RESPONSE OF *ANTHOXANTHUM ODORATUM* AND *A. ARISTATUM* TO DIFFERENT HABITAT TYPES AND NUTRIENT CONCENTRATIONS IN SOIL

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ABSTRACT

Anthoxanthum odoratum is a small tussock grass, which grows abundantly on a wide scale in numerous habitats, from mesotrophic and eutrophic fens and wet grasslands, forests, to dry grasslands and swards. In contrast, *A. aristatum* is characterised by a narrow ecological scale, and occurs mostly in oligotrophic, segetal habitats, rarely on sandy road sides. This specificity caused that in some regions in Central Europe, the species is observed to disappear from certain sites. The effect of habitat parameters on *Anthoxanthum odoratum* and *A. aristatum* occurrence and distribution was analysed in west-central and northern Poland. Additionally, variability of morphological traits of the examined grasses in different types of habitats was studied. Habitat conditions and morphological traits of *Anthoxanthum odoratum* and *A. aristatum* were analysed in different types of habitats. The study on *A. odoratum* included three types of habitats, i.e. forest, grasslands and fallow lands, while *A. aristatum* was analysed in segetal habitats (arable land), forest and fallow lands. In total, 22 populations of *Anthoxanthum odoratum* and *A. aristatum* were studied. In our experiments, *A. odoratum* and *A. aristatum* were generally associated with a high range of N concentrations in soil. *Anthoxanthum aristatum* usually grows in sites with low nitrogen concentrations, except for coniferous forest habitat where N concentrations were high and comparable to the concentrations found in forest sites with *A. odoratum*. Our study suggests that phosphorus plays the most important role in plant distribution and growth of *Anthoxanthum* species. This factor seems to play a more important role in the spread of *Anthoxanthum* species and their competitiveness than nitrogen concentrations in the soil. Stoichiometric indices, N:P and N:K ratios, strongly correlated with plant species traits and well characterised habitats.

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KEYWORDS: *Anthoxanthum odoratum*, *A. aristatum*, N:P, N:K, morphological traits.

1. INTRODUCTION

In the Polish flora the genus *Anthoxanthum* L. is represented by three species: *A. odoratum* L. s.s., *A. alpinum* Á. Löve & D. Löve and *A. aristatum* Boiss. *Anthoxanthum odoratum* (Sweet Vernal Grass) is a eurybiont, broadly distributed Eurasian species, a common perennial, deciduous, tussock-forming grass [1, 2]. In North America and Australia, it is classified as an invasive species [3, 4], whereas in Europe it is considered to be a native species, widely distributed. *Anthoxanthum odoratum* grows abundantly on a wide scale in numerous habitats, from mesotrophic and eutrophic fens and wet grasslands, forest, to dry grasslands and sward. Apart from natural habitats, this species has adapted to habitats destroyed by human activities (road sides, waist land, etc.). It is an euapophythic species – native, fully adapted to conditions in habitats created and sustained as a result of human activities. The wide ecological range of *Anthoxanthum odoratum* is confirmed by the fact that this species is characterised by good growth in various trophic conditions, observed in controlled conditions [5].

Anthoxanthum aristatum (Annual Vernal Grass) is characterised by a narrow ecological scale, and occurs mostly in oligotrophic, segetal habitats, rarely on sandy road sides. This specificity caused that in some regions in Central Europe (especially Germany), the species is observed to disappear from certain sites [6]. In Poland, *A. aristatum* entered at the end of the 19th century from the west, almost simultaneously via Silesia and Pomerania [7, 8].

In the following decades, it spread across central Poland towards the eastern border of the country, reaching it in the last decade (Fig. 1) [9, 10]. Currently, *Anthoxanthum aristatum* is in a chorological phase of expansion [11] and

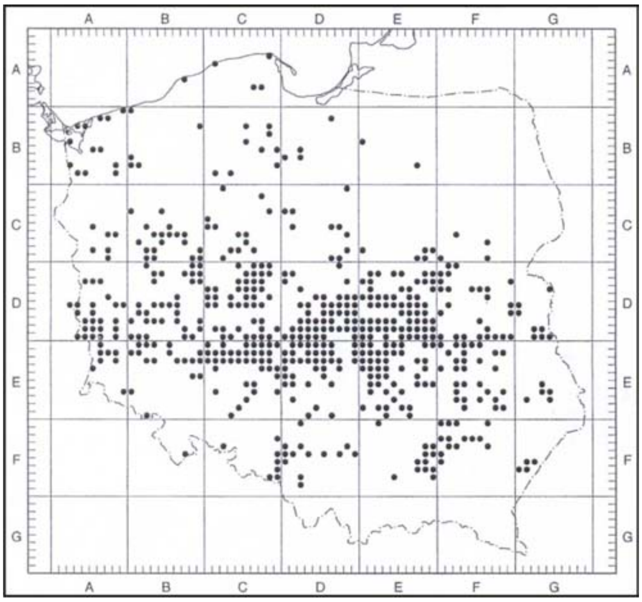

FIGURE 1 - Distribution of *Anthoxanthum aristatum* in Poland [10].

has achieved the status of an epecophyte, i.e. a species of foreign origin which occupies only sites created by man and which remains under constant and strong human pressure [12].

These species are characterised by a changing ecological scale, although in the literature [13] and in nature (Drapikowska et al., field observation) hybrids between *A. odoratum* and *A. aristatum* have been observed. However, site conditions accompanying the spread of such hybrids, even these species, have not been well recognized. The distribution and environmental conditions of *Anthoxanthum* grasses have been analysed in Europe [14, 15], although these conditions are not known in Poland.

The aim of the study was to analyse the effect of habitat parameters on *Anthoxanthum odoratum* and *A. aristatum* occurrence, and to test variability of morphological traits of the examined grasses in different types of habitats.

2. MATERIAL AND METHODS

2.1. Site selection

The study was carried out in Wielkopolska and Pomerania regions, in the west-central and northern parts of Poland, during flowering of grasses, from June to August 2009. Habitat conditions and morphological traits of *Anthoxanthum odoratum* and *A. aristatum* were analysed in different types of natural habitats. The study on *A. odoratum* included three types of habitats, forest, grasslands and wasteland, while *A. aristatum* was analysed in arable land (segetal habitats), forest and wasteland. In total, 22 populations of *Anthoxanthum odoratum* (14 populations) and *A. odoratum* (8 populations) were studied in north-west Poland (the Notecka Primeval Forest, *Nowy Tomyśl Sandr, Zielonka* Primeval *Forest, and Poznań, Ostrów Wlkp, Szczecinek surroundings) (Fig. 2). A* more detailed description of the studied sites can be found in *Table 1.*

2.2. Habitat study

Soil samples were collected in sites with dominance of *Anthoxanthum* species. Five soil samples were taken randomly from soil depths of 0–10 cm on each plot. Soil samples were obtained by using a 100 cm^3 (5-cm diameter) core sampler. Each sample was divided into two subsamples. One of the subsamples was frozen immediately for further analyses, and the second one was dried. Dried material was saved for chemical analysis.

