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Habitat factors influencing the competitive ability of *Calamagrostis epigejos* (L.) Roth in mountain plant communities

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Abstract: The aim of this study was to assess how the expansion of *Calamagrostis epigejos* influences the species composition and diversity of forest, clearing, and meadow communities as well as how habitat factors influence biometric variability and features determining the potential of *Calamagrostis epigejos* for expansion in the studied communities. The study was conducted in the central part of the Sudetes Mountains (SW Poland). Four types of communities with *C. epigejos* occurrence were chosen: a beech forest (*Luzulo luzuloidis-Fagetum*), a Norway spruce monoculture, a clearing community belonging to the *Epilobietea angustifolii* class, and a mesic mountain meadow of the *Arrhenatheretalia* order. In each of the studied communities, randomized selection of 10 plots (1 × 1 m) was performed. On these plots relevés were sampled, a biometric study was conducted, and soil samples were collected. The research revealed a significant influence of *C. epigejos* expansion on the species composition, diversity, and productivity in the herb layers of the studied communities. It also indicated a strong positive influence of sunlight availability and studied physicochemical properties of soil on the expansion ability of *C. epigejos*.

Key words: *Arrhenatheretalia* order, beech forest, *Epilobietea angustifolii*, Polish Sudetes Mountains, soil features, spruce forest

1. Introduction

Wood small-reed (*Calamagrostis epigejos* (L.) Roth) belongs to stoloniferous perennial grass species with high morphological and physiological plasticity (Gloser and Gloser, 1996; Jańczyk-Węglarska, 1996). It possesses some features of expansive species such as a rapid growth rate (Rebele and Lehmann, 2001) and long stolons (Gloser et al., 2004). In Europe, the species' range extends from the coastal belt of the Atlantic Ocean to the Urals (Hultén and Fries, 1986). This species is particularly common in Germany, Poland, and the Czech Republic (Rebele and Lehmann, 2001).

C. epigejos shows a broad range of tolerance to various environmental factors. It is able to colonize and spread on both dry and flooded sites, with a broad range of acidity (pH 2.8–8.2), and on sandy soils poor in nutrients, as well as on nutrient-rich soils, both on insolated and shaded sites. It occurs in various forest and nonforest natural habitats, as well as in disturbed urban and industrial sites (Rebele and Lehmann, 2001). According to Rothmaler (1988), in ruderal habitats wood small-reed occurs mainly in *Epilobietea angustifolii*, *Urtico-Sambucetea*, *Trifolion medii*, and *Ammophilon boreale* communities.

Adaptability to different habitats and competitive strength arise from its ability to create different ecotypes (Jańczyk-Węglarska, 1996). Another important feature of *C. epigejos* in this context is efficient nitrogen uptake from the soil, high accumulation of this element in the roots and shoot bases, and the capacity for its effective translocation from aerial shoots before their dieback to underground storage organs (Gloser, 2002, 2005; Gloser et al., 2004; Kavanová and Gloser, 2005). That efficient nitrogen usage allows *C. epigejos* to grow very fast and to produce a large biomass.

In Central Europe *Calamagrostis epigejos* is very frequent, though not always dominant in plant communities. It is especially visible in shadow forest communities (Rebele and Lehmann, 2001). Patches dominated by *C. epigejos* and fast expanding are a common phenomenon within various plant communities in open areas with soils rich in nutrients (Rebele and Lehmann, 2001; Pruchniewicz and Żołnierz, 2014, 2017). This problem is especially marked in seminatural grassland managed mainly by mowing (Gloser and Gloser, 1999). In recent years rapid and aggressive expansion of wood small-reed within grassland communities has led to changes in species composition

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(Stránská, 2004; Kavanová and Gloser, 2005; Holub et al., 2012) and the loss of their previously high species diversity (Pruchniewicz and Żołnierz, 2017). The expansion mechanism of *Calamagrostis epigejos* and its effects on species composition still remain poorly understood (Pruchniewicz and Żołnierz, 2017). However, it may be connected with very high production of aboveground and underground biomass, which leads to shading of slower growing species and production of a thick layer of slowly degrading litter preventing germination of seeds (Dolečková and Osbornová, 1990; Holub et al., 2004).

