

THE CLIMATIC PATTERNING OF SPHAGNUM SECT. SPHAGNUM
SPECIES DISTRIBUTION IN THE EAST EUROPEAN PLAIN
КЛИМАТ КАК ФАКТОР ОПРЕДЕЛЕНИЯ АРЕАЛОВ ВИДОВ SPHAGNUM
SECT. SPHAGNUM НА ВОСТОЧНО-ЕВРОПЕЙСКОЙ РАВНИНЕ

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Abstract

The purpose of this research is to correlate distribution of *Sphagnum* species with local climatic factors in the East European Plain. Six species of *Sphagnum* from section *Sphagnum*, i.e., *S. magellanicum*, *S. centrale*, *S. palustre*, *S. papillosum*, *S. austinii*, and *S. affine* were selected. The graded data on their abundance and the species number for 138 localities were mapped into unit squares of 10×10 km by using GRID coverage, to construct several delineated zones of occurrence/abundance. For analysis, the matrix was augmented by extended data from the BIOCLIM database. Regression analysis revealed strong correlation between species distribution and temperature, while abundance of the species showed high correlation with maximum relative humidity in two months, August and September, being especially high for most common species, *S. magellanicum* (0.85 and 0.83) and *S. centrale* (0.81 and 0.76). Distribution area of *Sphagnum palustre* is restricted by precipitation in the whole warm part of the year, while *Sphagnum papillosum* avoids regions with low relative humidity in early summer. The local number of species correlates with relative humidity in summer. The developed technique demonstrates a possible way of applying the climatic data to the analysis of the bryophyte distribution in extensive territories.

Резюме

Изучается значимость климатических факторов на распространение шести видов *Sphagnum* секции *Sphagnum*: *S. magellanicum*, *S. centrale*, *S. palustre*, *S. papillosum*, *S. austinii*, *S. affine* на территории Восточно-Европейской равнины. Корреляционный и регрессионный анализы выявили значимую зависимость между влажностью воздуха и месячных осадков, с одной стороны, и встречаемостью видов и видовым разнообразием секции *Sphagnum*, с другой. Построены карты распространения видов, отражающие их обилие, а также число видов секции *Sphagnum*. Они иллюстрируют более высокую встречаемость как отдельных видов, так и их общего числа на северо-западе и западе данной территории, где в летний и осенне-летний период влажность воздуха выше и осадков больше, чем в остальной части региона. Особенно высоки коэффициенты корреляции между встречаемостью и суммой осадков августа и сентября у двух видов – *S. centrale* (0.81 и 0.76 соответственно) и *S. magellanicum* (0.85 и 0.83). Распространение *S. papillosum* сдерживает продолжительный засушливый период весны и начала лета. В распространении *S. palustre* ведущую роль играет количество осадков всего теплого периода. Для местного разнообразия видов определяющими факторами являются осадки и относительная влажность воздуха в летние месяцы.

KEYWORDS: biogeography, ecology, ARCGIS, BIOCLIM

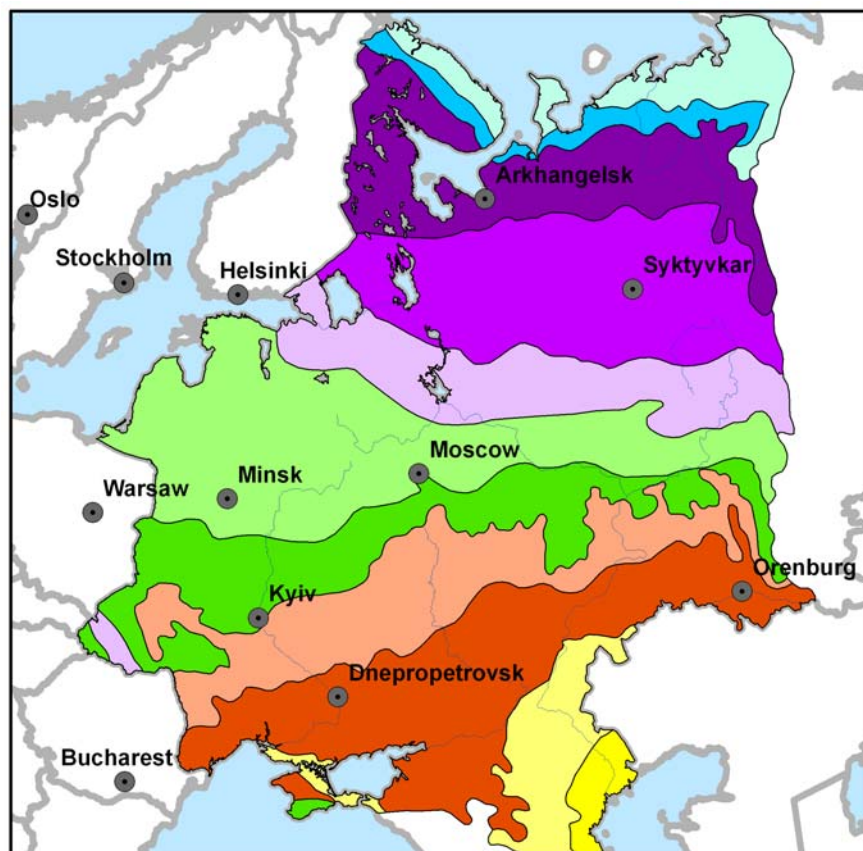
INTRODUCTION

Sphagnum mosses are hygrophytes, so their distribution is associated primarily with wetland habitats, such as bogs and mires (Mazing *et al.*, 1990), although in boreal forests they may dominate in the moss carpet as well. On the local scale, *Sphagnum* distribution depends largely on soil moisture and nutrient conditions (Vitt *et al.*, 1975; Chee & Vitt, 1989; Gignac *et al.*, 1991; Wojutin *et al.*,

2013). On the global scale, however, the distribution patterns of *Sphagnum* correlate mainly with the climatic parameters (Gignac & Vitt, 1990; Gignac *et al.*, 1991; Ignatov, 1993; Melosik, 2006).

Sphagnum bodies are mostly composed of empty hyaline cells, and they may accumulate moisture in tens to hundreds times of their dry weight. The growth of *Sphagnum* starts in spring and continues till autumn, although

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Vegetation zones

Tundra	Middle Taiga	Broadleaves Forests	Semidesert
Forest-Tundra	South Taiga	Forest-Steppe	Desert
North Taiga	Mixed Forests	Steppe	

Fig. 1. The East European Plain, taken in the present work, and vegetation zones by Kurnae (1973)

in a dry summer period their growth stops. The growth declines in October, interrupts by cold weather and snow (Savich-Lyubitskaya, 1952; Maksimov, 1982; Grabovik & Antipin, 1982; Grabovik, 1994). According to Grabovik (1994; 2003) and Grabovik & Antipin (2015), the intensity of *Sphagnum* growth in Karelia is strongly dependent on the annual rainfall: in wet years, *Sphagnum*'s annual increment was significant, while in dry years it was very low. Luken (1985) found a similar correlation in Alaska: in the areas with the same temperature, annual increment had a positive correlation with the highest rainfall. Being grown in artificial conditions at 100% humidity and room temperature, *Sphagnum* growth was maximum (Clymo, 1965; Smolyanitsky, 1977; Popov, 2012). The latter facts point at the importance of the air humidity just above the ground for *Sphagnum* growth.

Data on the environmental parameters patterning the distribution of *Sphagnum* species are rather general. Species diversity is higher in humid areas (Daniels & Eddy, 1990; Mazing *et al.*, 1990; Ignatov, 1993), while xeric areas have no or almost no species of the genus. Particular studies were conducted to identify an impact of climatic factors on the distribution of *Sphagnum* mosses, but they were done for limited areas (Gignac & Vitt, 1990;

Vitt, 1990; Gignac *et al.*, 1991; Melosik, 2006). These works are of considerable interest, because they are based on the statistical analysis of data of meteorological stations and focus on trends in species distribution in a certain type of climate (oceanic, subcontinental, *etc.*).

The East European Plain (EEP) represents a convenient territory for the study of *Sphagnum* species distribution. Being ca. 2000×2000 km, it has enough contrasting gradients of climatic conditions, from suboceanic to rather continental, and from north boreal types of vegetation to the broad-leaved zone and then to the steppes and semi-deserts. Distribution of *Sphagnum* species within the EEP was studied by Kudryashov (1940; 1945). He delimited several zones, including those where *Sphagnum* have continuous distribution, zones of dominance of eutrophic species from the section Subsecunda, which are located to the North and South of the forest zone. The present study has the same aim; however, it expands the usage of data on spatial distribution of the climatic parameters.

MATERIAL AND METHODS

The study area is shown in Figs. 1–2. It roughly corresponds to the East European Plain, somewhat overlapping to neighboring areas. Eleven vegetation zones are represented in its territory according to Kurnae (1973).

