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# NUTRIENT DEMAND AND ELEMENTAL STOICHIOMETRY OF PLANTS IN WETLAND ECOSYSTEMS IN THE BIEBRZA VALLEY, POLAND\*

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## ABSTRACT

The study was conducted in the wetland ecosystems in the Biebrza Valley, on peat soils with a varying degree of peat mineralization. The aim of this work was to assess differences between the content of elements in wetland plants and the effect of these differences on the plant elemental stoichiometry. The content of particular elements in a mass unit and the sum of the content of elements in the unit, i.e. in the biological yield, correspond with the nutrient demand of the plants. The content of N, P, K, Ca, Mg, Na and S in  $\text{mg kg}^{-1}$  d.w. was determined in aerial parts of various plant species (including leaves of shrubs), and the sum was calculated of all the concentrations of elements in  $\text{mmol}(+) \text{kg}^{-1}$ . The inter-elemental relationships were determined as: (i) an element: element ratio for each element, in  $(\text{mmol}(+) \text{kg}^{-1})$ , and (ii) the percent contribution of each element to the sum of elements. The values of nutrient demand for the species examined varied from about  $1000 \text{ mmol}(+) \text{kg}^{-1}$  d.w., to more than  $6000 \text{ mmol}(+) \text{kg}^{-1}$  d.w. Based on significant differences in the values of the sums of element, the species analyzed were split into five groups: up to  $2300 \text{ mmol}(+) \text{kg}^{-1}$ ,  $2301\text{-}3500 \text{ mmol}(+) \text{kg}^{-1}$ ,  $3501\text{-}4500 \text{ mmol}(+) \text{kg}^{-1}$ ,  $4501\text{-}6000 \text{ mmol}(+) \text{kg}^{-1}$  and above  $6000 \text{ mmol}(+) \text{kg}^{-1}$ , respectively. Meanwhile, the stoichiometry presented in the form of either an element: element ratio or the percent contribution of each element to the sum of elements did not differ significantly between plants with various nutrient demands.

**Keywords:** peat mineralization, wetland plant species, relationships between elements.

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## INTRODUCTION

The production of crop biomass in a given space at a given time is driven by multiple factors. All the factors contribute to controlling the rate of biomass production, the quantity of elements utilized for this production, as well as the plant's elemental stoichiometry. According to STERNER and ELSER (2002), the yield understood in the biological sense, as a mass unit produced with the use of a definite quantity of elements, corresponds to the nutrient demand and depends on properties of plant species. According to Liebig's theory of nutrient accumulation in plants, the plant's nutrient demand may be described using the content of individual elements required for producing a mass unit and the sum of the content of all elements in the biological yield (OSTROWSKA 1987).

The physiological role of an element in a plant affects its stoichiometry. At the lowest variable carbon content in plants (THOMAS, MALCZEWSKI 2007, STOLARSKI et al. 2008), it is other elements that determine the relationships between C and the other elements. In both biological yield and crop biomass, the elemental stoichiometry of a plant may be and, in fact, is significantly disturbed, compared to the plant's nutritional requirements, either by the real or supposed deficiencies or excesses of respective elements in the plant's growth environment. The excess of elements is caused mainly by the anthropogenic supply of one element, ignoring the plant's demand for other elements (OSTROWSKA, POREBSKA 2002, 2009).

Nitrogen (N) is a particular element that interferes with the elemental stoichiometry (OSTROWSKA, POREBSKA 2009), not only in plants. An inflow of N to the aquatic environment disturbs the balance between N and P, which results in an increased value of the N:P ratio along with an increase in the production of nitrogen-rich toxins by phytoplankton (VAN DE WAAL et al. 2014). According to GÜSEWELL (2005), the negative impact of high N deposition on species diversity in wetlands might be mitigated by P fertilisation.

SARDANS et al. (2012) suggest that plant growth conditions are not the only factor responsible for the relationships between elements, as the latter also depend on properties of a species, its development phase and/or element distribution within a plant, thus on the plant part examined. Plant metabolism was suggested by RIVAS-UBACH et al. (2012) to be the main factor behind the plant's elemental stoichiometry.