In this study we decided to test the hypothesis that the ability of *Calamagrostis epigejos* to expand in plant communities is determined by habitat factors. The crucial question of our study was how the habitat factors influence the ability of *C. epigejos* to produce high aboveground and underground biomass. That, we assume, should be the essence of the mechanism of its expansion in various affected communities and the main reason for its competitive strength. We decided to carry out our study in four different plant communities affected by *C. epigejos* to investigate the influence of various configurations of environmental factors.

Specifically, we addressed the following questions:

I. How does the expansion of *Calamagrostis epigejos* influence the species diversity and composition of forest, clearing, and meadow communities?

II. How do habitat factors influence the biometric variability as well as the ability of *Calamagrostis epigejos* to produce high above- and underground biomass, which in turn leads to the dominance of this species in the communities?

2. Materials and methods

2.1. Study area

The study was conducted in the central part of the Sudetes Mountains (SW Poland) in the Sowie, Bardzkie, and Suche Mountains. This part of the Sudetes Mts. encompasses low ranges with gentle slopes. Four localities were chosen for the survey within the Sudetian lower mountain forest belt. The mean altitude of those localities is 575 m a.s.l. Deciduous forests with European beech (*Fagus sylvatica*) are the potential plant community for that area. However, during the last two centuries they have been converted into artificial Norway spruce stands in most parts. The mesic meadows of the *Arrhenatheretalia* order dominate in the deforested areas. The climate is predominantly shaped by air masses from the Atlantic Ocean. The mean annual temperature in the study area is around 5.5 °C and the mean precipitation ranges between 700 and 800 mm (WBO, 2005). The soil cover mainly consists of brown and acid brown soils derived from igneous and metamorphic rocks as well as from sedimentary rocks (Olędzki, 2007).

2.2. Data collection

The survey was conducted in four types of plant communities with the occurrence of *Calamagrostis epigejos*: a mountain beech forest (*Luzulo luzuloidis-Fagetum*), an artificial Norway spruce monoculture, a clearing community (*Epilobietea angustifolii*), and a mesic mountain meadow community of the *Arrhenatheretalia* order (Appendix). In the forest communities cover of *C. epigejos* remains at a consistently low level. All studied communities are a common element of the landscape in the area. On the other hand, these habitats differ significantly, which has given us an opportunity to carry out our study in a broad variety of environmental factors. The first surveyed community was an acidophilous beech forest (*Luzulo luzuloidis-Fagetum*) with some *Quercus petraea*, and *Acer platanoides* in the canopy layer. The second forest community was a monoculture of Norway spruce (*Picea abies*) artificially introduced into the habitat of a mountain acidophilous beech forest. The third community represented clearing vegetation belonging to the *Epilobietea angustifolii* class. The fourth studied community represented mesic mountain meadow vegetation of the *Arrhenatheretalia* order. The study was carried out on ten patches of each of the four studied communities dispersed through the area. Within each patch we randomly established a set of 10 plots (1 × 1 m) from which the vegetation data of the herb layer were sampled. The percentage scale was used as the measure of the species cover. In each plot we selected 20 individual ramets of *C. epigejos*, whose total height was visually evaluated as nearest to the average for the local population. In collected specimens the following parameters were measured with an accuracy of 1 mm: panicle length, length of the blade, and diameter of the blade. For each specimen we also recorded the mass of blades (g), panicle weight (g), mass (g), and the number of leaves, as well as underground and aboveground biomass. The measurements of the studied biometric features of *C. epigejos* were conducted using fresh specimens. The biomass was determined after drying them at 85 °C to a constant weight. The underground biomass of *C. epigejos* was collected from the depth of 0–15 cm in five replications using the 10 × 10 cm frame. The block of soil was dug out and then in the laboratory all underground parts of *Calamagrostis epigejos* were carefully washed out under tap water. Another set of five subplots (10 × 10 cm) randomly scattered through each studied patch was used for collecting samples of the biomass of the accompanying species and samples of plant necromass. Samples of accompanying species' aboveground biomass were taken with the distinction of broadleaf forbs and graminoids.