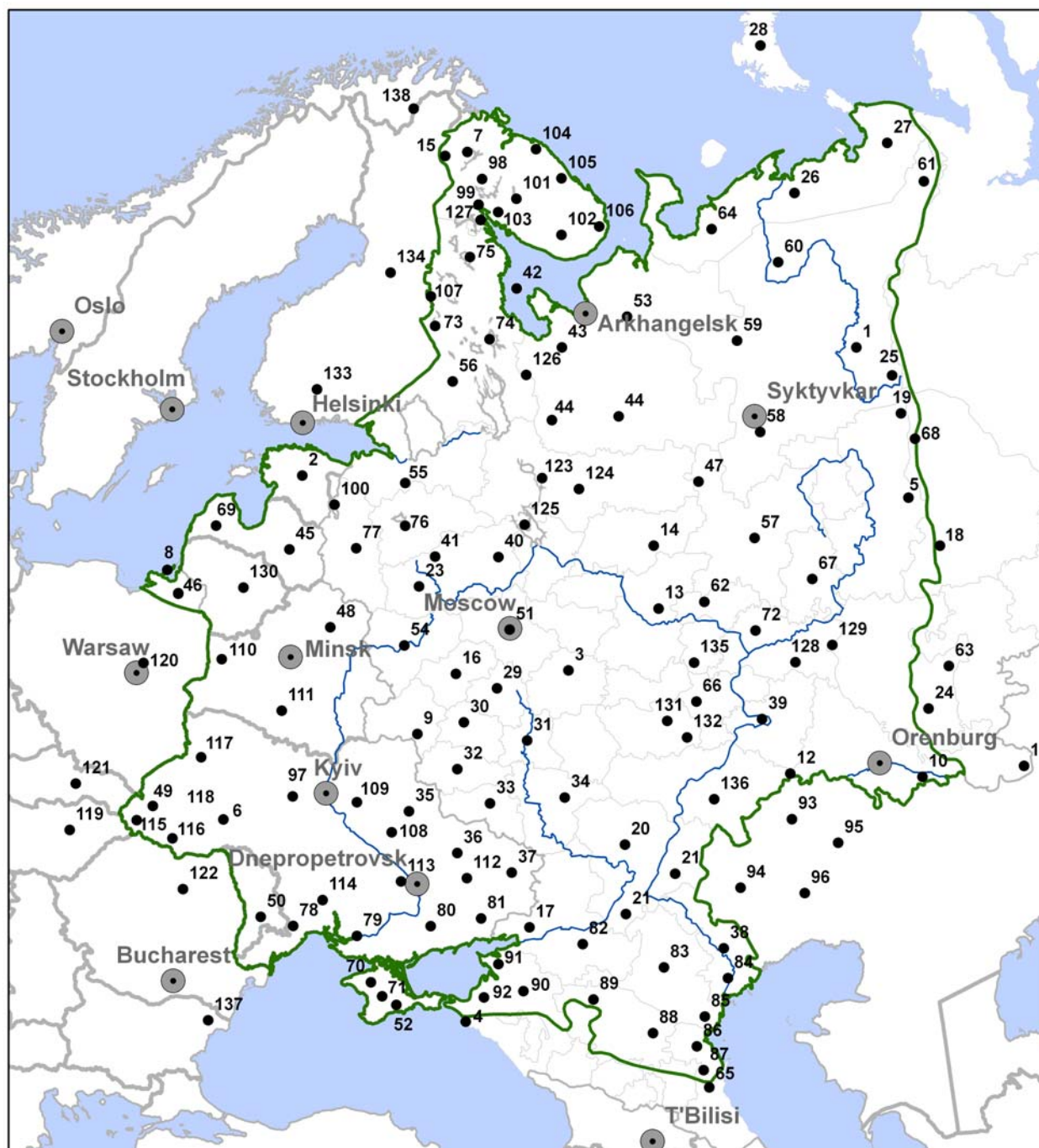


Fig. 2. The local bryofloras used in the analysis of species distribution in the territory approximately corresponding to the East European Plain: 1 – Zheleznova, 1994; Shubina & Zheleznova, 1995; 2 – Ingerpuu & Vellak, 1995; 3 – Volosnova *et al.*, 2000; 4 – Ignatova *et al.*, 2005; 5 – Ignatova *et al.*, 1995; 6 – Boljukh, 1995; 7 – Likhachev & Belkina, 1999; 8 – Dolnik & Napreenko, 2007; 9 – Anishchenko, 2007; Popova, 2002; 10–12 – Spirina & Zolotov, 2004; 13 – Popov *et al.*, 2004; 14 – Fedosov & Popov, 2004; 15 – Belkina & Likhachev, 2004; 16 – Teleganova, 2008; 17 – Sereda & Ignatov, 2008; 18 – Dyachenko *et al.*, 1996; Bezgodov, 2002; 19 – Ignatova *et al.*, 1996; 20–22 – Suragina, 2001; 23 – Ignatov *et al.*, 1998; 24 – Zolotov & Baisheva, 2003; 25 – Zheleznova & Shubina, 1997; 26–28, 138 – Afonina & Czernyadjeva, 1995; 29 – Popova, 2002; Volkova, 2006; 30–37 – Popova, 1999, 2002; 38 – Suragina *et al.*, 2002; 39 – Popov, 2002; 40–41 – Notov *et al.*, 2002; 42–44 – Churakova, 2002; 45, 69 – Abolin, 1968; Strazhdina, 2012; 46 – Napreenko & Razgulyaeva, 1999; 47, 57 – Zheleznova, 2014; 48, 110, 111 – Pidoplichko, 1948; Rykovski & Maslovski, 2009; 49, 115, 116, 118 – Zerov, 1964; Zerov & Partyka, 1975; 50, 78 – Simonov, 1978; 51 – Ignatov & Ignatova, 1994; Ignatov *et al.*, 2011; 52, 70, 71 – Partyka, 2005; 53 – Ignatov *et al.*, 1998; Popov & Buryanina, 2012; 54 – Ignatov & Ignatova, 2003; 55, 76, 77 – Boch & Kuzmina, 1985; 56 – Elina *et al.*, 1984; 58–61 – Zheleznova, 1994; 62 – Chernyadjeva, 2001; Chernyadjeva *et al.*, 2013; 63 – Baisheva *et al.*, 2015; 64 – Zheleznova & Shubina, 2015; 65 – Abakarova *et al.*, 2015; 66 – Blagoveschenskii & Blagoveschenskaya, 1982; 67 – Rubtsova,

Table 1. Variables from the database BIOCLIM used in analyses

Codes	Explanation
tm 01-12	Mean monthly temperature, °C (for each month)
pr 01-12	Monthly precipitation, mm (for each month)
reh 01-12	Relative humidity, % (for each month)
pr_a	Annual precipitation, mm
amt	Annual Mean Temperature
pr_wtm	Precipitation of Wettest Month
pr_drm	Precipitation of Driest Month
pr_wtq	Precipitation of Wettest Quarter
pr_drq	Precipitation of Driest Quarter
pr_wmq	Precipitation of Warmest Quarter
pr_clq	Precipitation of Coldest Quarter
t_wtq	Mean Temperature of Wettest Quarter
t_drq	Mean Temperature of Driest Quarter
t_wmq	Mean Temperature of Warmest Quarter
t_clq	Mean Temperature of Coldest Quarter

Bryophytes have been actively studied in this territory in recent decades, accumulating a sufficiently dense coverage of local floras. The main data for the foregoing analysis were obtained from the annotated lists of mosses. These lists commonly evaluate species abundance in the area. Altogether, data from 138 localities were collected, including some with zero values for all species (*i.e.* lacking all species of *Sphagnum* sect. *Sphagnum*). Localities were selected so that to be most evenly spread within this territory and overlap slightly beyond the boundaries of the study area to minimize errors from the boundary effects (Fig. 2). For each locality, the abundance of every selected species was ranked by the following scale:

- 0 – absent;
- 1 – very rare (1–2 records).
- 2 – rare (3–7 records).
- 3 – sporadic (more than 7 records).
- 4 – frequent, but not always present in suitable habitats.
- 5 – common and always present in suitable habitats.

These estimates of species abundance were used for composing GRID-covers with the resolution of 10 km in one pixel. GRID-covers are continuous surfaces. They are based on points with three coordinates X, Y and Z (where X and Y are geographic coordinates, and Z is the species abundance in the given point). The space between the known points is filled by approximations by the kriging method, which estimates the unknown values in the most optimal way based on a system of spatial regression equations, varying from point to point, *i.e.* the value of each point is weighted by the distance and the value of neigh-

bor points. Details of its implementation in ARCGIS is discussed by Lurie (2010) and Popov (2013).

The GRID coverage maps with grade data were obtained for six species: *Sphagnum magellanicum*, *S. centrale*, *S. palustre*, *S. papillosum*, *S. austinii*, and *S. affine*. Afterwards, these coverages were transformed to a relation table with 44370 lines (number of squares of 10×10 km). An original matrix had six columns performing the species frequency in a given 10 x 10 sq. km, obtained from interpolation by the kriging approximation. An additional seventh column showed a number of species (out of six) in each of the 10×10 km square. Finally, this matrix was augmented with the climatic data.

Climatic variables selected for the explanation of the species distribution patterns are listed in Table 1. We chose climatic variables that are recommended for the living being distribution analysis in the program BIOCLIM (2009, <http://www.andra.fr/bioclim>, accessed as of 15 February 2016). In total, the present analysis includes 48 climate variables (Tabl. 1) calculated by this program from the global network of meteorological stations and averaged over the years 1950–2000 (Hijmans *et al.*, 2005).

For each of 48 variables we also built a GRID coverage with a resolution of 10 km in one pixel (the pixel pitch in DB BIOCLIM is 10' along the arc of the WGS 84 ellipsoid, which is approximately equal to 10 km in the projected form). Each GRID coverage was composed in Azimuthal Equidistant Projection (Central Meridian 45°E, chief of the parallel – 55°N).

Further, the matrix was used for the regression analysis. Climatic parameters (*cf.* Table 1) were accepted as the predictors, while the abundance of each species expressed as a continuous numeric scale was the response. The method of polynomial multiple regression was used, as a nonlinear dependence was detected between the values of the predictors and the values of response, as well as because of nonnormal distribution of climatic variables. All operations on spatial objects were performed in packages ARCGIS and ERDAS, correlation and regression analysis were done in STATISTICA 6.0.

The final analyzed matrix includes 44370 lines (number of 10×10 km squares) and 55 columns. Columns represent 48 variables from the BIOCLIM, abundance of six selected species involved in the analysis, and a number of species (out of six) per a given 10 x 10 km square.