Our previous results showed that under the crop's growth conditions the main factor interfering with the plant's elemental stoichiometry is selective fertilization, i.e. using only one or a few elements (OSTROWSKA, POREBSKA 2002, 2009). Under natural conditions, the amounts of nutrients utilized by plants depend on the soil quality and the anthropogenic deposition of various elements. In the case of peat soils, nutrient availability to plants depends mainly on the degree of peat mineralization, as discussed in another paper (SIENKIEWICZ et al., in press).

The aim of this study was to assess differences between plant species of wetland ecosystems, developed on peat soils in the Biebrza Valley, Poland, in terms of nutritional requirements of plants and their effect on the stoichiometry of elements associated with the degree of peat mineralization.

## MATERIAL AND METHODS

The study was conducted in the wetland ecosystems of the Biebrza Valley, on peat soils with varying degrees of peat mineralization. The study plots were situated along three transects located in the southern, middle and northern basins of the Biebrza Valley, so as to represent locally typical plant communities and soil properties.

The plant communities varied in terms of the hydrological conditions and degree of peat mineralization in the habitats they occupied. On each study plot, the plant communities were syntaxonomically determined based on the plant species composition.

Soil for analysis was sampled from the three transects at two depths: 0-20 cm and 20-40 cm. The aerial parts of herbaceous plants and leaves of shrubs were sampled from plants growing around the soil profiles. About 100 soil samples, 40 samples of herbaceous plants and circa 10 samples of shrub leaves were analyzed. A summary of the results of soil properties, i.e. the total and dissolved content of macro- and microelements, bulk density, pH, water retention, soil C and N, was previously presented by SIENKIEWICZ et al. (2014). In the present work, we focused on the assessment of plant communities in relation to the peat mineralization, measured by the soil total organic carbon content (TOC).

In the plant samples, after prior preparation (drying, milling), the content of N, P, K, Ca, Mg, Na, S, Mn, Fe, Al, Cu and Zn was determined using the ICP-OES method. In the soil samples, the total content of organic C (TOC) was determined by the combustion method at 1000°C, using a TOC-5000A autoanalyzer (a Shimadzu model), while the total nitrogen content was determined using the Kjeldahl's method.

The content of respective elements in plants is given in mmol(+) kg<sup>-1</sup> d.w. The results were statistically analyzed. The variability of the content of each element was analyzed with ANOVA, and significance of differences was determined by the Tukey's test at  $p = 0.05$ . The elemental stoichiometry in the biomass was limited to macroelements, with the exception of carbon, and the relationship between the elements was shown as a percentage of each element in the sum of all elements per mass unit. In this way, the inter-elemental relationships could be compared in the biological yield of each species. The relationships in mmol(+):mmol(+) between each pair of elements were calculated in parallel.

Altogether, *ca* 50 species of plants were analyzed, and 24 species (at least three samples of each) were selected for comparison of differences between species.

## RESULTS

The analysis of peat soils in the Biebrza Valley showed significant variations in the degree of peat mineralisation, measured by the TOC content. The content of TOC increased from south to north of the Biebrza Valley, from *ca* 3% to *ca* 50%, and this was accompanied by the differentiation of plant communities, from species rich (Transect A) to species poor and even very poor (Transect B) – Figure 1. In all the species examined, the differences in the content of respective elements ranged from 4-5-fold for N, 5-6-fold for P, over 15-fold for K, over 20-fold for Mg, to as much as 40-fold for Ca (Table 1). The coefficients of variation for the mean content of N, P, S and the means of the element sums ranged from 32% to 46%, while those for the content of K, Ca and Mg were from 54% to 88% (Table 1).

The elemental stoichiometry reflects variation in the content of individual elements in the analyzed species, although differences in the values of the element: element ratios are slightly smaller than those in the element content. For example, the N content in the analyzed plants differed 4-5 fold, while the Ca content – approximately 40-fold, whereas the values of the N:Ca ratio varied by 20-30 fold. The values of the element: element ratios, calculated for 53 species on the basis of the average nutrient content, were as follows: N:P – 17.5, N:K – 2.9, N:Ca – 3.1, N:Mg – 5.2, P:K – 0.16, P:Ca – 0.18, P:Mg – 0.30 and Ca:Mg – 1.7.