From each of the plots, soil samples were collected from the depth of 0–15 cm in five replications. The samples were later dried at room temperature and, after a constant mass was obtained, they were sifted through a 2-mm mesh sieve. Afterwards, the following characteristics of the samples were measured according to methods described by Allen (1989) and Radojević and Bashkin (2006): loss on ignition after heating 2 g of soil in a muffle furnace at 600 °C for 6 h followed by cooling overnight; pH in water (w/v); total nitrogen content using the Kjeldahl method; and exchangeable forms of phosphorus determined colorimetrically after extraction in 0.5 M sodium bicarbonate at pH 8.5. Soluble forms of potassium, calcium, and magnesium were extracted with 1 M ammonium acetate (pH 7.0). A Varian SpectrAA 200 atomic absorption spectrometer was used for determinations of metals. It was set in emission measurement mode for calcium and potassium and in atomic absorption mode for magnesium. Soil texture was determined areometrically.

Light conditions were expressed on a scale of 1–3, where 1 represented full shade (surfaces getting up to 25% of daylight), 2 represented penumbra (surfaces getting up to around 50% of daylight), and 3 represented full sunlight (surfaces getting up to 100% of daylight).

2.3. Statistical analysis

Detrended correspondence analysis (DCA) was used in order to reveal the main environmental gradients on the basis of the species composition of vegetation. The length of the gradient represented by the first DCA canonical axis was 3.4 SD; therefore, canonical correspondence analysis (CCA) was chosen to assess the impact of *Calamagrostis epigejos* on the species composition of the studied communities. Values of aboveground and underground biomass of *C. epigejos* were used as environmental variables. The significance of the variables was tested with the Monte Carlo permutation test with stepwise variable selection. The log-transformed vegetation data were used in all ordination analyses. Ordination analyses were performed using the CANOCO v. 5.03 package (ter Braak and Šmilauer, 2012).

The Shannon–Wiener diversity index was calculated according to the following formula: $H' = -\Sigma (p_i \ln p_i)$, and the Shannon–Wiener evenness index was calculated as follows: $J' = H'/\ln S$, where $pi = n_i/N$; n_i = the abundance of the species expressed as percentage of its cover; N = the sum of abundances of all species; and S = the total number of species. The MVSP v. 3.131 package (Kovach Computing Services, 2004) was used for calculations of all diversity indices.

In statistical analyses the Shapiro–Wilk test was used to check the normal distribution of data. The data for which a normal distribution was obtained were analyzed using parametric methods: one-way ANOVA with post hoc testing of significance of differences using Tukey's HSD test or Pearson correlation analysis (r). The data for which a normal distribution was not found were analyzed using nonparametric methods: the Kruskal–Wallis test and Spearman's rank correlation (Rs). The Levene test was used to verify the assumption of equality of variances.

In order to determine the relationship between the studied biometric features of *Calamagrostis epigejos* as well as to eliminate collinearity and overfitting of variables in the multiple regression analyses, principal correspondence component analysis (PCA) was used.

Multiple regression analyses were used to evaluate the effect of tested environmental variables on the expansion ability of *C. epigejos*. Calculations were made for log transformed and standardized data. The final analysis of residuals showed their normal distribution (Shapiro–Wilk test), lack of autocorrelation (Durbin–Watson test), and the linear character of the model. All statistical analyses were conducted using STATISTICA v. 12 (StatSoft Inc., 2014) software.

3. Results

3.1. The influence of *Calamagrostis epigejos* expansion on the diversity and species composition of studied communities

Significant positive correlations were noted between the underground biomass of *Calamagrostis epigejos* and necromass, as well as biomass of accompanying grasses and forbs (Table 1). A positive correlation was also noted for the aboveground biomass of *Calamagrostis epigejos* and biomass of accompanying herb species. A decrease of the Shannon–Wiener diversity index was observed along with the increasing cover of *Calamagrostis epigejos*. The increase of the evenness index and increases of necromass and biomass of accompanying grass and herb species (Table 1) were caused by growing abundance of *C. epigejos*. The mean number of species occurring in plots in the forest communities ranged from 4.0 m^{-2} (*Luzulo luzuloidis-Fagetum*) to 4.3 m^{-2} (monoculture of spruce). In clearing and meadow communities the mean number of species reached values of 5 and 6.8 m^{-2}, respectively.