The dataset was further developed by delineating zones of abundance for each species. The technique com-

2015; **68** – Dyachenko & Dyachenko, 2010; **72** – Ignatov *et al.*, 2005; Ariskina, 1978; **73** – Maksimov & Kuznetsov, 2009; **74, 75** – Abramov & Volkova, 1998; **79, 80, 112, 113** – Boiko, 2009; **83, 85** – Doroshina, 2011; **97, 117** – Zеров, 1964; **98, 99** – Belkina & Likhachev, 1997, 2010; **100** – Andreeva & Filipieva, 2005; **101–106** – Shljakov & Konstantinova, 1982; **107** – Boichuk, 2001; **108–109** – Gapon, 1997; **119** – Papp *et al.*, 2009; **120** – Stebel, 2012; Melosik, 2006; **121** – Dite *et al.*, 2007; **122** – Erzberger *et al.* (http://abpa.ektf.hu/uploads/papers/finalpdf/ABPA_2_from73to95.pdf); **123** – Karmazina, 2013; **124** – Filippov & Boichuk, 2015; **125** – Volkova *et al.*, 1994; **126** – Boichuk *et al.*, 2002; **127** – Bogdanova, 1981; **128–129** – Ariskina, 1978; **131** – Serebrjakova, 2009; **132** – Doroshina-Ukrainskya, 1999; **134** – Popova, 1999; **135** – Popov *et al.*, 2001; **81, 82, 84, 86, 87, 88, 89, 90, 91, 92, 93, 94, 95, 96, 136, 137** – zero data, because of the lack any data in literature for south steppe and semidesert adreas; **130, 133, 134, 138** – Söderström, 1998.

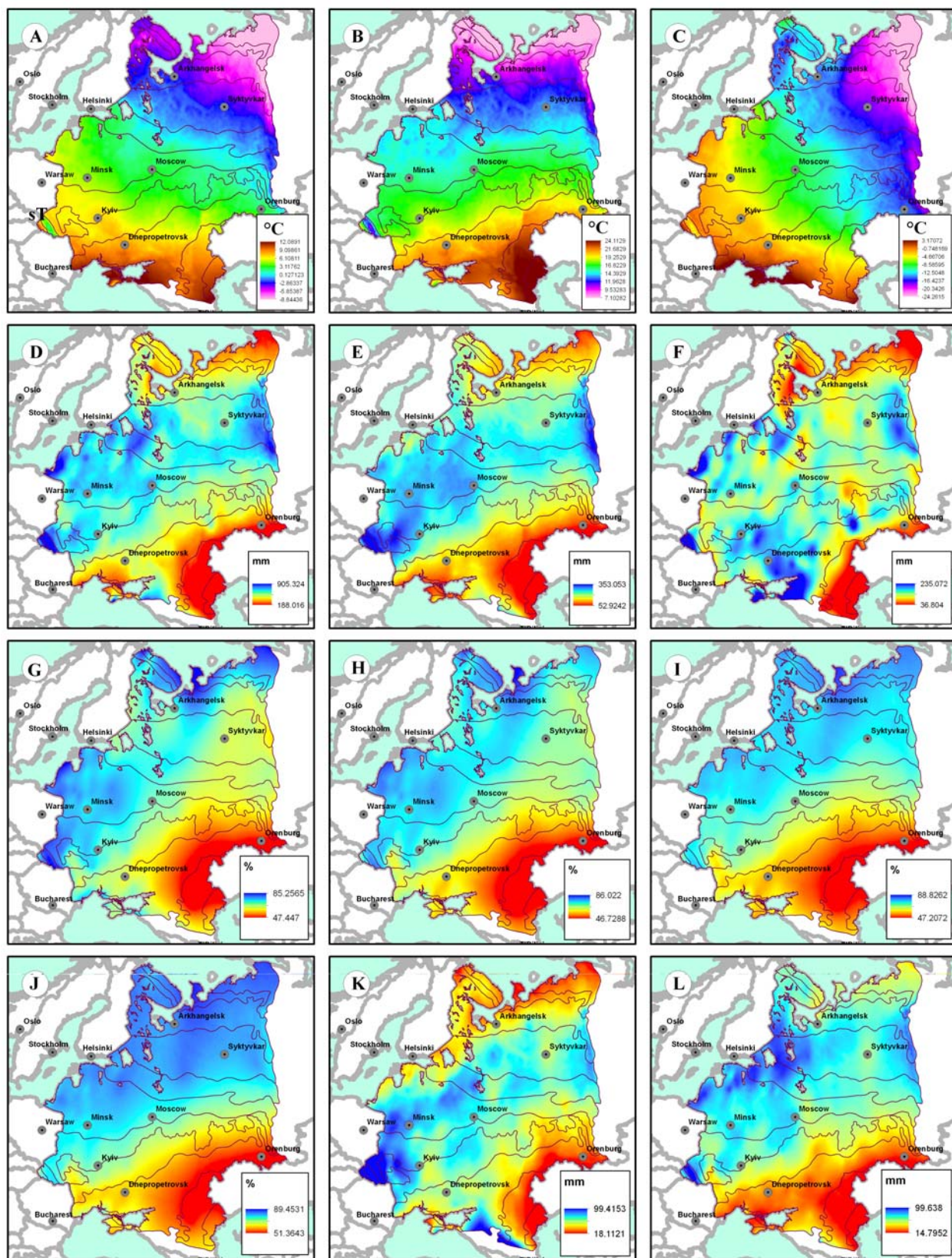


Fig. 3. Distribution of some important climatic variables on the territory of the East European Plain. A – average annual temperature; B – average temperature of the warmest quarter of the year; C – average temperature of the coldest quarter; D – annual precipitation; E – precipitation of warmest quarter; F – precipitation of coldest quarter; G – relative air humidity of June; H – relative air humidity of July; I – relative air humidity of August; J – relative air humidity of September; K – precipitation of May; K – precipitation of August. Brown lines indicate the boundaries of vegetation zones shown in Fig. 1.

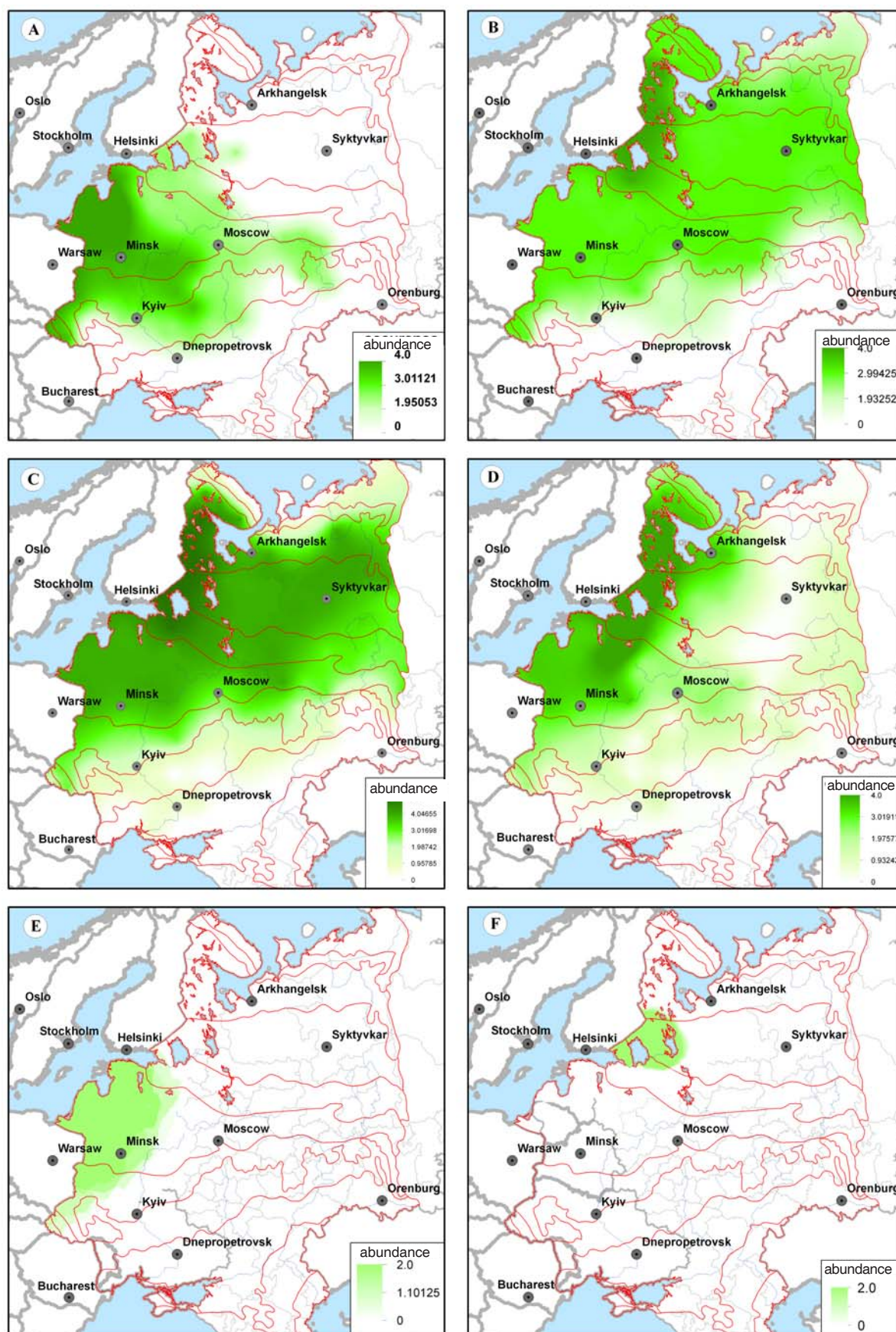


Fig. 4. The model maps of the *Sphagnum* section *Sphagnum* species distribution in the East European Plain: A – *S. palustre*; B – *S. centrale*; C – *S. magellanicum*; D – *S. papillosum*; E – *S. austinii*; F – *S. affine*. The limits between zones of abundance (cf. Fig. 5) are given by the kriging method