Total soil nitrogen, phosphorus and potassium concentrations were determined with a Kjeldahl procedure [17]. The N and P concentrations of the diluted digested material were determined colorimetrically on a Srecord 40, and the K concentration with flame emission spectroscopy, on a Sherwood Model 425. The pH in soil pore water was measured with a standard KCl pH-electrode. In the frozen samples, nitrate and ammonium contents were determined using Bremner methods [17]. N:P and N:K ratios were determined based on total N and P concentrations in soil.

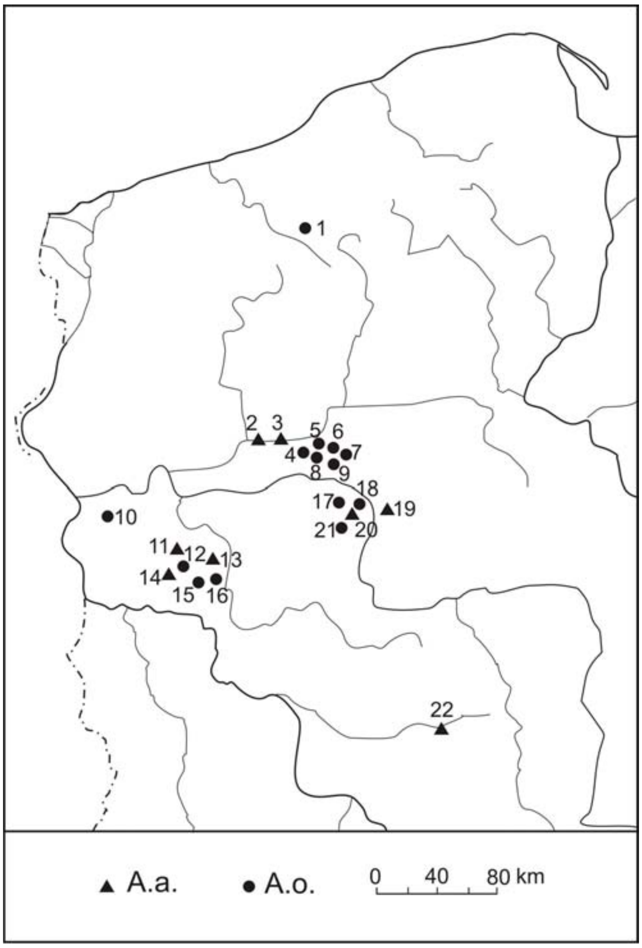

FIGURE 2 - Distribution of sampling sites with *A. odoratum* and *A. aristatum*.

TABLE 1 - Sampled populations of *Anthoxanthum odoratum* (*A.o.*) and *A. aristatum* (*A.a.*).

Site	Geographic position	Map number	Date of sampling	Habitat	Dominant species
Jasionna 1	N 52°46`42.6`` E 16°27`05.5``	4	21.05.2009	pine forest	*A.o., Deschampsia flexuosa, Juniperus communis, Pinus sylvestris*
Jasionna 5	N 52°47`17.6`` E 16°26`27.7``	8	21.05.2009	pine forest	*A.o., Deschampsia flexuosa, Pinus sylvestris, Vacinium myrtillus*
Ruchocki Młyn 1	N 52°10`58.9`` E 16°05`05.1``	15	14.05.2009	pine forest	*A.o., Deschampsia flexuosa, Pinus sylvestris, Vaccinium myrtillus*
Nowa Tuchorza 3	N 52°12`29.2`` E 16°04`31.9``	12	14.05.2009	pine plantation	*A.o., Deschampsia flexuosa, Festuca ovina, Pinus sylvestris*
Poznań 2	N 52°28`08.1`` E 16°55`33.5``	18	07.07.2009	pine plantation	*A.o., Calamagrostis epigejos, Padus serotina, Pinus sylvestris*
Kicin	N 52°28`12.7`` E 17°01`55.2``	19	07.07.2009	fallow-land	*Anthemis arvensis, A.a., Apera spica-venti, Stellaria media*
Storkowo	N 53°46`09.2`` E 16°29`23.3``	1	25.08.2009	fallow-land	*Achillea millefolium, A.o., Gnaphalium sylvaticum, Holcus mollis,*
Nowa Tuchorza 2	N 52°12`26.1`` E 16°04`36.1``	14	14.05.2009	the edge of a pine plantation	*A.a., Corynephorus canescens, Erophila verna, Spergula morisonii*
Ruchocki Młyn 2	N 52°00`22.8`` E 16°06`28.1``	16	29.05.2009	wet meadow	*Agrostis stolonifera, A.o., Hydrocotyle vulgaris, Ranunculus flammula*
Nowa Tuchorza 1	N 52°12`24.2`` E 16°04`38.3``	11	14.05.2009	arable land; in rye crops	*A.a., Erophila verna, Spergula morisonii, Teesdalea nudicaulis*
Barłożnia	N 52°09`27.5`` E 16°07`29.6``	13	07.07.2009	arable land; in rye crops	*Anthemis arvensis, A.a., Centaurea cyanus, Viola arvensis*
Świeca	N 51°33`19.7`` E 17°42`15.5``	22	04.07.2009	arable land; in rye crops	*A.a., Centaurea cyanus, Scleranthus annuus, Viola arvensis*
Poznań	N 52°27`58.5`` E 16°55`19.8``	20	07.07.2009	arable land; in rye crops	*A.a., Apera spica-venti, Vicia villosa, Viola arvensis*
Wrzeszczyna 1	N 52°52`08.6`` E 16°14`41.3``	2	21.05.2009	arable land; in rye crops	*A.a., Scleranthus annuus, Spergula morisonii, Teesdalea nudicaulis*
Wrzeszczyna 2	N 52°52`35.4`` E 16°14`19.7``	3	22.05.2009	arable land; in rye crops	*A.a., Spergula morisonii, Teesdalea nudicaulis, Viola arvensis*
Jasionna 3	N 52°46`39.6`` E 16°26`35.8``	6	21.05.2009	roadside in coniferous forest	*A.o., Entodon schreberi, Teesdalea nudicaulis, Veronica officinalis*
Jasionna 4	N 52°46`39.8`` E 16°26`35.3``	7	21.05.2009	roadside in coniferous forest	*Achillea millefolium, A.o., Deschampsia flexuosa, Entodon schreberi*
Debrznica	N 52°15`52.7`` E 15°03`36.7``	10	29.05.2009	roadside in coniferous forest	*A.o., Deschampsia flexuosa, Festuca ovina, Veronica officinalis*
Poznań 1	N 52°28`04.1`` E 16°55`36.5``	17	07.07.2009	forest roadside	*Achillea millefolium, A.o., Hieracium pilosella, Medicago lupulina*
Jasionna 2	N 52°46`51.6`` E 16°27`59.3``	5	21.05.2009	dry meadow	*A.o., Deschampsia caespitosa, Holcus lanatus, Poa pratensis*
Jasionna 6	N 52°45`35.3`` E 16°27`47.5``	9	21.05.2009	dry meadow	*A.o., Holcus lanatus, Poa pratensis, Potentilla anserina*
Poznań 3	N 52°27`54.2`` E 16°55`23.4``	21	07.07.2009	dry meadow	*A.o., Deschampsia caespitosa, Potentilla anserina, Poa pratensis*