CCA demonstrated that the variety of species composition was strongly influenced by the habitat gradients, which were related to the first two canonical axes (Figure 1). The eigenvalues for axes 1 and 2 were 0.3021 and 0.2835, respectively. The cumulative percentage variances of species data for those axes were 4.87 and 9.44. The results of the Monte Carlo permutation test followed by stepwise selection of the variables showed that the underground biomass of *Calamagrostis epigejos* had a significant impact on the species composition (lambda = 4.8%; F = 1.9; P = 0.008). On the other hand, no significant influence of the aboveground biomass of *Calamagrostis epigejos* was noted (lambda = 49.1%; F = 1.9; P = 0.062).

Table 1. Spearman's rank correlations between under- and aboveground biomass of *Calamagrostis epigejos* and its cover and the Shannon–Wiener diversity index (H'), evenness index (J'), biomass of accompanying forbs and grasses, and plant necromass. Asterisks denote Spearman correlation coefficients (Rs) significant at *P ≤ 0.05, **P ≤ 0.01, and ***P ≤ 0.001.

	H'	J'	Grasses biomass	Forbs biomass	Necromass
Underground biomass		–0.409**	0.352	0.781***	0.352**
Aboveground biomass		–0.494***		0.529***	
Cover	–0.464**	–0.609***	0.323*	0.456**	0.536***