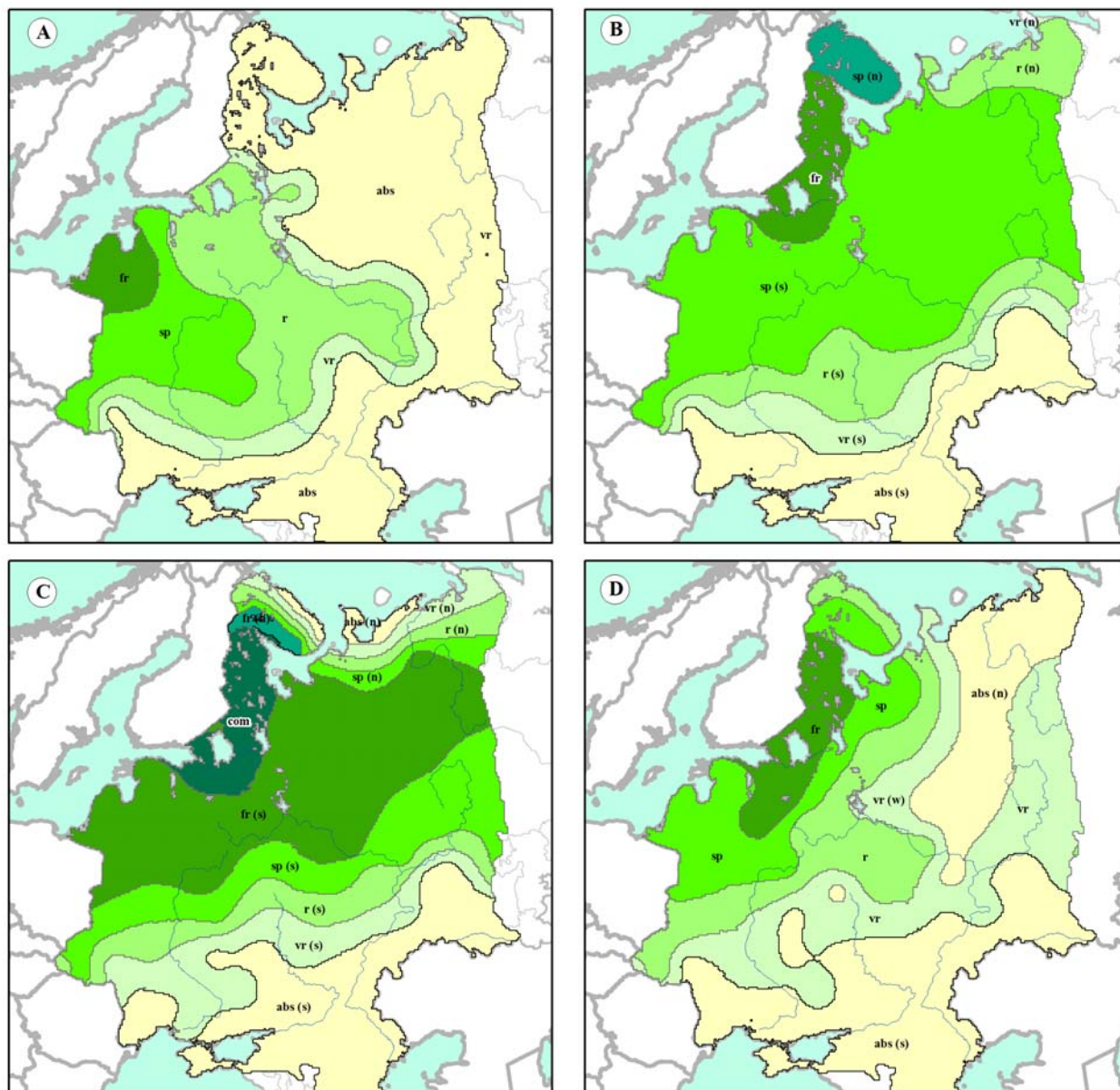


Fig. 5. Zones of abundance of species of *Sphagnum* sect. *Sphagnum* in the East European Plain: abs – species is absent; vr – very rare; r – rare; sp – sporadic; fr – frequently; com – common, or widely distributed; (n) the Northern subzone, (s) – southern subzone. A – *S. palustre*; B – *S. centrale*; C – *S. magellanicum*; D – *S. papillosum*. The limits between zones of abundance given by the method of “natural breaks” are shown in boxes in Fig. 4.

prised the conversion to the integer coverage by the method of “Natural breaks”: the border between the classes was installed in the place where it achieved the best grouping of close values and the maximum difference of values between the classes. Thus the limits between the “integer” values were slightly shifted from continuous values (cf. Fig. 4). The boundaries between the abundance zones of species determined in this way (cf. Fig. 5) were used to calculate the average values of each of 48 climatic variables within every zone of abundance, for each species. The regression analysis of this second matrix was implemented to find the impact of each variable on patterning the distribution of each species.

RESULTS

Patterns of spatial variation and interrelation of climatic factors in the East European plain

The climate maps of EEP in Fig. 3 illustrate gradual decrease of the temperature to the north and the increase of moisture to the west, towards the Atlantic Ocean. However, the overall patterns are complex, being in a rather good congruence with the general vegetation zonation. Being in general sublatitudinal, the boundaries of the zones bend first southwesterly and then towards the southeast, delimiting semi-desert and desert territories by a semicircle.

Variation of mean annual temperature is nonlinear. In southern parts of EEP, isotherms are sublatitudinal, in

its northern parts they bend from northwest to southeast (Fig. 3, A). Winter isotherms are sublongitudinal, (Fig. 3, C), while summer isotherms have a sublatitudinal direction (Fig. 3). However, the temperature distribution is affected not only by the direct solar radiation, but also by the circulation of air masses and the presence of large water bodies (Alisov, 1956).

There are two atmospheric fronts in the EEP: the Arctic and the Atlantic ones. In summer Atlantic air masses dominate, while in winter winds from the Arctic prevail. Especially noticeable is an increase of precipitation at the Valday Upland and in the Smolensko-Moskovskaya Upland, where the Atlantic air leaves a considerable portion of its humidity (Figs. 3, D, E).

Relative humidity in the north (Arkhangelsk Province) and Northwest (Karelia) is quite high, over 60%, especially in summer (Figs. 3 G-I). In general, relative humidity in the cold time of the year is uneven and in the warm period it increases towards the oceanic regions, so its contours overlap beyond the boundaries of vegetation zones and isotherms of the warm period (Fig. 3, G-J).

Amount of monthly precipitation of the warm period in early summer is highest in the Middle zone of EEP (Fig. 3, K). In late summer, precipitation is maximum in the Northwest (Fig. 3, L).

No correlation has been revealed between mean annual temperature and annual precipitation, precipitation and temperature of summer and winter across localities (Table 2). However, the cross-comparison of (a) monthly relative humidity with (b) monthly rainfall and (c) average monthly temperature reveals an interesting and definite pattern. Among others, a strong positive correlation between monthly rainfall and relative humidity is observed in the late summer to mid-autumn period, *i.e.*, August to October (Table 3). In the same period, there is a strong negative correlation between rainfall and temperature (Table 4). In other words, the higher hydration is achieved in the more northern areas of EEP. However, strong negative correlation between monthly mean temperatures and relative humidity does not change during the whole year (Table 3); this fact indicates that the saturation of air with water vapor is always higher in the north of EEP.

Thus, in the autumn and summer periods relative humidity depends directly on the rainfall and indirectly on the temperature. This rule is especially important in a view of the second peak of active growth of *Sphagnum* during the vegetation period (Grabovik & Antipin, 1982).

Patterns of distribution of species of the section *Sphagnum* on the East European Plain

Six *Sphagnum* species of the section *Sphagnum* known in EEP are characterized by rather different distribution patterns (Figs. 4, 5). The role of different climatic variables in their patterning is shown in Table 5. Already simple visual comparison of maps of distribution of moisture factors (Fig. 3G, L) and occurrence of *Sphagnum* species (Fig. 4, 5) reveals that *Sphagnum* are more diverse in more

humid areas in the Northwest of European Russia and in the Baltic States. Most important are the high rainfall and relative humidity in autumn and summer. However, the obtained data reveal some more details explaining species patterning.

Contribution of climatic variables to the explanation of species distribution is summarized in Figs. 6–9. Table 6 provides data confirming a high level of explanatory capability of the climatic data.

DISCUSSION

Sphagnum palustre

This species occurs in the forest, forest-steppe and steppe zones in the Central and Western regions of EEP (Fig. 4A). It reaches the highest frequency at its western borders (Fig. 5A), however its abundance never exceeds 4 in local floras. Correlation analysis shows that most important factors determining its distribution are the amount of precipitation in summer and the sum of precipitation for months of spring and summer (Table 5). Strong correlation with precipitation is observed already in March and April (Table 5), unlike other species of the section *Sphagnum* discussed here. Since that time *Sphagnum palustre* begins its first peak of active growth (Grabovik & Antipin, 1982), which seems to be most important for this species. Unlike *S. magellanicum*, *S. centrale* and *S. papillosum*, there is a positive correlation of the abundance of *S. palustre* with temperature characteristics, but it is weak for the summer period and rather strong for winter months (Table 5). This means that *S. palustre* reaches the highest abundance in regions with short, warm winters. Fig. 6 shows that the relative humidity in summer months remains about the same in the area where *S. palustre* occurs, never dropping below 60%.

The comparison of Fig. 3 and 5A indicates that the northern boundary of «very rare» zone of *S. palustre* is parallel to the isotherms of winter temperatures, while its southern border depends on summer temperatures and follows isolines of relative humidity in late summer. This means that *S. palustre* is sensitive to the decrease of winter temperatures (and, apparently, related to a reduction in the duration of the winter period) and to the increase of summer temperatures (and the associated decrease in precipitation and humidity), and these factors restrict the distribution of this species. The larger part of its distribution is confined to the areas with maximum relative humidity and precipitation of the warm period (Fig. 3, D, E, G, K).