The mineral composition of the species varied in terms of the content of individual elements, but it was possible to isolate groups of species with similar element content. Based on the values of the sums of the elements in the biological yield, five groups of species were distinguished, which varied in the level of nutrient requirements as follows: to 2300 mmol(+) kg<sup>-1</sup>, 2301-3500 mmol(+) kg<sup>-1</sup>, 3501-4500 mmol(+) kg<sup>-1</sup>, 4501-6000 mmol(+) kg<sup>-1</sup> and above 6000 mmol(+) kg<sup>-1</sup>. Such a division of species was statistically confirmed, since there were significant differences between the above groups in the values of elemental sums, while differences between species inside the groups were insignificant (Table 2).

The percent contribution of the N-content to the sum of elements was found to vary significantly between the above groups of species. Significant differences were also observed in the content of the remaining elements between the plant species which showed the lowest nutrient demand (the sum of elements – up to 2300 mmol(+) kg<sup>-1</sup>) and between those with the highest demand (the sum of elements > 6000 mmol(+) kg<sup>-1</sup>) – Table 2.

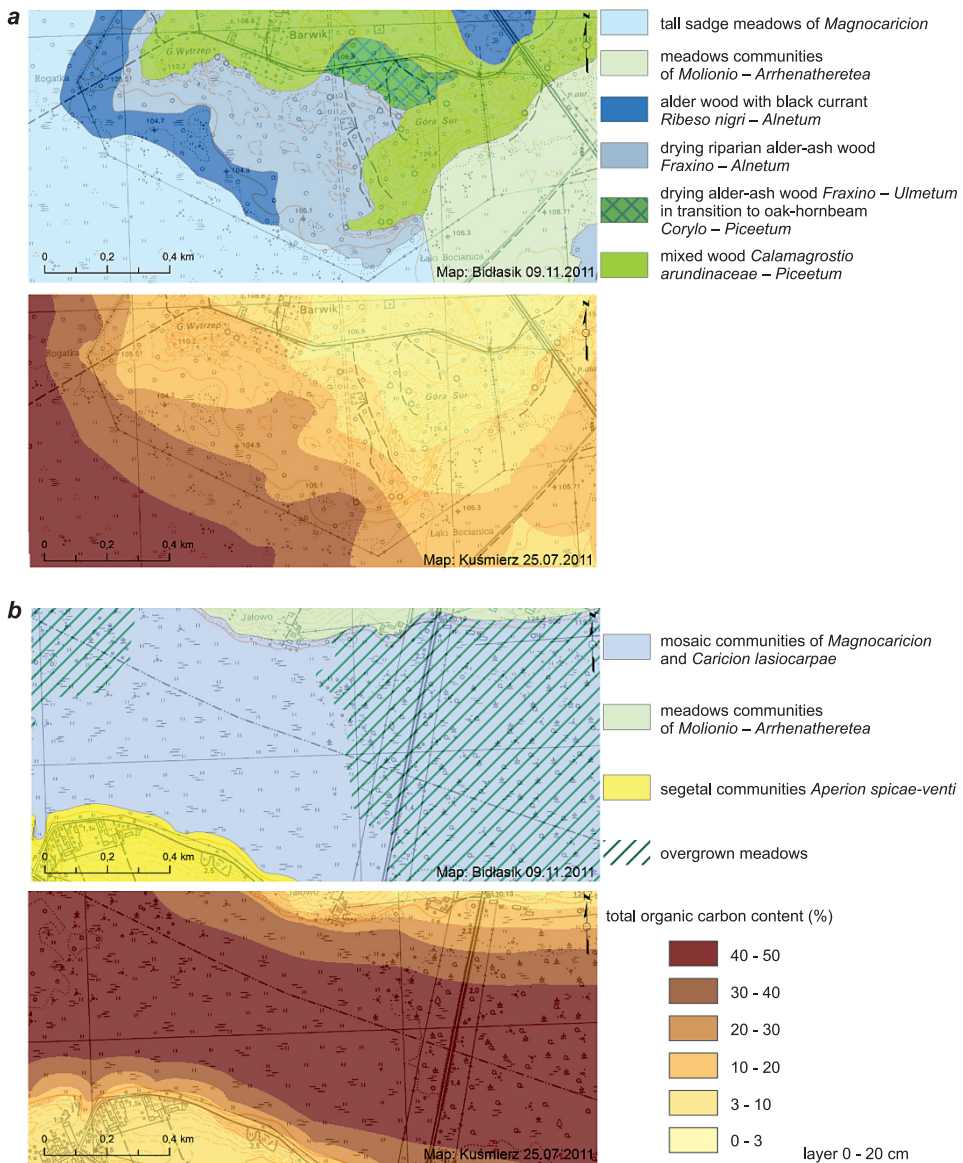


Fig 1. Vegetation and C content in the layer of 0-20 cm of peat soils in Transect 1 (a) and Transect 2 (b). Sources: Basic geodata (Topographic map of Poland in the 1:10 000 scale):  
 a – plant communities: tall sedge meadows, meadow communities of *Molinio – Arrhenatheretea*, drying riparian alder-ash wood, drying alder-ash wood *Fraxino – Ulmetum* in transition to oak-hornbeam *Corylo – Piceetum*, mixed wood *Calamagrostio arundinaceae – Pinetum*, alder wood with black currant *Ribeso nigri – Alnetum*;  
 b – plant communities: mosaic communities of *Magnocaricion* and *Caricion lasiocarpae*, meadow communities of *Molinio – Arrhenatheretea*

Table 1

Content of elements in different plant species in mmol(+) kg<sup>-1</sup>

Plant	N	P	K	Ca	Mg	Na	S	Sum