2.3. Morphometric traits

The plant material of *A. odoratum* and *A. aristatum* was collected from each study site. Out of each population, 30-35 tufts were collected for morphometric studies. From the 24 analysed traits of generative organs [18], the five traits best differentiating populations of *A. odoratum* and *A. aristatum* were selected for the present study (Table 2).

2.4. Statistical analyses

Analyses of environmental databases were initiated by testing the distribution of environmental variables, using the W-value according to Shapiro-Wilk criteria [19]. To assess the normal distribution, most of the variables were transformed, mainly through square root or logarithmic conversion (Table 3). To test differentiation of environmental

TABLE 2. List of morphometric traits of *Anthoxanthum odoratum* and *A. aristatum* used in the present study.

Trait number	Traits' description
panicle	
1	panicle length
2	number of nodes in a panicle
3	length of the fifth internode
spikelet	
4	length of a spikelet on the second branching from a panicle top
5	number of spikelets on the second branching from a panicle top

TABLE 3 - Variables recorded in the soil database.

Parameter		Units	Transformation	Shortcode
Habitat parameters				
1.	Nitrogen	mg N·g^{-1}soil	ln (x+1)	N
2.	Phosphorus	mg P·g^{-1}soil	ln (x+1)	P
3.	Potassium	mg K·g^{-1}soil	ln (x+1)	K
4.	N:P	-	ln (x+1)	NP
5.	N:K	-	ln (x+1)	NK
6.	Ammonium	mg N-NH_4^+ ·100g^{-1}soil	$\sqrt{x}$	N-NH4
7.	Nitrate	mg N-NO_3^- ·100g^{-1}soil	$\sqrt{x}$	N-NO3
8.	pH	-	ln (x+1)	pH

factors between species and habitat types, an analysis of variance (ANOVA) was performed. Additionally, a factor analysis (principal component analysis – PCA) was used to uncover the structure of environmental matrices and reveal directions of ecological variability. Principal components, revealed within the PCA analysis, were used with canonical correspondence analysis (CCA) as selected environmental variables against the selected morphometric traits of *Anthoxanthum* species [20]. All statistical analyses were performed using Statistica [19] and CANOCO [21] software.

3. RESULTS

Principal component analysis (PCA) yielded a simplified habitat description of the analysed matrix. Primary components PCA1 and PCA2 explained altogether 75.83% of total variation, of which the former factor described 41.72% and the second one 34.11% of variation (Fig. 3). Table 4 presents the principal components and their corresponding eigenvalues after varimax rotation.

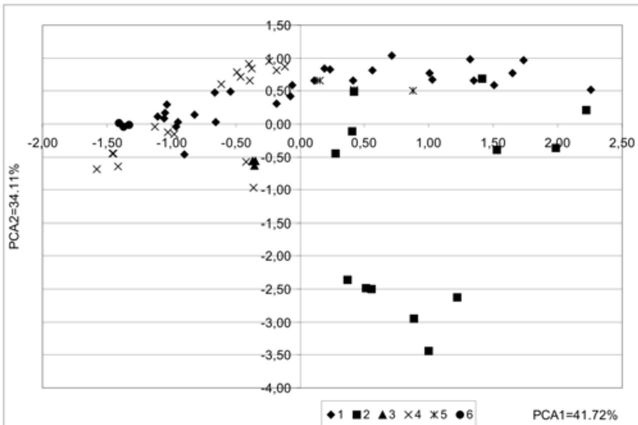

FIGURE 3 - Graphic picture of the principal component analysis based on soil parameters for *A. odoratum* s.s. and *A. aristatum* populations from different habitats.
Abbreviations: *A. odoratum*, 1 – forest, 2 – grassland, 3 – wasteland; *A. aristatum*, 4 – arable land, 5 – forest, 6 – wasteland. Full names of environmental variables are given in Table 2.

TABLE 4 - Correlation coefficients between six parameters and first two principal components (PCA1 and PCA2). Values given in boldface are statistically significant at the level p<0.01.

Parameter	Values of principal components	
	1	2
mg N·g^{-1}soil	0.82	-0.26
mg P·g^{-1}soil	-0.75	0.03
mg K·g^{-1}soil	0.67	0.62
N:P	0.87	-0.25
N:K	0.11	-0.90
pH	-0.17	-0.84
Variance explained	2.50	2.05
% of total variance explained	41.72	34.11

The first principal component was strongly associated with nitrogen (positively, r=0.82) and phosphorus (negatively, r=0.75) concentrations in the soil; therefore it can be defined as the gradient indicating nutrient availability to plants. It is most strongly, positively associated with the stoichiometric index N:P (r=0.97). The second principal component extracted was strongly related to pH (r= 0.84) and the N and K concentration ratio (r=0.90).

Significant differences between habitat components for *A. odoratum* and *A. aristatum* were found with respect to nutrient concentrations, particularly phosphorus and nitrogen (Table 5). *Anthoxanthum odoratum* occurred at the site with low phosphorus content in the soil (2.26 mg P·g^{-1}± 1.70) compared to the site characteristic for *A. aristatum* (6.21 mg P·g^{-1}±3.72) (Fig. 4, 5). Nitrogen concentrations varied from 2.10 to 66.61 mg N·g^{-1} in sites with *A. odoratum* (average 19.24 mg N·g^{-1}) and from 6.13 to 13.30 mg N·g^{-1} in sites with *A. aristatum* (8.74 mg N·g^{-1}). The highest variation and biggest values were noted in sites with *A. odoratum* (Fig. 4).