Thus, *S. palustre* tends to be common in areas with the suboceanic climate. Gignac & Vitt (1990) also referred this species as suboceanic, basing on their studies of transect crossing the different types of climate in Western Canada.

The regression analysis shows that the occurrence of *S. palustre* in the EEP is determined by climatic factors at 90.6% (Table 6).

Table 2. The Pearson correlation coefficient between indicators of moisture and temperature for different periods of the year (the transcript notation see table. 1) (all values at level $p < 0.05$).

	pr_wtq	pr_wtm	pr_wmq	pr_drq	pr_drm	pr_clq	pr_a
t_wtq	-0.359535	-0.289570	-0.291563	0.016944	-0.033481	0.076180	-0.348773
t_wmq	-0.388909	-0.318326	-0.355634	0.096391	0.045213	0.166367	-0.353339
t_drq	-0.230896	-0.195838	-0.232799	0.310200	0.279664	0.383091	-0.154659
t_clq	0.020720	0.038853	0.004990	0.362679	0.281148	0.265806	-0.010605
amt	-0.147676	-0.110268	-0.141448	0.290921	0.219295	0.257793	-0.148296

Table 3. The Pearson correlation coefficient between the monthly rainfall, average monthly temperature and average monthly relative humidity (transcript notation see table. 1) (all values at level $p < 0.05$)

	reh01	reh02	reh03	reh04	reh05	reh06	reh07	reh08	reh09	reh10	reh11	reh12
pr01	-0.0417											
pr02		-0.5141										
pr03			-0.3250									
pr04				0.0338								
pr05					0.1886							
pr06						0.3913						
pr07							0.4952					
pr08								0.7379				
pr09									0.7744			
pr10										0.7324		
pr11											0.3021	
pr12												-0.0757
tm01	-0.7885											
tm02		-0.8297										
tm03			-0.7693									
tm04				-0.7228								
tm05					-0.6130							
tm06						-0.6231						
tm07							-0.8150					
tm08								-0.9020				
tm09									-0.8662			
tm10										-0.7951		
tm11											-0.8983	
tm12												-0.8405

Table 4. The Pearson correlation coefficient between the monthly rainfall and average monthly temperature (the transcript notation see table. 1) (all values at level $p < 0.05$)

	pr01	pr02	pr03	pr04	pr05	pr06	pr07	pr08	pr09	pr10	pr11	pr12
tm01	0.1325											
tm02		0.5014										
tm03			0.3768									
tm04				0.1978								
tm05					-0.0202							
tm06						-0.0878						
tm07							-0.3257					
tm08								-0.6737				
tm09									-0.7627			
tm10										-0.6793		
tm11											-0.1717	
tm12												0.2513

Sphagnum centrale

This species occurs in all zones, from tundra to steppe, but its frequency declines both to the south and to the north of the forest zone. Its maximum abundance was found in the Northwestern region of European Russia (Figs. 4, 5). Maximum abundance in local floras reaches 4 according to the adopted scale.

The abundance of *S. centrale* has fairly strong positive correlation with the precipitation and relative humidity in the period from late summer to mid autumn (August–October) and negative correlation with the temper-

ature in this period. Thus, its distribution covers the whole forest zone, generally following patterns of precipitation and humidity in EEP (Fig. 3). Negative correlation of its occurrence with summer temperatures results in the increase of its abundance towards the Northwest.

Southern border of the area where *S. centrale* is rare (*i.e.*, zones *r(n)* and *r(s)* in Fig. 5) are parallel to the isotherms of the warm period of the year (Fig. 3B). The area of its maximum frequency more or less coincides with the zone of maximum rainfall in August (Fig. 3L), and in September and October. Thus, the limiting climatic fac-

Table. 5. The Pearson correlation coefficient between the values of climatic factors and species abundance and number of species (count_sp). Bold highlighted values of $r > 0.5$ in absolute value. The statistically significant values are marked by asterisk * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. All values for *Sphagnum affine* are non significant at $p > 0.05$.

	<i>palustre</i>	<i>centrale</i>	<i>magellanicum</i>	<i>papillosum</i>	<i>austinii</i>	<i>affine</i>	count_sp
reh04	-0.03**	0.58***	0.62***	0.50***	0.26*	0.05	0.39***
reh05	0.04***	0.44***	0.4***	0.44***	0.40*	0.01	0.34***
reh06	0.29***	0.52***	0.51***	0.60***	0.53***	0.04	0.54***
reh07	0.29***	0.67***	0.67***	0.71***	0.52***	0.05	0.63***
reh08	-0.02***	0.69***	0.72***	0.57***	0.26*	0.08	0.45***
reh09	-0.08***	0.72***	0.74***	0.53***	0.18*	0.08	0.42***
reh10	-0.14***	0.70***	0.74***	0.42***	0.05*	0.02	0.36***
pr_wtq	0.53***	0.64***	0.66***	0.63***	0.50***	0.15	0.75***
pr_wtm	0.53***	0.61***	0.60***	0.58***	0.41*	0.15	0.72***
pr_wmq	0.53***	0.62***	0.63***	0.60***	0.48*	0.09	0.73***
pr_drq	0.49***	0.14***	0.18***	0.27***	0.34*	0.10	0.41***
pr_drm	0.44***	0.13***	0.19***	0.25***	0.30*	0.09	0.38***
pr_clq	0.40***	0.07*	0.10***	0.15***	0.18*	0.11	0.29***
pr_a	0.49***	0.62***	0.66***	0.58***	0.46*	0.15	0.69***
tm01	0.44***	-0.31***	-0.33***	0.03**	0.40*	0.05	0.09***
tm02	0.47***	-0.27***	-0.29***	0.04**	0.41*	0.05	0.12***
tm03	0.45***	-0.34***	-0.34***	-0.07**	0.36*	0.04	0.05***
tm04	0.29***	-0.60***	-0.61***	-0.32**	0.13*	-0.04	-0.20***
tm05	0.22***	-0.66***	-0.67***	-0.40***	0.01*	-0.04	-0.29***
tm06	0.16***	-0.69***	-0.70***	-0.46***	-0.06*	-0.05	-0.34***
tm07	0.06***	-0.71***	-0.71***	-0.55***	-0.18*	-0.05	-0.44***
tm08	0.20***	-0.67***	-0.67***	-0.42***	0.00*	-0.03	-0.30***
tm09	0.26***	-0.63***	-0.63***	-0.34***	0.12*	-0.02	-0.24***
tm10	0.39***	-0.46***	-0.46***	-0.13***	0.31*	0.02	-0.04***
tm11	0.42***	-0.38***	-0.39***	-0.05*	0.36*	0.04	0.02***
tm12	0.43***	-0.34***	-0.36***	0.00***	0.37*	0.05	0.06***
pr01	0.27***	-0.01***	0.03***	0.04**	0.05*	0.08	0.14***
pr02	0.40***	-0.08**	-0.06***	0.07**	0.18*	0.09	0.18***
pr03	0.52***	0.25***	0.30***	0.39***	0.48*	0.16	0.48***
pr04	0.54***	0.24***	0.28***	0.36***	0.40*	0.09	0.50***
pr05	0.45***	0.37***	0.39***	0.34***	0.36*	-0.03	0.50***
pr06	0.53***	0.39***	0.42***	0.45***	0.42*	0.00	0.58***
pr07	0.54***	0.61***	0.60***	0.54***	0.40*	0.08	0.71***
pr08	0.31***	0.81***	0.85***	0.73***	0.40*	0.16	0.72***
pr09	0.10***	0.76***	0.83***	0.56***	0.25*	0.13	0.55***
pr10	0.01***	0.72***	0.76***	0.47***	0.05*	0.14	0.42***
pr11	0.34***	0.58***	0.62***	0.50***	0.29*	0.15	0.54***
pr12	0.43***	0.23***	0.26***	0.25***	0.26*	0.15	0.38***
amt	0.36***	-0.51***	-0.51***	-0.21***	0.26*	0.00	-0.09***
t_wtq	0.17***	-0.62***	-0.64***	-0.42***	-0.09*	-0.06	-0.29***
t_wmq	0.17***	-0.69***	-0.70***	-0.46***	-0.06*	-0.04	-0.34***
t_drq	0.25***	-0.50***	-0.51***	-0.25***	0.17*	0.01	-0.18***
t_clq	0.45***	-0.28***	-0.31***	0.04***	0.40*	0.04	0.11***

Table. 6. Indicators of the quality of the regression analysis

	Multiple R	R ²	St. err.	F	df	p-level
<i>S. palustre</i>	0.95199461	0.90629374	0.352617792	8863.66	48,43990	0.000000
<i>S. centrale</i>	0.97774316	0.95598168	0.254552183	19903.47	48,43990	0.000000
<i>S. magellanicum</i>	0.97324380	0.94720350	0.370147647	16441.86	48,43990	0.000000
<i>S. papillosum</i>	0.95854016	0.91879923	0.327381372	10369.87	48,43990	0.000000
<i>S. austinii</i>	0.91858434	0.84379719	0.097454125	4950.64	48,43990	0.000000
<i>S. affine</i>	0.69103505	0.47752944	0.111912753	837.62	48,43990	0.000000
Count_sp	0.96623643	0.93361283	0.349143500	12888.29	48,43990	0.000000