<i>Aegopodium podagraria</i>	2643	102	764	760	1392	2	131	5794
<i>Angelica sylvestris</i>	2057	138	1046	1148	695	2	312	5398
<i>Asarum europaeum</i>	2071	130	828	1395	420	2	146	4992
<i>Athyrium filix-femina</i>	2077	129	748	306	415	8	169	3852
<i>Calamagrostis arundinacea</i>	1886	113	811	168	205	1	127	3312
<i>Calluna vulgaris</i>	864	33	102	200	134	2	44	1379
<i>Caltha palustris</i>	1571	110	1018	1475	319	n.d.	257	n.d.
<i>Carex acutiformis</i>	1529	76	302	195	186	9	144	2440
<i>Carex nigra</i>	1836	112	323	201	240	2	135	2849
<i>Carex paradoxa (appropinquata)</i>	1186	52	551	247	135	2	103	2276
<i>Carex riparia</i>	1523	94	506	182	190	90	156	2742
<i>Cicuta virosa</i>	2664	118	1603	1395	528	2	178	6488
<i>Comarum palustre</i>	1700	110	556	555	395	11	134	3461
<i>Convallaria majalis</i>	1855	106	805	422	238	2	111	3539
<i>Deschampsia flexuosa</i>	1379	63	263	99	75	1	68	1948
<i>Dryopteris carthusiana</i>	2146	154	553	418	335	8	173	3787
<i>Equisetum fluviatile</i>	1664	177	926	870	262	17	331	4247
<i>Eriophorum vaginatum</i>	1574	93	446	71	134	1	103	2422
<i>Festuca ovina</i>	1207	66	459	70	66	1	82	1952
<i>Filipendula ulmaria</i>	1919	138	617	484	697	4	166	4025
<i>Galeobdolon luteum</i>	2647	141	992	881	582	4	181	5429
<i>Geranium robertianum</i>	2514	134	1108	1065	278	6	191	5296
<i>Geum rivale</i>	1250	100	372	1115	862	2	101	3802
<i>Hepatica nobilis</i>	1736	63	559	710	455	2	150	3675
<i>Humulus lupulus</i>	3586	181	872	1245	653	1	256	6794
<i>Impatiens noli-tangere</i>	2673	152	1195	1384	861	6	190	6461
<i>Lathyrus vernus</i>	2729	87	377	900	281	7	102	4483
<i>Lazula pilosa</i>	1200	84	556	212	265	1	78	2396
<i>Ledum palustre</i>	1093	53	171	309	151	2	55	1834
<i>Majanthemum bifolium</i>	2214	131	856	359	287	2	237	4088
<i>Melampyrum pratense</i>	1871	113	449	535	257	1	124	3350
<i>Menyanthes trifoliata</i>	2436	185	1100	407	215	39	193	4575
<i>Molinia caerulea</i>	1636	53	485	93	136	1	96	2499
<i>Oxalis acetosella</i>	1930	88	603	560	372	3	159	3715
<i>Phalaris arundinacea</i>	1657	50	204	261	85	14	242	2513
<i>Phragmites australis</i>	1989	99	795	130	90	9	197	3309