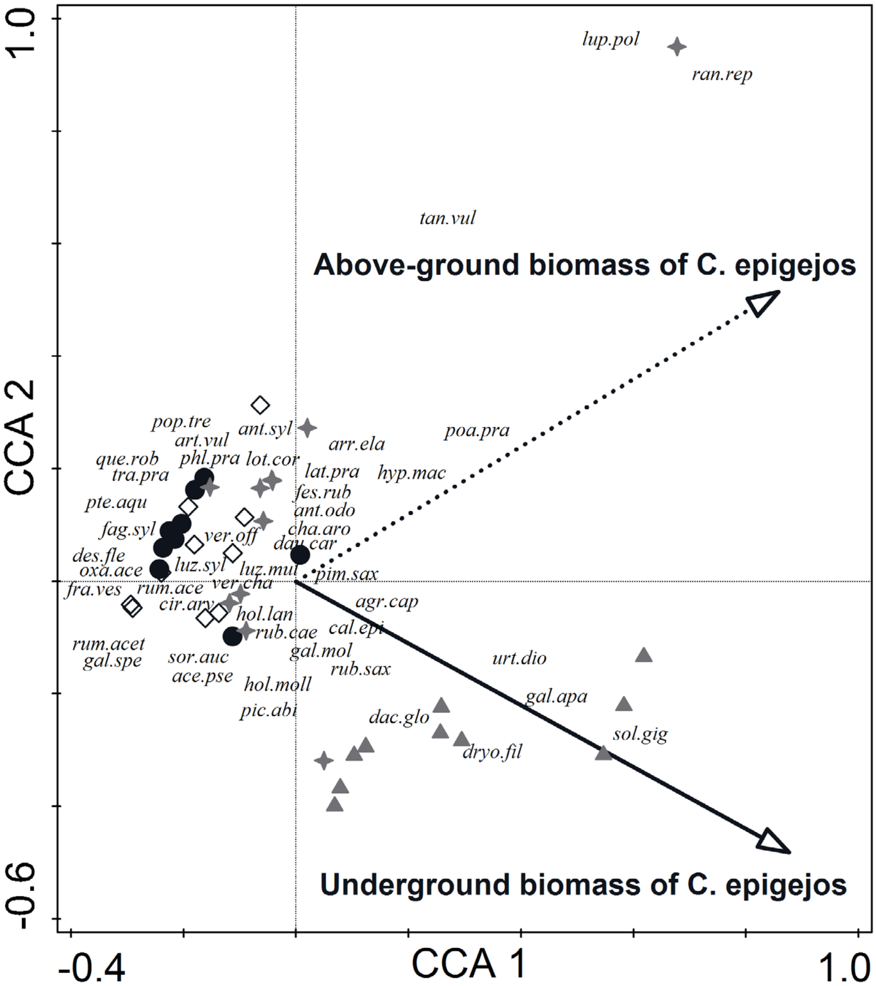

Figure 1. Results of CCA for the samples and species. The vector marked by a solid line reflects the variable selected as significant (P ≤ 0.05) by the Monte Carlo test. Black circles indicate the spruce forest, black diamonds the beech wood, gray triangles the clearing community (*Epilobietea angustifolii* class), and gray stars the mesic meadows community. Abbreviations of species names: ace.pse - *Acer pseudoplatanus*, agr.cap - *Agrostis capillaris*, ant.odo - *Anthoxanthum odoratum*, ant.syl - *Anthriscus sylvestris*, arr.ela - *Arrhenatherum elatius*, art.vul - *Artemisia vulgaris*, cal.epi - *Calamagrostis epigejos*, cha.aro - *Chaerophyllum aromaticum*, cir.arv - *Cirsium arvense*, dac.glo - *Dactylis glomerata*, dau.car - *Daucus carota*, des.fle - *Deschampsia flexuosa*, dryo.fil - *Dryopteris filix-mas*, fag.syl - *Fagus sylvatica*, fes.rub - *Festuca rubra*, fra.ves - *Fragaria vesca*, gal.spe - *Galeopsis speciosa*, gal.apa - *Galium aparine*, gal.mol -*Galium mollugo*, hol.lan - *Holcus lanatus*, hol.mol - *Holcus mollis*, hyp.mac - *Hypericum maculatum*, lat.pra - *Lathyrus pratensis*, lot.cor - *Lotus corniculatus*, lup.pol - *Lupinus polyphyllus*, luz.mul - *Luzula multiflora*, luz.syl - *Luzula sylvatica*, oxa.ace - *Oxalis acetosella*, phl.pra - *Phleum pratense*, pic.abi - *Picea abies*, pim.sax - *Pimpinella saxifraga*, poa.pra - *Poa pratensis*, pop.tre - *Populus tremula*, pte.aqu - *Pteridium aquilinum*, que.rob - *Quercus robur*, ran.rep - *Ranunculus repens*, rub.cae - *Rubus caesius*, rub.sax - *Rubus saxatilis*, rum.ace - *Rumex acetosa*, rum.acet - *Rumex acetosella*, sol.gig - *Solidago gigantea*, sor.auc - *Sorbus aucuparia*, tan.vul - *Tanacetum vulgare*, tra.pra - *Tragopogon pratensis*, urt.dio - *Urtica dioica*, ver.cha - *Veronica chamaedrys*, ver.off - *Veronica officinalis*.

3.2. The effect of different plant communities and environmental factors on the biometric variability of *Calamagrostis epigejos*

Based on the study, significant differences in morphological features of *C. epigejos* were demonstrated (Table 2). The highest coverage of *C. epigejos* was recorded in the clearing communities, while the lowest cover was noted in the forest and meadows communities (H = 18.768, P = 0.0003). Significant differences were observed between studied biometric parameters of *C. epigejos* growing in various communities: blade length (H = 19.179; P = 0.0003), panicle length (H = 17.843; P = 0.0005), blade diameter (H = 14.578; P = 0.0022), blade mass (H = 11.814; P = 0.008), panicle weight (H = 15.76; P = 0.0013), and underground (H = 28.128; P ≤ 0.001) and aboveground biomass (H = 12.449; P = 0.006). The highest values of the majority of studied biometric parameters were recorded in *C. epigejos* occurring in the clearing community, with the exception of the diameters of blades, which were the largest in grasses growing in the mountain mesic meadows. No significant difference was determined for the mass of leaves (H = 1.778; P = 0.620) and number of leaves (H = 8.33; P = 0.040).

The results of PCA are shown in Figure 2. As significant variables the following were selected: aboveground biomass, underground biomass, and cover of *Calamagrostis epigejos*. These variables were tested in multiple regression analysis.