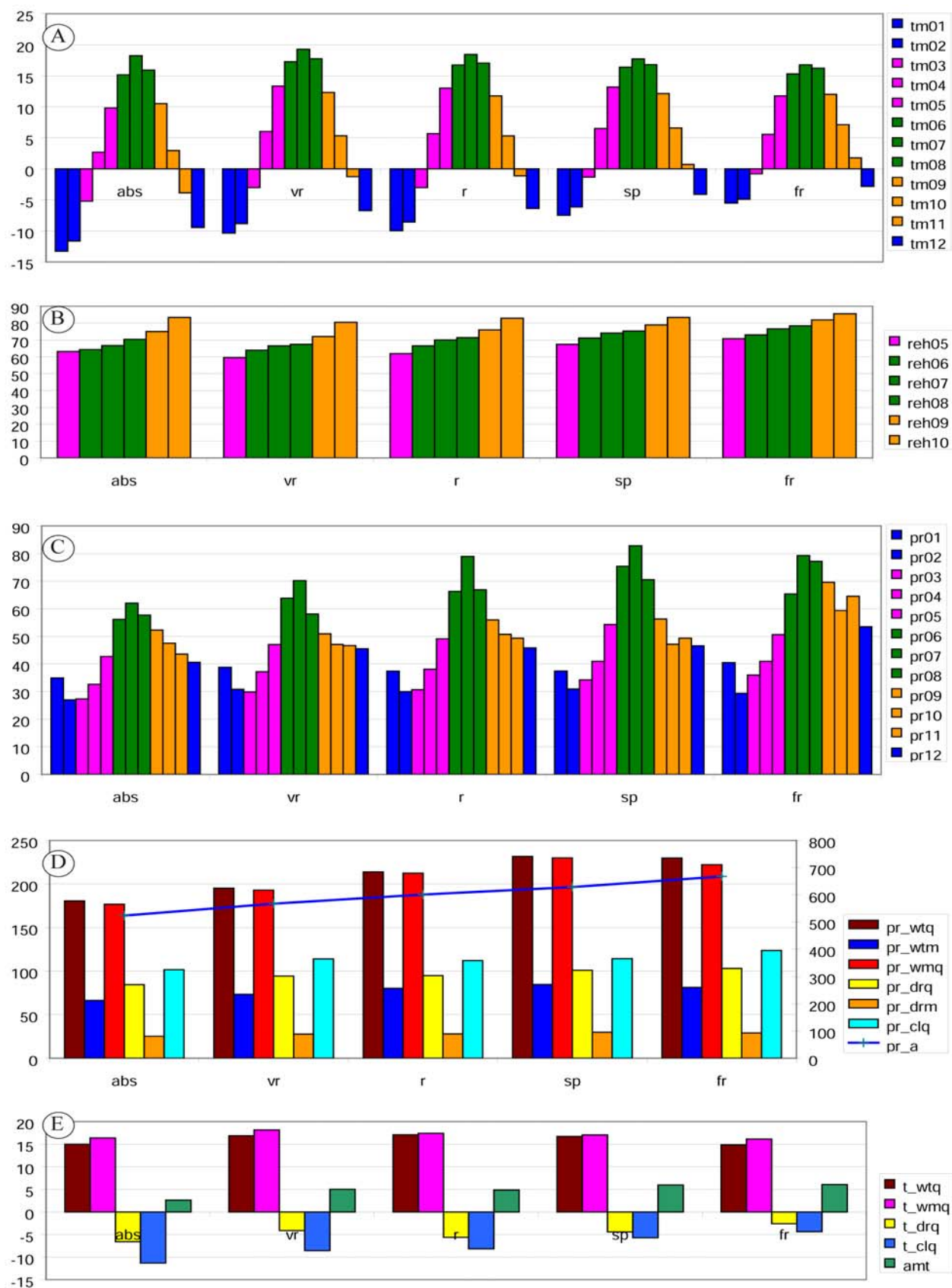


Fig. 6. Absolute values of climatic variables (see Table 1 for abbreviations) for *zones of abundance* (shown in Fig. 5) of *Sphagnum palustre*: A – temperature, monthly; B – relative humidity, warm months only; C – precipitation, monthly; D – precipitation (blue line indicates annual precipitation, with scale on the right; bars show precipitation by selected periods, their scales are on the left); E – temperature of selected periods.

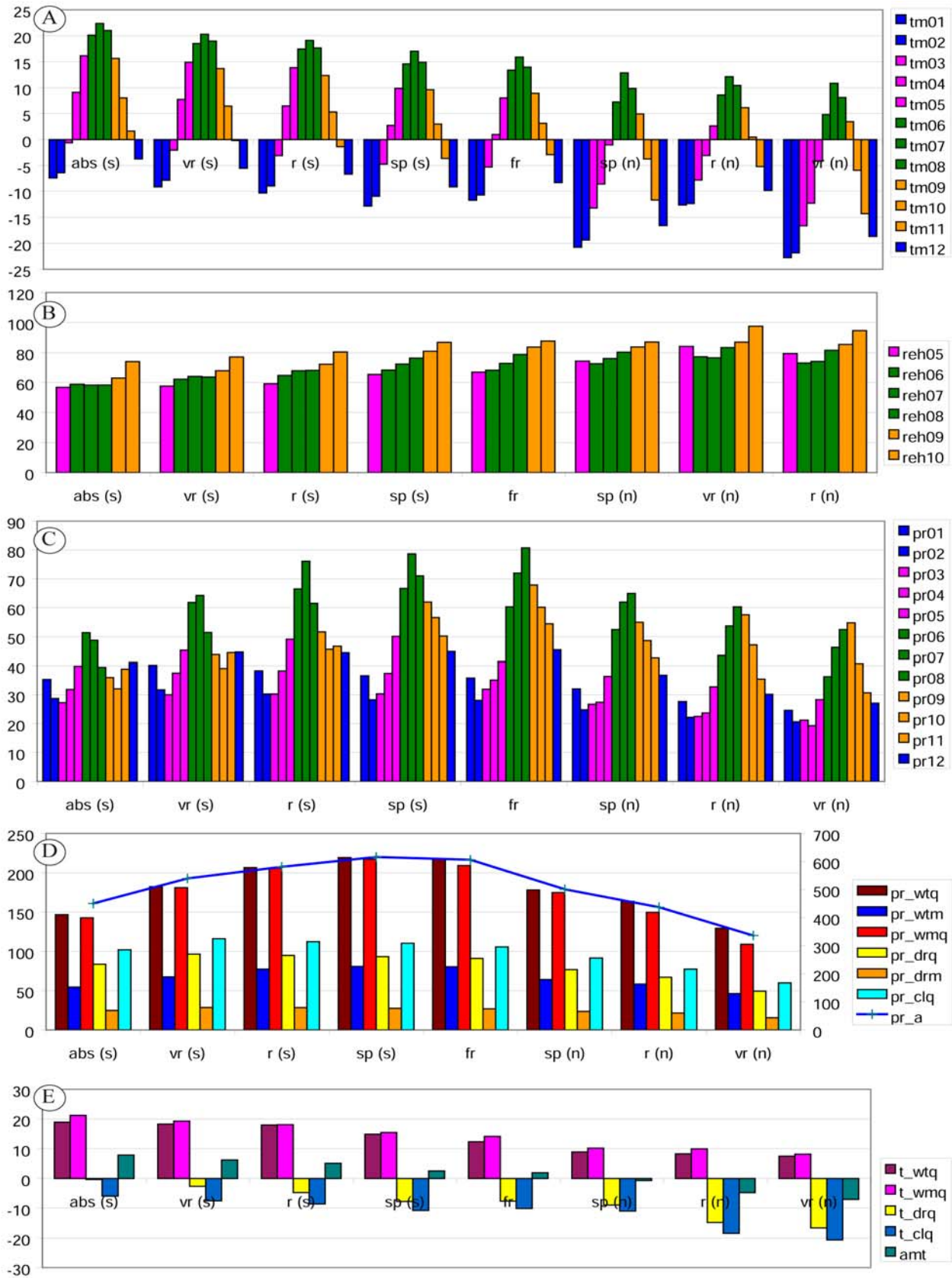


Fig. 7. Absolute values of climatic variables (see Table 1 for abbreviations) for *zones of abundance* (shown in Fig. 5) of *Sphagnum centrale*: A – temperature, monthly; B – relative humidity, warm months only; C – precipitation, monthly; D – precipitation (blue line indicates annual precipitation, with scale on the right; bars show precipitation by selected periods, their scales are on the left); E – temperature of selected periods.