cont. Table 1

<i>Pteridium aquilinum</i>	1364	123	744	157	173	1	89	2651
<i>Pulmonaria obscura</i>	1700	259	1605	665	176	1	130	4536
<i>Ranunculus acris</i>	2014	151	559	985	382	45	178	4315
<i>Ribes nigrum</i>	2116	139	445	1133	361	2	315	4511
<i>Rubus caesius</i>	2471	146	746	388	669	2	152	4575
<i>Rubus idaeus</i>	2193	93	532	924	519	3	113	4377
<i>Rumex obtusifolius</i>	3136	182	1505	456	447	5	305	6036
<i>Salix aurita</i>	1829	120	364	650	257	2	238	3460
<i>Sambucus nigra</i>	3764	137	785	960	873	1	297	6817
<i>Scirpus silvaticus</i>	1693	89	764	210	144	4	168	3072
<i>Stellaria holostea</i>	1969	91	842	525	424	1	146	3998
<i>Thelypteris palustris</i>	1604	81	389	308	491	3	107	2983
<i>Trientalis europaea</i>	1314	85	897	219	368	1	126	3012
<i>Urtica dioica</i>	2082	78	333	3080	770	3	320	6666
<i>Vaccinium myrtillus</i>	1180	61	234	381	177	2	103	2138
<i>Vaccinium uliginosum</i>	1136	50	168	179	136	1	97	1767
<i>Vaccinium vitis-idaea</i>	857	45	137	265	127	1	56	1488
Mean ( $n = 53$ )	1904	109	660	610	366	7	162	3824
SD	618	43	355	533	262	14	74	1453
V(%)	32	40	54	88	72	219	46	38

SD – standard deviation; V(%) – coefficient of variation

The differentiation between the species with various nutrient demand, assessed according to the content of elements (Table 2), and the percentages of elements in their sum (Table 3), was slightly varied. The percentages of elements in their sum reflect the overall stoichiometry of elements in their mutual interactions. For example, an increase in the share of N in the sum of elements was concurrent with a decline in the share of the remaining elements and vice versa; this regularity is particularly evident in the case of N and Ca.

The comparison of particular species in terms of percentages of elements in their total sum showed similar relationships as did the comparison of groups of species having different nutrient requirements. Significant differences between the shares of the individual elements in their sum were found mainly for the N contribution (Table 4). At the high (> 60%) share of N in the element sum, the share of other elements decreased, particularly the share of Ca (up to several %) and, conversely, when the contribution of N was small, down to approximately 30%, the contribution of Ca increased, even as high as 46 % (Table 4).

Table 2

Mean content of elements in selected groups of plant species in mmol (+) kg<sup>-1</sup>

Sum of elemental content	Number of samples	N	P	K	Ca	Mg	Na	S
mmol(+) kg <sup>-1</sup>		(mmol(+) kg <sup>-1</sup> )						
< 2300	8	1128 <i>a</i>	57 <i>a</i>	250 <i>c</i>	285 <i>a</i>	147 <i>a</i>	1 <i>a</i>	86 <i>a</i>
2301-3500	16	1641 <i>b</i>	91 <i>b</i>	536 <i>a</i>	199 <i>a</i>	211 <i>a</i>	20 <i>a</i>	133 <i>b</i>
3501-4500	13	1965 <i>c</i>	113 <i>c</i>	655 <i>a</i>	584 <i>b</i>	428 <i>b</i>	6 <i>a</i>	159 <i>b</i>
4501-6000	9	2310 <i>d</i>	141 <i>d</i>	894 <i>b</i>	963 <i>c</i>	517 <i>b</i>	20 <i>a</i>	215 <i>c</i>
> 6000	6	2800 <i>e</i>	138 <i>d</i>	1021 <i>b</i>	1575 <i>d</i>	749 <i>c</i>	4 <i>a</i>	243 <i>c</i>

Means followed by the same letters do not differ significantly at  $p = 0.05$ .