The results of multiple regression (Table 3) calculated together with the correlation coefficients revealed a significant influence of environmental factors on the features of *C. epigejos* determining its capacity for expansion. In the case of aboveground biomass (R = 0.77, R^2 = 0.59, adjusted R^2 = 0.46, F = 4.75, P = 0.0005) significant effects of light, concentration of exchangeable phosphorus, and thickness of soil were noted. Negative effects were noted for pH and the percentage of the sand fraction. Positive influences on the underground biomass were noted for light, concentration of exchangeable phosphorus, and organic matter (R = 0.97, R^2 = 0.95, adjusted R^2 = 0.94, F = 86.10, P < 0.0001). Negative effects were observed for soil thickness and concentration of exchangeable potassium. The cover of *C. epigejos* was positively correlated with the light level (R = 0.84, R^2 = 0.70, adjusted R^2 = 0.65, F = 13.03, P < 0.0001). Negative correlations were noted for pH, percentage fraction of silt, and organic matter content.

4. Discussion

4.1. The influence of *Calamagrostis epigejos* expansion on the species diversity and composition of studied communities

The study revealed a significant influence of *Calamagrostis epigejos* expansion on the studied communities. However, the significant influence is restricted only to the underground, and not the aboveground, biomass of wood small-reed. Along with the expanding *Calamagrostis epigejos*, there was observed a positive effect of its underground biomass on increase of plant necromass, as well as biomass of forbs and grasses. Increase of forbs biomass was caused by increased *C. epigejos* aboveground

Table 2. Comparison of cover and some biometric features of *Calamagrostis epigejos* between studied communities. The table shows mean values with standard errors. Different letters in each row show significant differences obtained after the Kruskal–Wallis test (P ≤ 0.05).

		Spruce forest			Beech forest			Clearing			Mesic meadows		
		x	SE		x	SE		x	SE		x	SE	
Cover of *C. epigejos*	%	62.9	9.57	a	75.6	9.25	a	98.3	0.15	b	71.5	5.27	a
Blade length	cm	73.46	2.71	a	77.02	4.01	a	108.04	2.56	b	81.9	5.7	a
Panicle length	cm	16.63	0.48	a	17.44	1.51	a	22.81	0.64	b	14.83	1.53	a
Blade diameter	cm	1.71	0.19	a	2.13	0.23	ab	2.68	0.13	b	2.75	0.09	b
Blade mass	g	0.74	0.08	a	0.76	0.09	ab	1.37	0.19	b	1.05	0.08	ab
Panicle weight	g	0.29	0.03	ab	0.19	0.03	a	0.47	0.06	b	0.3	0.05	ab
Leaf mass	g	0.2	0.02	a	0.25	0.05	a	0.26	0.03	a	0.69	0.46	a
Number of leaves		2.4	0.16	a	2.6	0.16	a	2.3	0.15	a	2	0	a
Underground biomass	g	145	63.35	a	183	41.27	a	1539	123.43	b	492.16	88.02	ab
Aboveground biomass	g	1.22	0.08	a	1.20	0.15	a	2.09	0.27	b	2.03	0.44	ab