Stoichiometric indices of nitrogen and phosphorus concentration ratios in the soil showed significant species preferences for different nutrient availability. These differences were statistically significant between analysed species and between tested habitats (Table 5). N:P ratio effects were much stronger than the main effects (higher F-ratios in Table 5), i.e. variations of N:P ratios were lower than N and P concentrations. N:P ratios ranged from 0.4 to 47.7 for *A. odoratum* and from 0.6 to 25.7 in sites characteristic for *A. aristatum* (Fig. 6). No significant differences in potassium concentrations were found between the studied species

TABLE 5 - Analysis of variance of environmental factors between species and habitat types. Full names of environmental variables and type of transformations are given in Table 3.

	Species				*A. odoratum*				*A. aristatum*			
Variable	df	F	p	Sig.	df	F	p	Sig.	df	F	p	Sig.
N	1	6.11	0.016	*	2	7.35	0.002	**	2	13.12	0.001	**
P	1	20.14	0.000	***	2	2.58	0.089		2	9.42	0.003	**
K	1	0.00	0.993		2	2.60	0.086		2	3.73	0.050	
N:P	1	18.16	0.000	***	2	7.54	0.002	**	2	17.44	0.000	***
N:K	1	2.59	0.112		2	11.57	0.000	***	2	1.70	0.219	
$N\text{-}NH_4$	1	7.07	0.010	*	2	12.83	0.000	***	1	2.25	0.178	
$N\text{-}NO_3$	1	21.36	0.000	***	2	2.75	0.078		1	1.15	0.319	
pH	1	1.26	0.267		2	10.55	0.000	***	1	6.18	0.042	*

Level of significance * p<0.05; ** p<0.01; *** p<0.001

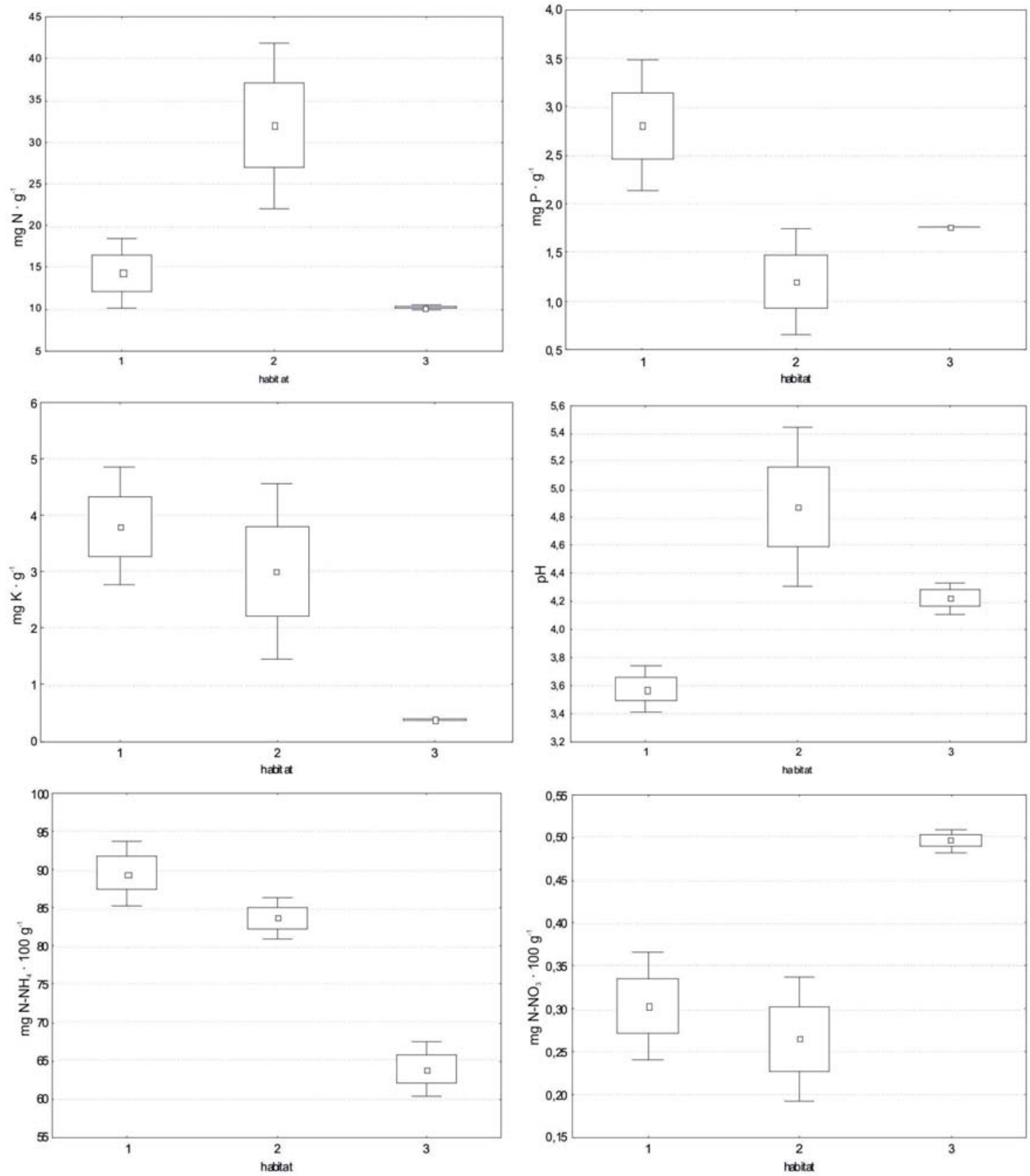

FIGURE 4 - Variability of environmental parameters among different habitat types with *Anthoxanthum odoratum*. Types of habitats: 1 – forest, 2 – grassland, 3 – wasteland. The plot indicates mean value ±standard error and ±1.96 standard error. Full names of variables and their description are in Table 3.

