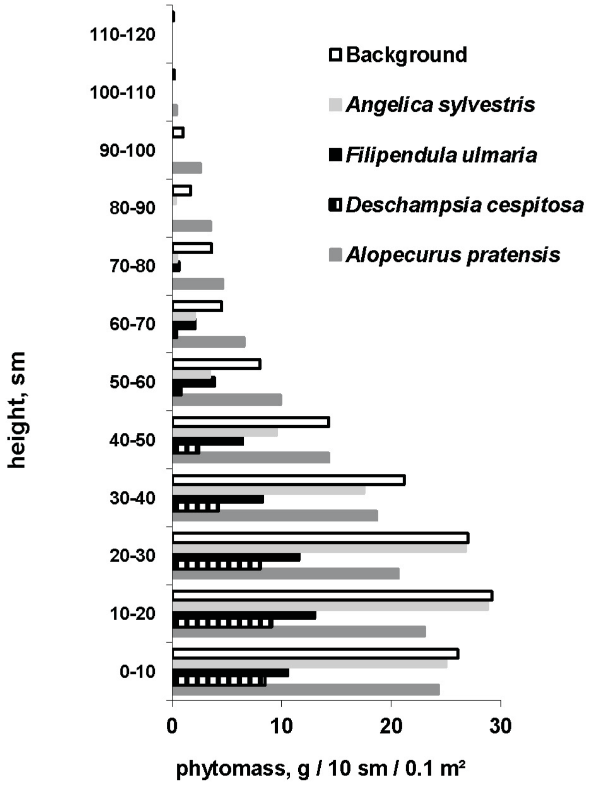

Fig. 2. Distribution of associated species overground phytomass in height classes in the plots with dominants (*Alopecurus pratensis*, *Filipendula ulmaria*, *Deschampsia cespitosa*, *Angelica sylvestris*) and in background plots without dominants.

Positive relations were discovered by other authors. The mechanisms of their occurrence are different: creation of microsites with favourable microenvironment, the phenomenon of "hydraulic lift" and others (Mirkin *et al.*, 1967; Uranov and Mikhailova, 1974; Zaugolnova and Mikhailova, 1978; Caldwell, 1990; Leffler *et al.*, 2005; Peach and Zedler, 2006; Liste and White, 2008).

CONCLUSIONS

In the studied wet meadow community, dominant plant species are represented by *Alopecurus pratensis*, *Filipendula ulmaria*, *Deschampsia cespitosa*, *Angelica sylvestris,* and *Anthriscus sylvestris*. The edificator role of dominants was estimated from differences in the abundance of associated species. Not all dominants were recognised as edificators. Also, edificator effects significantly vary in their level and duration and depend on the biomorph. Perennials *Alopecurus pratensis*, *Filipendula ulmaria* and *Deschampsia cespitosa* are strong constant edificators. The short-lived monocarpic *Angelica sylvestris* is a weak seasonal dominant and edificator. Edificators have a negative effect on the abundance of associated species (their percent cover, number, phytomass, and height). Monocarpic *Anthriscus*

Table 4

SPEARMAN CORRELATION COEFFICIENTS FOR THE RELATIONSHIPS OF DOMINANT SPECIES COVERS WITH THE SUMMED COVER OF DIFFERENT GROUPS OF ASSOCIATED SPECIES

Dominant species	Cover of grasses			Cover of forbs		
	tall	small	total	tall	small	total
Alopecurus pratensis	**– 0.42***	**– 0.21***	**– 0.45***	**– 0.17***	– 0.04	**– 0.18***
Filipendula ulmaria	**– 0.28***	0.04	**– 0.27***	**– 0.31***	**– 0.12***	**– 0.29***
Deschampsia cespitosa	**– 0.24***	0.02*	**– 0.23***	**– 0.36***	– 0.06*	**– 0.34***
Angelica sylvestris	**– 0.35***	– 0.02*	**– 0.36***	**– 0.27***	0.02	**– 0.23***
Anthriscus sylvestris	0.07	**0.25***	**0.12***	**– 0.16***	**0.32***	0.02

Values significant at $p < 0.05$ are marked in bold; * denotes groups of species whose covers significantly differs under the influence of dominants according to the Kruskal–Wallis Criterion ($p < 0.05$).

sylvestris likely does not exert edificator effects itself. Thus, in wet meadow plant communities, some dominant species might not function as edificators.

Plants species that are both dominants and edificators play a strong community role in wet meadow communities: they regulate abundance of the associated species and promote heterogeneity (complex mosaic) of meadows. Dominants with different ecological strategies (constant and season dominants edificator, dominants not edificator) create the sustainability of meadow plant communities. Species with a competitive life strategy are not always edificators (*Anthriscus sylvestris*), whereas some stress-tolerants can show edificator properties (*Deschampsia cespitosa*). The associated plant species usually display positive interactions between each other. It is possible that edificator effects and stress-tolerance of the majority of the associated species is evolutionary developed and is crucially important for wet meadow community structure.

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DOMINĒJOŠO SUGU IETEKME UZ PAVADOŠO SUGU DAUDZUMU MITRO AUGSTO LAKSTAUGU PĻAVU SABIEDRĪBĀS

Augu mijiedarbība mitro augsto lakstaugu pļavu sabiedrībās tika noteikta, nosakot dominējošās un edifikatorsugas. Tika identificētas piecas dominējošās sugas: *Alopecurus pratensis, Filipendula ulmaria, Deschampsia cespitosa, Anthriscus sylvestri* un *Angelica sylvestris*. Ne visas dominējošās sugas vienlaicīgi bija arī edifikatorsugas. Edifikatorsugām *Alopecurus pratensis, Filipendula ulmaria, Deschampsia cespitosa, Angelica sylvestris* bija negatīva ietekme uz vairākiem pavadošo sugu daudzuma indikatoriem: projektīvo segumu, augu skaitu, fitomasu un augstumu. Edifikatorefekts ticami atšķīrās pēc ietekmes līmeņa un ilguma un bija atkarīgs no dominējošo sugu bioloģiskām īpašībām.