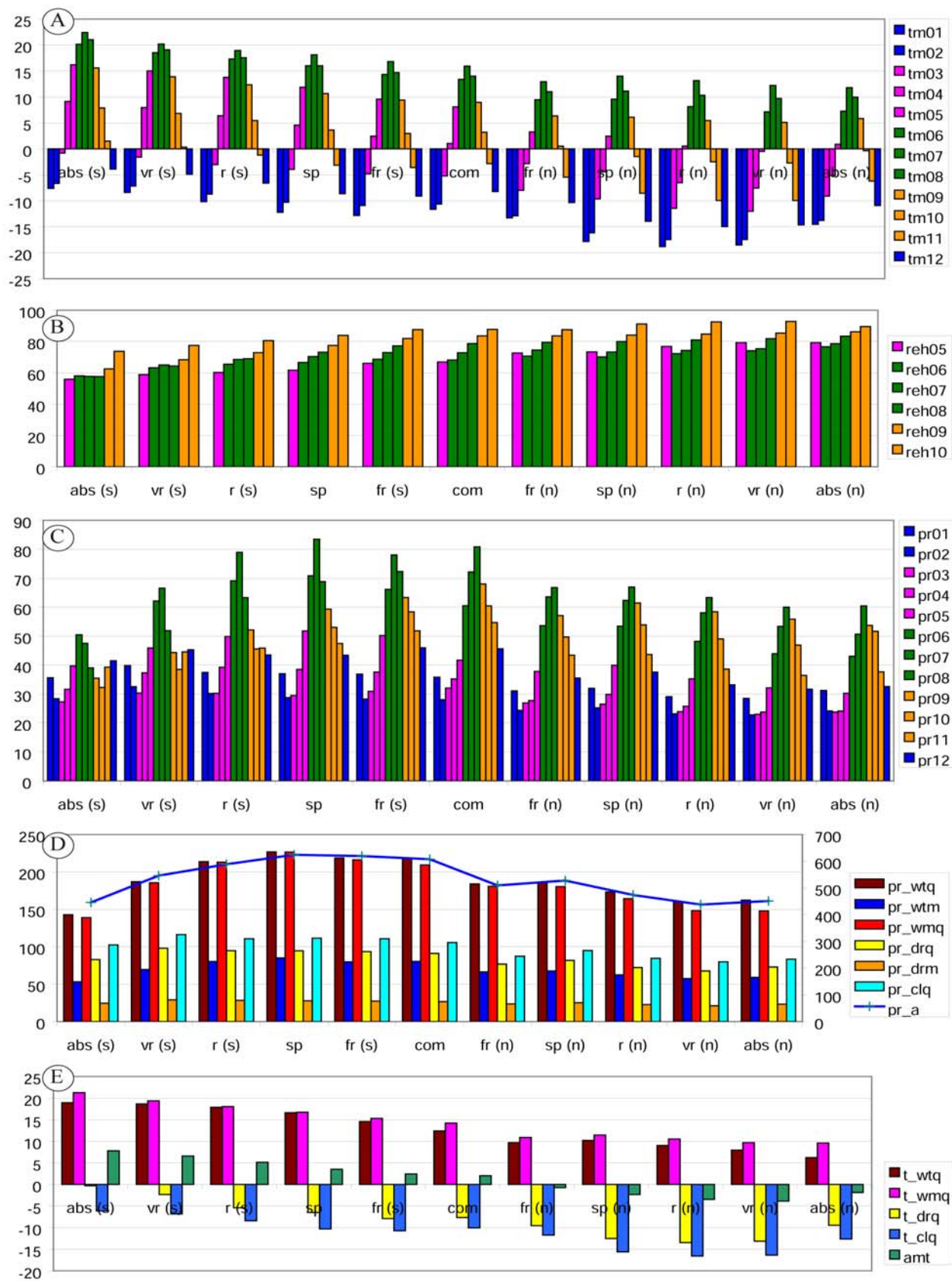


Fig. 8. Absolute values of climatic variables (see Table 1 for abbreviations) for *zones of abundance* (shown in Fig. 5) of *Sphagnum magellanicum*: A – temperature, monthly; B – relative humidity, warm months only; C – precipitation, monthly; D – precipitation (blue line indicates annual precipitation, with scale on the right; bars show precipitation by selected periods, their scales are on the left); E – temperature of selected periods.

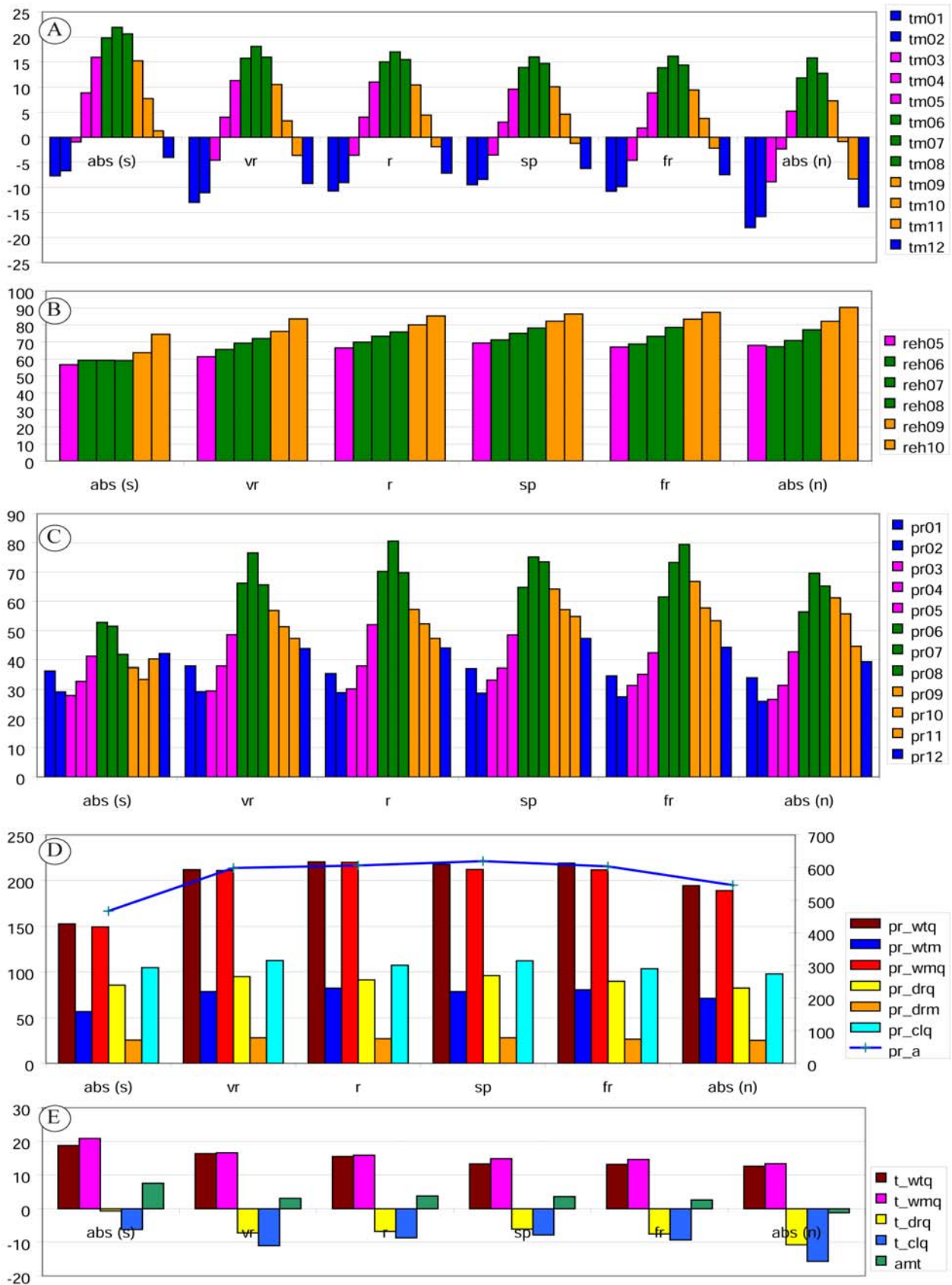


Fig. 9. Absolute values of climatic variables (see Table 1 for abbreviations) for *zones of abundance* (shown in Fig. 5) of *Sphagnum papillosum*: A – temperature, monthly; B – relative humidity, warm months only; C – precipitation, monthly; D – precipitation (blue line indicates annual precipitation, with scale on the right; bars show precipitation by selected periods, their scales are on the left); E – temperature of selected periods.

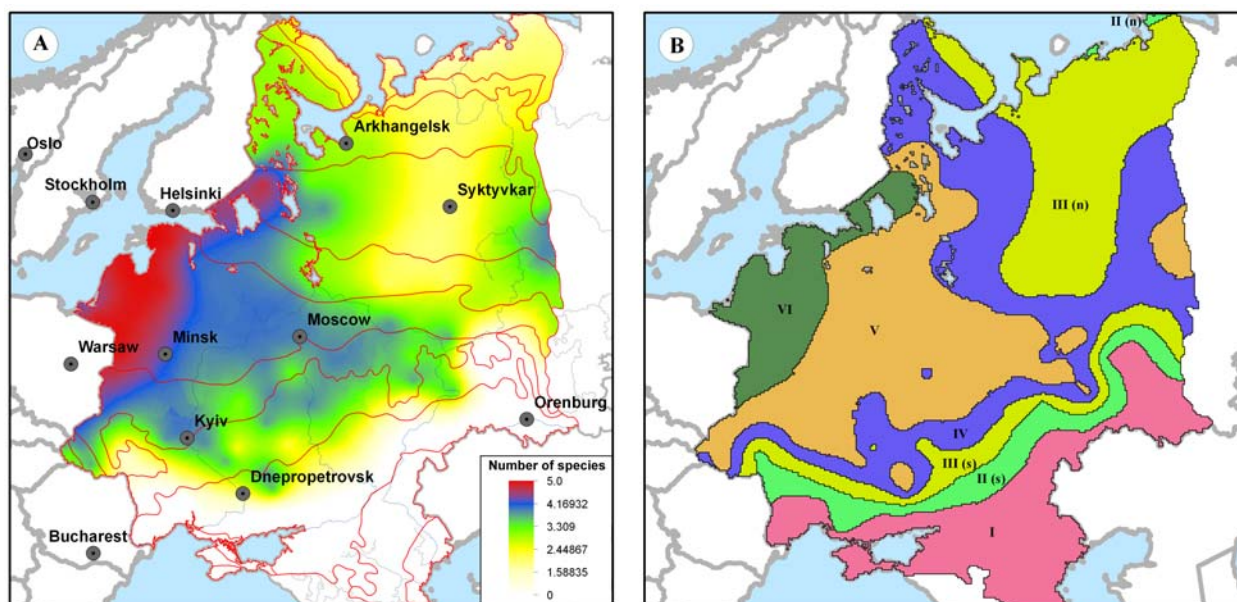


Fig. 10. Diversity of species of *Sphagnum* section *Sphagnum* in the territory of East European Plain. A – model map of species diversity; B – zones of diversity: zone I: 0 species; II: 1; III: 2; IV: 3; V: 4; and VI: 5 species; (n) Northern subzones, (s) – Southern subzones.

tors of *S. centrale* are summer temperatures, not too hot and not too cold, while the climatic optimum is determined by rainfall in autumn and summer. The requirements in humidity above 60% during the growing season and annual precipitation of 600 mm are apparent from Fig. 7. These conclusions are similar to those obtained by Melosik (2006) for Poland.