Table 3

Mean share (%) of elements in the sum of elemental content in five group of plant species

Mean sum total	N	P	K	Ca	Mg	Na	S
mmol(+) kg <sup>-1</sup>	(%)						
1889 <i>a</i>	57.7 <i>c</i>	2.8 <i>b</i>	12.3 <i>a</i>	15.2 <i>bc</i>	7.6 <i>ab</i>	0.1 <i>a</i>	4.3 <i>a</i>
3086 <i>b</i>	58.3 <i>c</i>	3.2 <i>b</i>	18.8 <i>b</i>	6.9 <i>a</i>	7.4 <i>a</i>	0.7 <i>b</i>	4.7 <i>a</i>
3949 <i>c</i>	50.3 <i>b</i>	2.9 <i>b</i>	16.8 <i>b</i>	14.9 <i>b</i>	10.9 <i>c</i>	0.1 <i>a</i>	4.1 <i>a</i>
4994 <i>d</i>	45.7 <i>a</i>	2.9 <i>b</i>	17.8 <i>b</i>	19.0 <i>cd</i>	9.9 <i>bc</i>	0.4 <i>ab</i>	4.3 <i>a</i>
6569 <i>e</i>	42.9 <i>a</i>	2.1 <i>a</i>	15.8 <i>b</i>	24.0 <i>d</i>	11.5 <i>c</i>	0.1 <i>a</i>	3.7 <i>a</i>

Means followed by the same letters do not differ significantly at  $p = 0.05$ .

Changes in the relationships between N and the remaining elements as well as other pairs of elements were observed. The highest differentiation was in the case of the following ratios: N:Ca, P:Ca and K:Ca (coefficients of variation: 87, 87 and 94%, respectively), while the lowest one was in the case of ratios: N:P and N:S (coefficient of variation: 21 and 27%, respectively) – Table 5.

## DISCUSSION

The elemental stoichiometry is governed by plant metabolism, i.e. the physiological role of each element (RIVAS-UBACH et al. 2012), and, in accordance with the ecological stoichiometry theory, the amount of individual elements consumed for the production of biological yield, i.e. mass units (STERNER, ELSER 2002). In other words, these are the nutritional requirements of a plant relative to each element and, according to Liebig, relative also to



Table 4

Sum of elemental content and the share of elements in their sum in selected plant species (mean values)