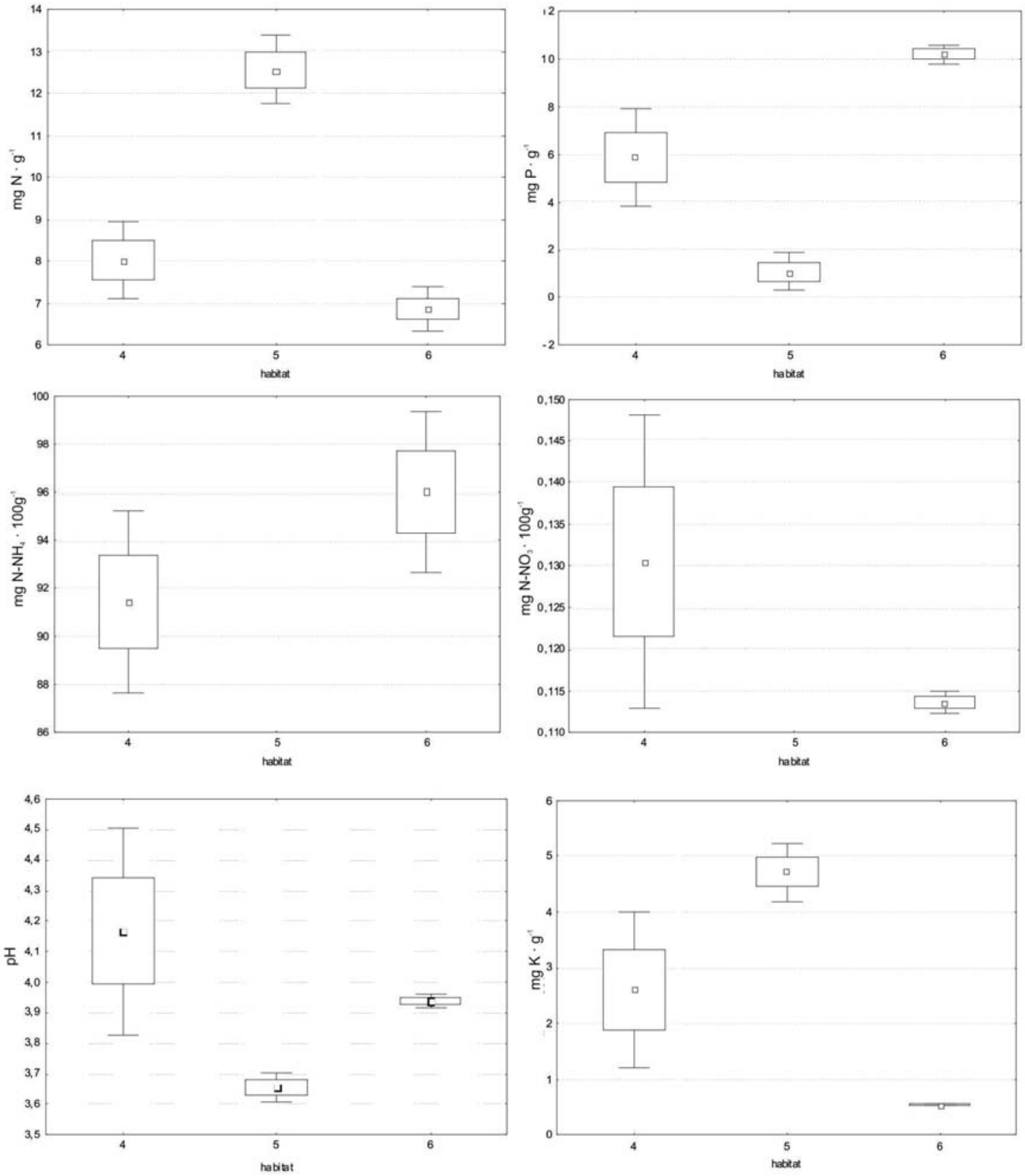

FIGURE 5 - Variability of environmental parameters among different habitat types with *Anthoxanthum aristatum*. Types of habitats: 4 – arable land, 5 – forest, 6 – sward. The plot indicates mean value ±standard error and ±1.96 standard error. Full names of variables and their description are in Table 3.

species (3.34±2.82 *A. odoratum*, 2.89±2.40 *A. aristatum*). Also, N:K did not show significant differences of the analysed sites between the two grasses; however, significant variability was observed between the analysed habitats with *A. odoratum* (Table 5, Fig. 7). Nitrate concentrations at the highest standing stock were higher in the habitat where *A. odoratum* was growing (0.31±0.15) than at the site where *A. aristatum* was growing (0.14±0.03).

Further analyses of nutrient concentrations indicate significant differences between the studied habitats of tested species (Table 5). In grasslands covered by *A. odoratum*, nitrogen concentrations were significantly higher compared to other habitats (forest and wasteland) (Table 5, Fig. 4). A similar pattern was observed at the site with *A. aristatum* (Table 5, Fig. 5). In forest, nitrogen concentrations were significantly higher in relation to wasteland and arable land.

The P concentrations at the site with *A. aristatum* were highest in the wasteland in comparison with arable fields and forest (Table 5, Fig. 5). However, significant changes of P concentrations in soil with *A. odoratum* between the analysed habitats were not detected. Also, potassium did

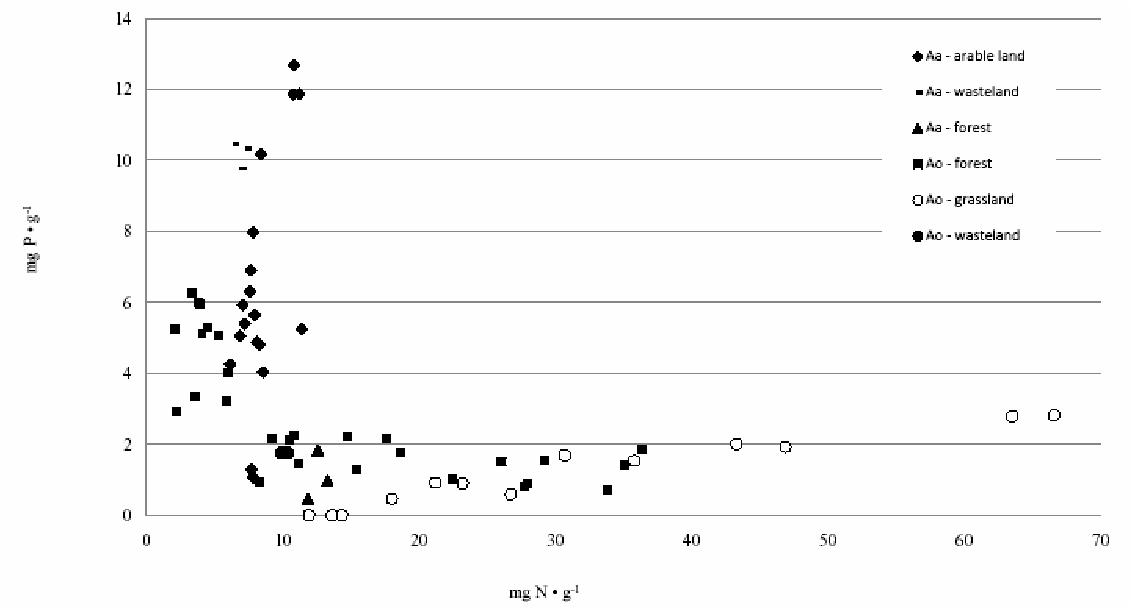

FIGURE 6 - Relationships between N concentrations and P concentrations in the soil among different habitat types with *Anthoxanthum odoratum* (Aa) and *A. aristatum* (Ao).