The regression analysis shows that the occurrence of *S. centrale* in EEP is determined by climatic factors at 95.5% (Table 6).

Sphagnum magellanicum

Distribution maps of *S. magellanicum* (Figs. 4, 5) show dependence of its distribution on temperature, precipitation and air humidity (Fig. 3).

Similar to *S. centrale*, *S. magellanicum* occurs from tundra to steppe zones, increasing its abundance to the Northwestern part of European Russia. Correlation analysis reveals the same trends as were detected for *S. centrale* (Table 5). Borders between zones of its sporadic / rare abundance follow summer temperatures, both in the north and in the south.

Contrary to *S. centrale*, *S. magellanicum* has a higher abundance in peatlands; it dominates in raised bogs and oligotrophic mires and often reaches the maximum value of abundance, 5 in local floras. Similar to other species, its abundant presence requires no less than 60% relative humidity during all months of the vegetation period (Fig. 8C) and no less than 550 mm of annual precipitation (Fig. 8D).

The regression analysis shows that the occurrence of *S. magellanicum* in EEP is determined by climatic factors at 94.7% (Table 6).

Sphagnum papillosum

This species is more common in oceanic climates and in the mountains, thus the boundaries of its abundance

zones cross boundaries of vegetation zones and isotherms (Fig. 4, 5D). It has maximum abundance in the North-western parts of EEP, where it reaches the value 4 in local floras.

Its abundance positively correlates with relative humidity of all months of the growing season, although the strongest values of this correlation are in August to October, *i.e.* similar to other species. Apparently, it is less sensitive to temperature than to humidity, although it certainly avoids too cold and too hot regions. Its absence between the Urals and central regions of European Russia can be explained by extremely low humidity in the first half of summer (Fig. 3G-H).

The regression analysis shows that the occurrence of *S. papillosum* in the EEP is determined by climatic factors at 91.8% (Table 6).

Sphagnum austinii and *S. affine*

These two species were recorded in Russia only after Flatberg (1984) worldwide revision of the *S. imbricatum*-complex, and subsequent study of this group in Russia by Maximov (2007). Therefore, in the mapping of the distribution of these species, we primarily rely on the data of their distribution in the countries adjacent to Russia (Abolin, 1968; Ingerpuu & Vellak, 1995; Melosik, 2006; Dite *et al.*, 2007; Ingerpuu *et al.*, 2014). We refer the records of *Sphagnum imbricatum* in Belarus (Pidoplichko, 1948; Rykovskiy & Maslowski, 2009) and Kaliningrad Province (Napreenko, 1999) to *Sphagnum austinii*, based on the data on their distribution given by Maksimov (2007) and the presence of *S. austinii* in the neighboring western floras.

S. austinii and *S. affine* are extremely rare in EEP. This made impossible to conduct a multivariate analysis of their distribution data at a significance level of $p < 0.05$. Therefore, the results of correlation and regression

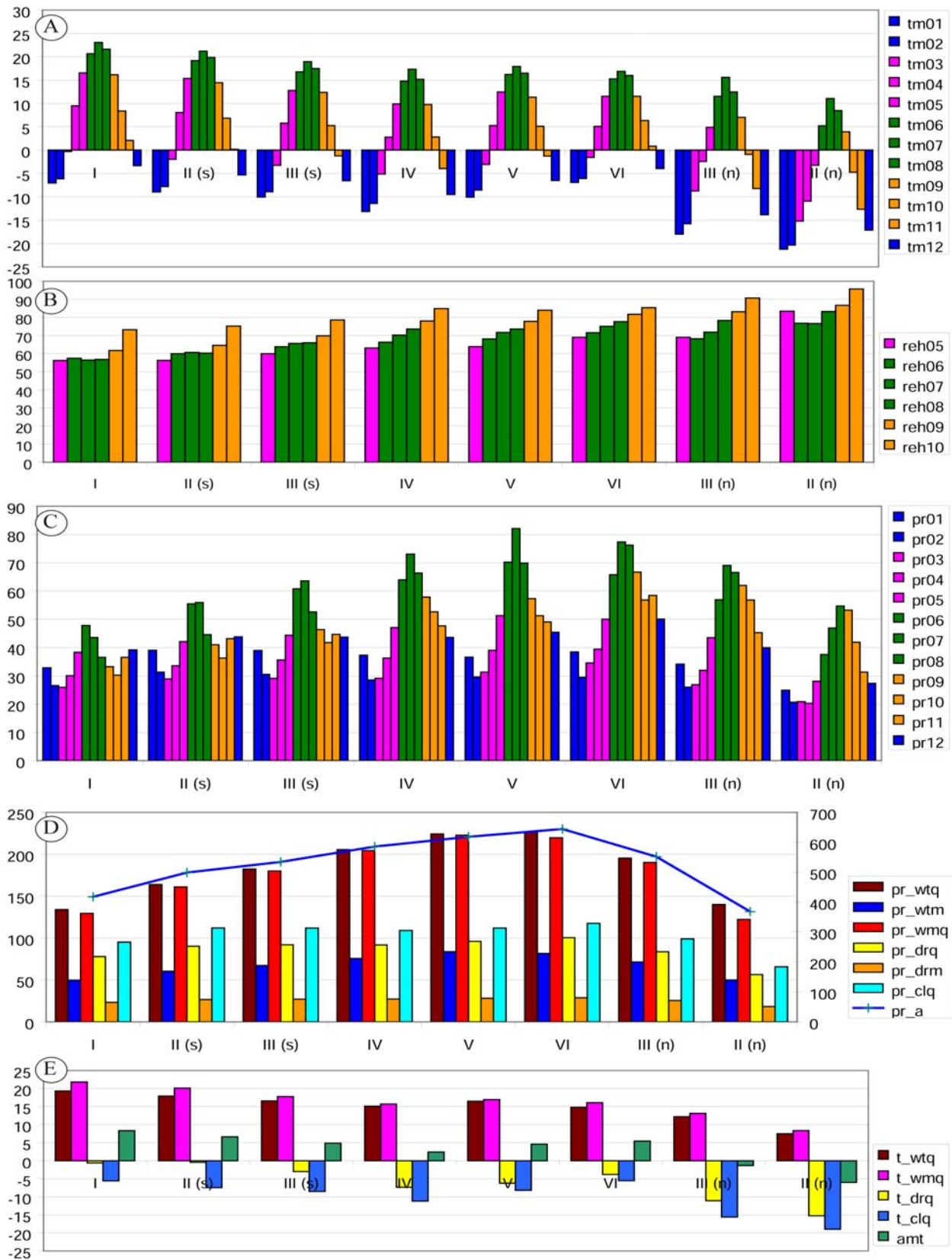


Fig. 11. Absolute values of climatic variables (see Table 1 for abbreviations) for the **zones of diversity** (shown in Fig. 10). Zones have the following number of species: I – 0; II – 1; III – 2; IV – 3; V – 4; VI – 5; (n) the northern subzone, (s) – southern subzone. A – temperature, monthly; B – relative humidity, warm months only; C – precipitation, monthly; D – precipitation (blue line indicates annual precipitation, with scale on the right; bars shows precipitation by selected periods, their scales are on the left); E – temperature of selected periods.

analyses presented in Tables 5 and 6 should be considered statistically unreliable. In other words, the question of the distribution of these species on the territory of EEP requires further research.

* * *

The maps of the species distribution presented above (Figs. 4–5) are similar in showing the great abundance of species in regions closer to the Baltic Sea. This looks natural, as they have most humid climate as compared with other parts of the study area. The areas where *Sphagna* are common are generally outlined by the values of annual precipitation not less than 550 mm, relative humidity not less than 60–70% and precipitation of warmest quarter of at least 150–200 mm.

Two species, *S. palustre* and *S. papillosum*, are rather sensitive to moisture. They start to decline when the annual precipitation become less than 600 mm and relative humidity – lower than 70% of (Figs. 6, 9). Such high values are atypical for the area as a whole, being more common near the Baltic Sea only. Apparently, *S. affine* and especially *S. austinii* also strongly depend on the more oceanic climate, despite the unreliable data due to species rarity. However, their range in Europe (Flatberg, 1984; Ros *et al.*, 2013) and absence in the eastern part of European Russia and Siberia (Maksimov, 2007) definitely indicate their oceanic or suboceanic ecology.

The diversity of species of the *Sphagnum* section *Sphagnum* in the territory of the East European Plain.

Maps in Fig. 10 show that the highest species diversity of section *Sphagnum* is in the western part of EEP, the wettest region within the study area. The leading factors found in the correlation analysis (Table 5) include the relative humidity, precipitation of the warm period and precipitation of the summer months. The pairwise analysis in Fig. 11C,D also confirms that number of species in the diversity zones depends primarily on precipitation.

In contrast to the higher abundance of individual species in wetter regions of EEP, the species diversity also increases in mountain areas, *e.g.*, in the Urals and Carpathians, which is a common pattern in mosses in general (Ignatov, 1993). A noteworthy zone of low species diversity between the Urals and Central regions of Russia, zone **III(n)** is explained by the rarity of *S. papillosum*, which can not tolerate extensive periods of low air humidity in late spring and in the first half of summer. Nold and thus relatively dry Arctic air masses affect this area (Alisov, 1956). In addition, the route of occasional dry air masses from Kazakhstan follows along the Cis-Urals, contributing to overall continentality of the region (Alisov, 1956).

In the south. *Sphagnum* species penetrate to the steppe zone, where peat mosses occur in floodplain swamps and in *Betula* stands in swampy depressions (Blagoveschenskij & Blagoveschenskaya, 1982; Boiko, 2009).

The regression analysis reaffirms that the number of

species in the East European Plain is generally determined by all climatic factors (Table 1) at a high significance level (93.3%) (Table 6).

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