Plant species	Sum (mmol(+) kg <sup>-1</sup> )	N	P	K	Ca	Mg	Na	S
<i>Angelica sylvestris</i>	5398	38.1 ab	2.5 bcd	19.4 ef	21.4 gh	12.8 efg	0.03 a	5.8 de
<i>Athyrium filix-femina</i>	3853	53.8 efg	3.4 de	19.4 ef	8.2 abcd	10.6 def	0.20 a	4.4 cd
<i>Calamagrostis arundinacea</i>	3312	56.9 fghi	3.4 de	24.5 f	5.1 abc	6.2 abc	0.04 a	3.9 abc
<i>Carex nigra</i>	2850	64.4 ijk	3.9 e	11.3 abc	7.1 abcd	8.4 bade	0.08 a	4.8 cd
<i>Carex paradoxa (appropinquata)</i>	2276	52.1 defg	2.3 abc	24.2 f	10.9 bcde	5.9 abc	0.07 a	4.5 cd
<i>Carex riparia</i>	2742	55.6 fgh	3.4 de	18.5 def	6.7 abcd	6.9 abc	3.32 b	5.7 de
<i>Conocharia majalis</i>	3540	52.5 defgh	3.0 bcde	22.7 f	11.9 cde	6.7 abc	0.05 a	3.2 ab
<i>Dryopteris carthusiana</i>	3788	56.8 fghi	4.1 e	14.7 bcde	10.9 bcde	8.8 bcde	0.21 a	4.6 cd
<i>Eriophorum vaginatum</i>	2423	65.0 jk	3.9 e	18.4 def	2.9 a	5.5 ab	0.05 a	4.2 bcd
<i>Filipendula ulmaria</i>	4025	47.4 cde	3.4 de	15.4 bcde	12.2 cde	17.4	0.10 a	4.1 abcd
<i>Galeobdolon luteum</i>	5429	48.2 de	2.7 bcd	19.0 def	16.1 efg	10.5 def	0.07 a	3.4 ab
<i>Impatiens noli-tangere</i>	6461	41.4 bc	2.4 bc	18.4 def	21.5 gh	13.4 f/g	0.09 a	2.9 ab
<i>Ledum palustre</i>	1835	59.5 hijk	3.0 bcde	9.3 ab	17.2 efgh	8.1 bcd	0.09 a	2.9 ab
<i>Molinia caerulea</i>	2499	65.3 k	2.1 ab	19.2 def	3.9 ab	5.6 ab	0.04 a	3.8 abc
<i>Oxalis acetosella</i>	3714	52.1 defgh	2.4 bc	16.1 cde	15.1 ef	10.0 cde	0.08 a	4.3 bcd
<i>Phragmites australis</i>	3309	60.1 hijk	3.0 bcde	24.0 f	3.9 ab	2.7 a	0.28 a	6.0 de
<i>Ribes nigrum</i>	4511	47.3 cd	3.1 cde	10.1 ab	24.8 h	7.9 bcd	0.04 a	6.9 e
<i>Rubus idaeus</i>	4377	49.7 def	2.1 a	12.1 bc	21.6 gh	11.9 efg	0.08 a	2.6 a
<i>Stellaria holostea</i>	3998	49.3 def	2.3 bc	21.0 ef	13.1 de	10.7 def	0.03 a	3.7 abc
<i>Thelypteris palustris</i>	2983	53.8 defgh	2.7 bcd	13.1 bcd	10.3 abcde	16.5 gh	0.10 a	3.6 abc
<i>Urtica dioica</i>	6667	31.2 a	1.2 a	5.0 a	46.3 i	11.5 defg	0.04 a	4.8 cd
<i>Vaccinium myrtillus</i>	2138	54.4 fgh	2.9 bcd	10.6 ab	19.1 fgh	8.4 bcd	0.07 a	4.6 cd
<i>Vaccinium uliginosum</i>	1768	64.0 ijk	2.7 bcd	9.5 ab	10.3 abcde	7.8 bcd	0.04 a	5.6 de
<i>Vaccinium vitis-idaea</i>	1488	57.5 ghij	3.0 bcde	9.0 ab	18.1 efgh	8.6 bcde	0.06 a	3.8 abc

If next to the mean values at least one letter is the same the species difference between them is not significant ( $P < 0.05$ ).

Table 5

Stoichiometry of elements [mmol(+):mmol(+)] in plant species (listed in Table 4,  $n = 24$ ) with different nutrient demand

Parameter	N:P	N:K	N:Ca	N:Mg	N:S	P:K	P:Ca	P:Mg	K:Ca	K:Mg	Ca:Mg
Min.	13.9	2.0	0.7	2.7	6.5	0.09	0.03	0.10	0.11	0.43	0.53
Max.	31.1	6.7	22.2	22.2	19.9	0.35	1.31	1.11	6.28	8.87	4.00
Mean	19.3	3.8	6.2	7.0	13.0	0.20	0.33	0.37	1.94	2.17	1.51
V(%)	21	41	87	60	27	40	87	58	94	82	54

V(%) – coefficient of variation

the sum of elements (the so-called Liebig's barrel), consumed for building a mass unit (OSTROWSKA 1987).