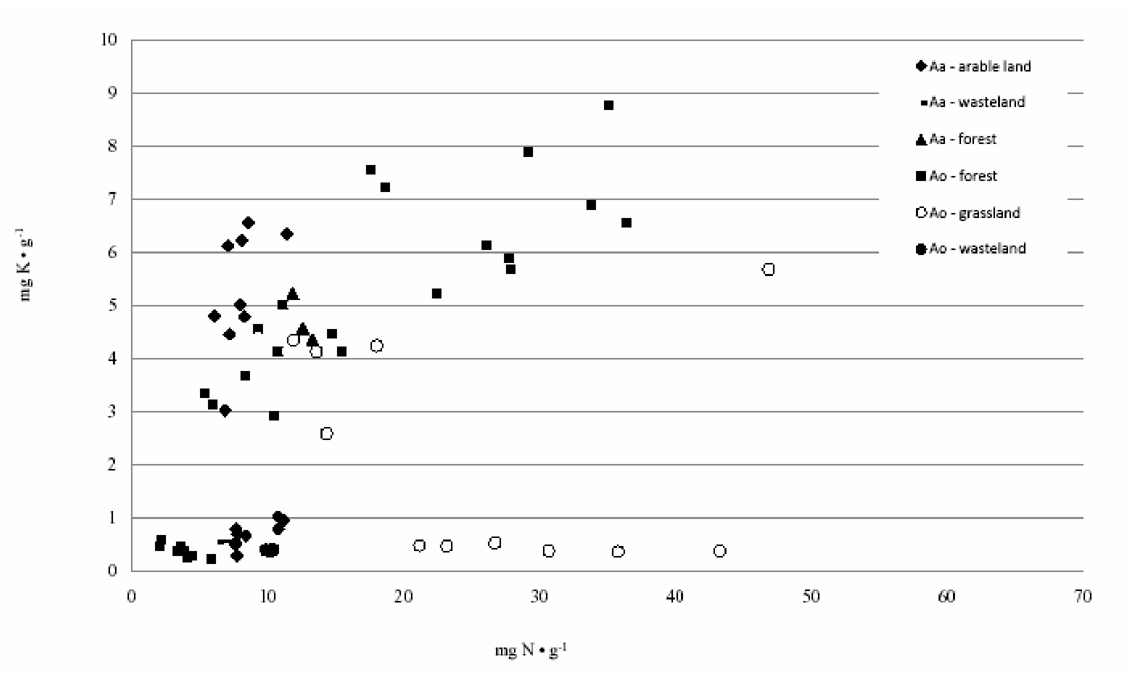

FIGURE 7 - Relationships between N concentrations and K concentrations in the soil among different habitat types with *Anthoxanthum odoratum* (Aa) and *A. aristatum* (Ao).

not show significant differences between analysed habitats. However, N:K concentration ratio indicated an influence of K on N concentrations in soil with *A. odoratum* (Fig. 4, 7).

The most significant variations among tested habitats were observed in the N:P ratio (Table 5, Fig. 6). *A. aristatum* preferred sites with high N:P ratio in comparison with the wide range of occurrence of *A. odoratum*. The smallest N:P and N:K ratios were found in wasteland (N:P – 5.76 *A. odoratum*, 0.67 *A. aristatum*) and forest (N:K – 6.03 *A. odoratum* and 2.69 *A. aristatum*), respectively (Fig. 6, 7).

Forms of nitrogen: ammonium and nitrate, as well as pH varied significantly between sites covered by *A. odoratum*. Particularly, at sites with high human pressure, low ammonium and high nitrate concentrations were observed (Fig. 4, 5). A correlation between pH and NH_4^+ was detected ($r= -0.67$, $p<0.05$).

To investigate the relationship between habitat factors and grass traits, canonical correspondence analysis (CCA) was performed (Fig. 8). PCA principal components were used as environmental variables. It was found that there were two dominant environmental variables explaining species traits variability. The results were analysed with the Monte Carlo permutation test. Their value amounted to CA= 0.02. The level of significance was at 0.05.

On the basis of canonical analysis (Fig. 8), it was found that there was a positive relationship between N:K ratio and panicle length (trait no. 1), as well as between N and trait no. 1, P and length of the fifth internode of the panicle (trait no. 3). On the other hand, a much weaker relationship was observed between the length of the spikelet on the second branching from the panicle top (trait no. 4), the number of spikelets on the second branching from the panicle top (trait no. 5) and the level of P and K concentrations.

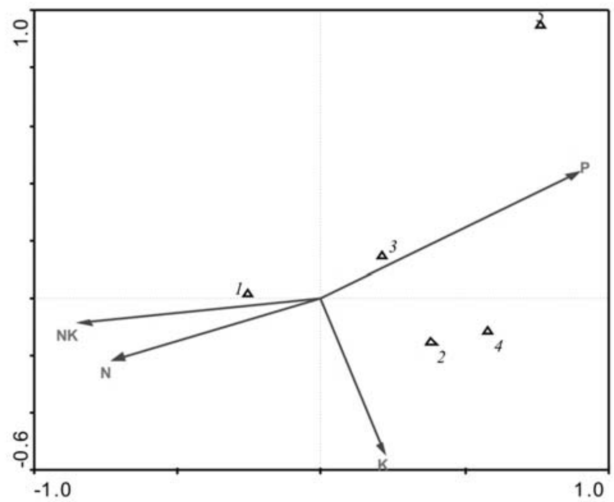

FIGURE 8 - Canonical correspondence analysis (CCA) plot for plant response parameters of *Anthoxanthum odoratum* and *A. aristatum* and environmental parameters.

4. DISCUSSION

Anthoxanthum odoratum occurred at sites with a very wide range of nitrogen concentrations in the soil. This broad amplitude of *A. odoratum* with respect to nutrient availability and ecological flexibility to grow in different types of habitats has been recognised in many studies [11, 23, 24]. However, most of the studies analysed the occurrence of plant species with respect to nitrogen concentrations. According to Ellenberg et al. [25], *A. odoratum* has a broad amplitude with respect to nitrogen (no nutrient indicator value, on a scale from 1 to 9), whereas *Anthoxanthum aristatum* is characteristic for sites of lower fertility (Ellenberg – nutrient indicator value of 3). In our study, *A. odoratum* and *A. aristatum* were generally associated with a high range of N concentrations in soil. *Anthoxanthum aristatum* usually grows in sites with low nitrogen concentrations, except for coniferous forest habitat where N concentrations were high and comparable to the concentrations found in forest sites with *A. odoratum*. In the literature, *A. odoratum* is also observed among pine trees where it is typically sparsely distributed, whereas in open areas it is present in greater abundance [26]. Moreover, *A. aristatum* was restricted mostly to ruderal sites and was not observed widely in coniferous forest [9, 11, 12]. It seems that *A. aristatum* increased its preferences and adapted to higher N concentrations.