The analysis of the aerial parts of *ca* 50 plant species, from the wetland communities in the Biebrza Valley, showed considerable variation between plant species in terms of their nutrient demand, i.e. the sum of consumed elements, which ranged from below 1000 mmol(+) kg<sup>-1</sup> to more than 6000 mmol(+) kg<sup>-1</sup>. A decreasing trend was observed in the nutrient demand of wetland plant species with the increasing TOC content in peat soils, i.e. a decrease was observed in the quantity of elements accumulated in the biological yield. A similar correlation was noted by WANG and MOORE (2014). The study by LAWNICZAK (2011) showed that N deficiency was the main factor limiting plant growth in wetlands, and similar results were obtained in plants growing on less mineralized soils in the Biebrza Valley.

Based on the statistical analysis, the species were divided into five groups, significantly differing in their nutrient requirements. Species with similar nutrient requirements could hardly be linked with specific plant families. In the previous studies (OSTROWSKA, POREBSKA 2002), significant differences with respect to nutrient requirements were found between the species belonging to such families as: *Poaceae*, *Chenopodiaceae*, *Fabaceae* and *Cruciferae*, although there were significant differences between species within the respective families. Generally, the monocotyledonous plants consumed less of elements than the dicotyledonous species to produce a mass unit. For example, GRZEGORCZYK et al. (2013) observed the ability of dicotyledonous plants to accumulate high concentrations of Ca and Mg, which resulted in low K:Ca and K:Mg ratios. Moreover, rapidly growing species consume more elements in a mass unit than slow growing species (POORTER, BERGKOTTE 1992).

We observed that as the TOC content in peat soil decreased, the number of species with ordinary (3000-4000 mmol(+) kg<sup>-1</sup>) and high (> 4000 mmol(+) kg<sup>-1</sup>) nutrient demands increased. Peat mineralization results in a decrease of the TOC content and an increase of the nutrients available to plants. It may be suggested that the C content in peat soils seems to be an indicator of the ability of plants to utilize elements. There are more useful indicators (SIENKIEWICZ et al. 2014, SIENKIEWICZ et al. in press) for

the assessment of the present peat mineralization or the soluble forms of C and N (DOC and DON). The ratio of C:N, however, suggests only the direction of the mineralization process (OSTROWSKA, POREBSKA 2015).

Differentiation of the elemental stoichiometry in various plant species is small, irrespective of the plants' nutritional requirements (OSTROWSKA, POREBSKA 2002). In the present study, slight differences were observed between the species with the smallest and the highest nutrient demand in the relationships between particular elements. This may be the result of these species growing on soils with various content of elements available for plants.

Relationships between elements in plants may be disturbed by various factors, mainly by deficiency or excess of particular elements in the plant growth habitat. The input of nitrogen to the environment (fertilization, deposition) seems to be the main factor that interferes with the relationships between elements. The reasons could be the physiological role of N in the biomass production and excessive input of N with fertilization. According to XIA and WAN (2008), the elevated N input to the environment (fertilization, deposition) in the last century has resulted in an increase of the N content in almost 30% of the analyzed 456 plant species. Notwithstanding the differences in plant species and growth conditions, the results obtained by HAN et al. (2011) on the elemental stoichiometry of 1900 plant species in China do not differ much from the relationships between the elements found in our study.

Numerous authors suggest that the relationships between C, N and P are the most important ones for the functioning of the different groups of organisms. Taking into account little variation of the C content in plants, we disregarded carbon in our study, as the ratios of C to the other elements are controlled by the remaining elements. It seems equally important that, in addition to the C:N:P ratio, the disturbed relationships between different elements in the environment may adversely affect the functioning of producers and consumers. Negative effects may occur in both natural ecosystems (semi-natural) and in crops, although the extent to which they are manifested and appear measurable may vary.

## CONCLUSIONS

The results indicate that:

- wild plants growing under natural conditions (or those close to natural) vary in terms of their nutrient requirements, from  $< 1000 \text{ mmol(+) kg}^{-1}$  to  $> 6000 \text{ mmol(+) kg}^{-1}$  of the sum of macronutrients accumulated in a mass unit;
- the occurrence of species having different nutrient requirements is associated with the nutrient availability, i.e. the degree of peat mineralization;

- the examined plant species with different nutritional requirements do not differ significantly in terms of their elemental stoichiometry; however, there were differences with regard to the inter-elemental relationships between the groups of species with small and high nutrient demands.

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