Significant differences of N concentrations between sites with *A. odoratum* and *A. aristatum* were observed, but these differences were not as pronounced as in the case of P concentrations in the soil. Our study suggests that phosphorus plays the most important role in plant distribution and growth of *Anthoxanthum* species. This factor seems to play a more important role in the spread of *Anthoxanthum* species and their competitiveness than nitrogen concentrations in the soil. The observed strong effects of P on plant species composition was in agreement with the results published by van der Hoek et al. [27], Bohner [28] or by Wassen et al. [29].

Studies by Koerselman and Meuleman [30] and Güsewell and Koerselman [31] demonstrated that stoichiometric indices (N:P and N:K ratios) provided better indicators of nutrients limiting plant growth than nutrient concentrations separately. Our study showed that N:P and N:K ratios strongly correlated with plant species traits and well characterised habitats. Variations of N:P ratios in the soil were lower than N and P concentrations independently. Although K concentrations did not show significant differences between species habitats, they could have influenced the N uptake. N:K ratios strongly and significantly correlated with plant traits, which suggested a combined influence of N and K concentrations on plant species performances. The results obtained in controlled conditions support the importance of the combined effect of N and K on grass species growth [5].

In natural habitats, K shortages are rare, and are usually combined with poor availability of N or P [32, 33]. This may explain the significant differences between habitats with *A. odoratum* in relation to N:K ratios and correlations between N:K ratios and plant traits.

In our study, soil pH poorly correlated with morphological traits of the examined *Anthoxanthum* species, and although this parameter is not a key factor affecting the spread and growth of these grasses, it can affect the nutrient cycle. Mainly, soil pH determines root growth [34], mineralisation rates in soil and mineral nutrient availability [35]. This impact of pH was confirmed in our study by negative correlations between pH and NH_4^+.

Correlations between inorganic nitrogen forms and traits of studied grasses at the studied sites were not observed, although available inorganic nitrogen forms are the most important for plant growth [36]. In many natural, seminatural and agricultural ecosystems, NH_4^+ is the predominant N source [37, 38], but in high concentrations has a toxic effect on plant growth [39]. However, lack of a correlation between nitrogen forms and plant traits could have been due to single measurements which reflect only concentrations of inorganic nitrogen forms at the time of sampling. Concentrations of NH_4^+ and NO_3^- in soil are controlled by a number of factors, such as pH, temperature, organic matter, etc. [40, 41] and vary considerably during the vegetation season. The studies of Güsewell and Koerselman [31], and Verhoeven and Aerts [42] suggested that measurements of inorganic nutrients in soil do not really reflect nutrients available for plant growth. Some species have the ability to solubilise "unavailable" phosphorus [43] or organic nitrogen [44]. This suggests that nutrient concentration in plants may better reflect the amount of nutrients available for plant growth than nutrients measured in soil.

Changes in nutrient availabilities caused by human impact affect species composition and disturbances of plant communities [44, 45]. These differences between studied species also result from their diverse life-cycle strategies. *A. odoratum* is adapted to habitats where the distribution of plant species is controlled by moderate intensities of stress and disturbance (C-S-R strategies) [1, 2]. In contrast, *A. aristatum* appears to prefer sites degraded by man frequently characterised by a shift in nutrient availability. In the case of arable land where *A. aristatum* occurred, phosphorus availability was high, and the N:P ratio was relatively low. In forest sites, a slight shift of N:P ratio was observed, which explains the increased capability of *A. aristatum* to occupy new sites or the ability to create hybrids with *A. odoratum* in order to increase its range.

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REFERENCES

[1] Grime, J.P. (1974) Vegetation classification by reference to strategies. Nature, 250: 26-31.

[2] Grime, J.P. (1979) Plant, strategies and vegetation processes. John Wiley & Sons, Inc., Somerset, N.J., 222 pp.

[3] Csurhes, S. and Edwards R. (1998) Potential environmental weeds in Australia: Candidate species for preventative control. Biodiversity Group. Environment Australia, Canberra. 208 pp.

[4] Mack, R.N. (2000) Assessing the extent, status and dynamism in plant invasions: current and emerging approaches. [In:] Mooney, H.A. and Hobbs, R.J. (eds). The Impact of Global Change on Invasive Species, Island Press, Covelo 141-168.

[5] Lawniczak, A.E., Güsewell, S. and Verhoeven, J.T.A. (2009) Effect of N:K supply ratios on the performance of three grass species from herbaceous wetlands. Basic and Applied Ecology 10(8), 715-725.

[6] Schneider, Ch., Sukopp, U. and Sukopp, H. (1994) Biologisch-ökologische Grundlagen des Schutzes gefährdeter Segetalpflanzen. Schr. f. Vegetation 26, 1-356.

[7] Rola, Z. and Kuźniewski, E. (1979) Einfluß der Intensivierung und Spezialisierung der Pflanzenproduktion auf die Verunkrautung. Unkrautbekämpfung in der industrimäßigen Pflanzenproduktion. 1: Allgemeine Grundlagen, Wiss. Beitr. Martin-Luther-Univ., Halle-Wittenberg 22-27.

[8] Tokarska-Guzik, B. (2005) The Establishment and Spread of Alien Plant Species (Kenophytes) in the Flora of Poland. Prace Nauk. UŚ w Katowicach 2372, 1-192.

[9] Ciosek, T.M. and Skrzyczyńska, J. (1997) *Anthoxanthum aristatum* (Poaceae) in the Nizina Południowopodlaska and its neighbourhood (Poland). Fragm. Flor. Geobot. 42(2), 344-348.

[10] Zając, A. and Zając, M. (eds.). (2001) Distribution Atlas of Vascular Plants in Poland. Edited by Laboratory of Computer Chorology, Institute of Botany, Jagiellonian University, Cracow.

[11] Jackowiak, B. (1999) Modele roślin synantropijnych i transgenicznych. Phytocoenosis 11(N.S.). Sem. Geobot. 6, 3-16.

[12] Latowski, K. E(2005) Ecological-biological reasons and sources of the invasive propensity of *Anthoxanthum aristatum* Boiss. Thaiszia – J. Bot. Košice 15(1), 143-152.

[13] Falkowski, M. (ed.). (1982) Trawy polskie. 565 pp. PWRiL, Warszawa.

[14] Flegrova, M. and Krahulec, F. (1999) *Anthoxanthum odoratum* and *A. alpinum* life history parameters at two different altitudes. Folia Geobotanica 34, 19-31.

[15] Pimentel, M., Sahuquillo, E. and Catala´n, P. (2007) Genetic diversity and spatial correlation patterns unravel the biogeographical history of the European sweet vernal grasses (*Anthoxanthum* L., Poaceae). Molecular Phylogenetics and Evolution 44, 667-684.

[16] Bremner, J.M. and Mulvaney, C.S. (1982) Nitrogen-Total. [In:] Page, A.L. (ed.). Methods of soil analysis, Part 2. Chemical and microbiological properties. American Society of Agronomy, Madison, 595-624.

[17] Ostrowska, A., Gawliński, S. and Szczubiałka, Z. (1991) Metody analizy i oceny właściwości gleb i roślin. Inst. Ochr. Środ., Warszawa.

[18] Drapikowska, M., Szkudlarz, P., Celka, Z., Pierścińska, J. and Jackowiak B. (2008) Preliminary results of the studies on morphological diversity of lowland populations of species from the genus *Anthoxanthum* L. Scripta Facultatis Rerum Naturalium Universitatis 186, 236-242.

[19] StatSoft. (2007) Inc. STATISTICA (data analysis software system). version 8.0. www.statsoft.com

[20] Ter Braak, C.J.F. and Prentice, I.C. (1988) A theory of gradient analysis. Adv. Ecol. Res. 18, 271-317.

[21] Ter Braak, C.J.F. and Šmilauer, P. (1998) CANOCO reference manual and user's guide to Canoco for Windows: software for canonical community ordination (version 4). Microcomputer Power, Ithaca, USA.

[22] Hegi, G. (1965) Illustrierte Flora von Mittel-Europa. Lehmann Verlag, München.

[23] Snaydon, R.W. and Davies, M.S. (1972) Rapid population differentiation in a mosaic environment. II. Morphological variation in *Anthoxanthum odoratum*. Evolution 26, 390-405.

[24] Snaydon, R.W. and Davies, M.S. (1976) Rapid population differentiation in a mosaic environment. Populations of *Anthoxanthum odoratum* at sharp boundaries. Heredity 37, 9-25.

[25] Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W. and Paulissen, D. (1991) Zeigerwerte von Pflanzen in Mitteleuropa. Scripta Geobotanica 18, 1-248.

[26] Grant, M.C. and Antonovics J. (1978) Biology of ecologically marginal populations of *Anthoxanthum odoratum*. I. Phenetics and dynamice. Evolution 32, 822-838.

[27] van der Hoek, D., Mierlo, A.J.E.M. and van Groenendael, J.M. (2004) Nutrient limitation and nutrient-driven shifts in plant species composition in a species-rich fen meadow. Journal of Vegetation Science 15(3), 389-396.

[28] Bohner, A. (2005) Soil chemical properties as indicators of plant species richness in grassland communities. Grassland Sci. Eur. 10, 48-51.

[29] Wassen, M.J., Olde Venterink, H., Lapshina, E.D. and Tanneberger, F. (2005) Endangered plants persist under phosphorus limitation. Nature 437, 547-550.

[30] Koerselman, W. and Meuleman, A.F.M. (1996) The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. Journal of Applied Ecology 33, 1441-1450.

[31] Güsewell, S. and Koerselman, W. (2002) Variation in nitrogen and phosphorus concentrations of wetland plants. Perspectives in Ecology, Evolution and Systematics 5, 37-61.

[32] Roem, W.J. and Berendse, F. (2000) Soil acidity and nutrient supply ratio as possible factors determining changes in plant species diversity in grassland and heathland communities. Biological Conservation 92, 151-161.

[33] Olde Venterink, H., Pieterse, N.M., Belgers, J.D.M., Wassen, M.J. and de Ruiter P.C. (2002) N, P, and K budgets along nutrient availability and productivity gradients in wetlands. Ecological Applications 12, 1010-1026.

[34] Brouwer, R. (1978) Soil physical conditions and plant growth. In: Freysen, A.H.J. and Woldendorp J.W. (eds). Structure and Functioning of Plant Populations, North Holland Publ. Comp., Amsterdam, 189-213.

[35] Vermeer, J.G. and Berendse, F. (1993) The relationship between nutrient availability, shoot biomass and species richness in grassland and wetland communities. Vegetatio 53, 121-126.

[36] Salsac, L., Chaillou, S., Morot-Gaudry, J.F., Lesaint, C. and Jolivoe, E. (1987) Nitrate and ammonium nutrition in plants. Plant Physiol. Biochem. 25, 805-812.

[37] Vitousek, P.M., Gosz, J.R., Grier, C.C., Melillo, J.M. and Reiners W.A. (1982) A comparative analysis of potential nitrification and nitrate mobility in forest ecosystems. Ecol. Monogr. 52, 155-177.

[38] Blew, R.D. and Parkinson D. (1993) Nitrification and denitrification in a white spruce forest in southwest Alberta, Canada. Can. J. For. Res., 23: 1715-1719.

[39] Britto, D.T. and Kronzucker, H.J. (2002) NH_4^+ toxicity in higher plants: a critical review. J. Plant Physiol. 159, 567-584.

[40] Rice, E.L. and Pancholy S.K. (1972) Inhibition of nitrification by climax ecosystems. Amer. J. Bot, 59, 1033-1040.

[41] Lodhi, M.A.K. (1978) Inhibition of nitrifying bacteria, nitrification, and mineralization of spoil soils as related to their successsional stages. Bull. Torrey Bot. Club 106, 284-289.

[42] Verhoeven, J.T.A. and Aerts, H.H.M., (1987) Nutrient dynamics in small mesotrophic fens surrounded by cultivated land. II. N and P accumulation in plant biomass in relation to the release of inorganic N and P in the peat soil, Oecologia 72, 557-561.

[43] Perez-Corona, M.E., van der Klundert, J. and Verhoeven, J.T.A. (1996) Availability of organic and inorganic phosphorus compounds as phosphorus sources for *Carex* species, New Phytologist 133, 225-231.

[44] Jonasson, S., Michelsen, A., Schmidt, I.K. and Nielsen, E.V. (1999) Responses in microbes and plants to changed temperature, nutrient, and light regimes in the arctic, Ecology 80, 1828-1843.

[45] Geerts, R.H.E.M. and Oomes, M.J.M. (2000) Kan de Spaanse ruiter het Wageningse Binnenveld heroveren? De Levende Natuur 101, 71-75.

[46] Güsewell, S., Bailey, K., Roem, W. and Bedford, B.L. (2005) Nutrient limitation and botanical diversity in wetlands: can fertilisation raise species richness? Oikos 109, 71-80.

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