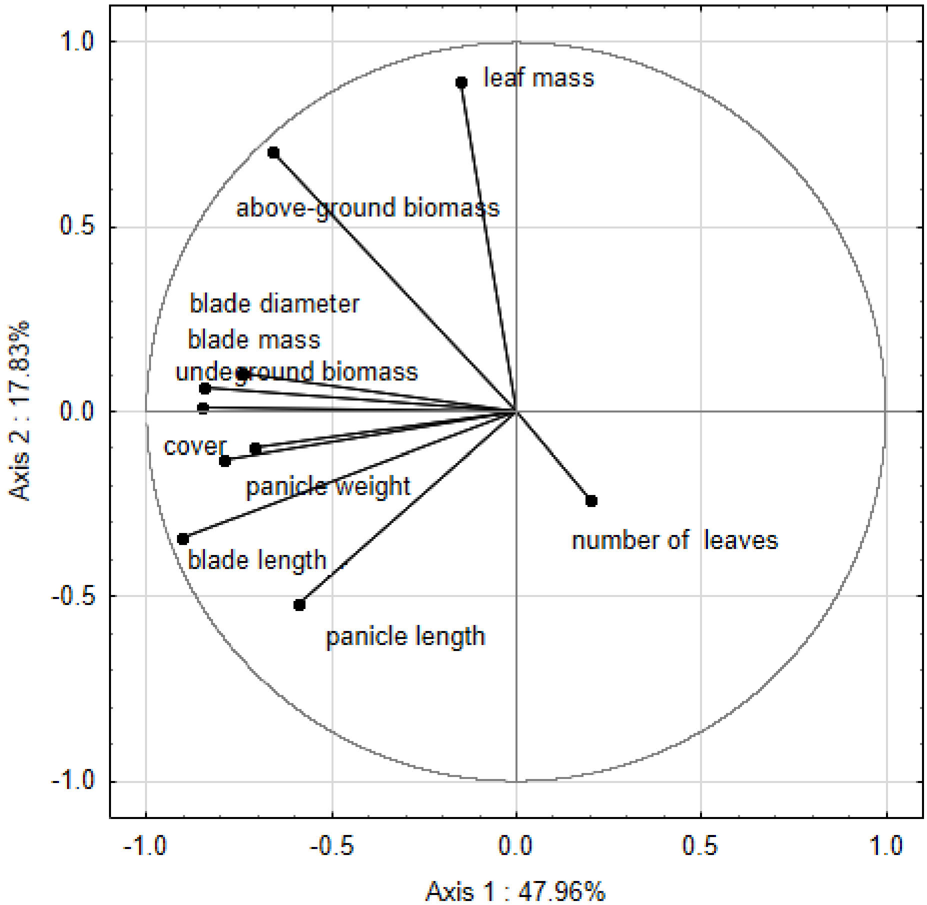

Figure 2. Results of PCA in the first and second canonical axes. The analysis was prepared for all biometric features and cover of *C. epigejos*.

biomass. An increase of *C. epigejos* cover was noted along with a decrease of Shannon–Wiener diversity and evenness indices.

Similarly to the previous results (Pruchniewicz and Żołnierz, 2017), there was observed an increase of necromass and biomass of accompanying species of grasses and forbs. *C. epigejos* is a highly competitive species limiting the occurrence of other taxa (Somodi et al., 2008) and leading to a quick decrease in species richness wherever it occurs (Mudrák et al., 2010). The studied communities, both forest and meadow, were characterized by low diversity. According to Gloser and Gloser (1999) and Gloser et al. (2004), low species richness in communities dominated by *C. epigejos* is caused by a thick layer of plant necromass, which undergoes slow decomposition and successfully limits regenerative succession and the growth and development of forest species. This observation is confirmed by our research in clearing and meadow communities, where the mean number of species is higher. The decline of species diversity in grassland under the influence of *C. epigejos* may be explained by the shading of nearby plants (Somodi et al., 2008), increased soil fertility due to nutrient availability (Holub and Záhora, 2008), and a thick necromass layer limiting the germination and development of meadow species (Házi et al., 2011).

4.2. The influence of environmental factors on features determining the expansion ability of *Calamagrostis epigejos*

The high diversity of biometric parameters in various plant species is one of the main factors determining the possibilities of adaptation to the habitat conditions (Sultan, 1987). This phenomenon was spectacularly apparent in the study area, where significant differences in morphological features of *C. epigejos* were noted. In the case of aboveground biomass our study shows a significant effect of light, concentration of exchangeable phosphorus, and thickness of soil. A negative effect was noted for pH and the percentage of the sand fraction. There was observed a positive influence of light, concentration of exchangeable phosphorus, and organic matter content on underground biomass. A negative impact was noted for the soil thickness and concentration of exchangeable potassium.

Table 3. Summary of the multiple regression analysis for the biomass and cover of *Calamagrostis epigejos*.

	BETA	r	R^2	t	p
Aboveground biomass of *C. epigejos*					
Light	0.545	0.403	0.732	2.410	0.022
pH	–0.718	–0.405	0.844	–2.424	0.022
P	0.734	0.419	0.837	2.530	0.017
Share of sand	–0.803	–0.420	0.863	–2.535	0.017
Soil depth	0.450	0.389	0.638	2.311	0.028
Underground biomass of *C. epigejos*					
Light	0.951	0.922	0.684	13.473	<0.001
Soil depth	–0.363	–0.715	0.599	–5.793	<0.001
P	0.203	0.410	0.753	2.543	0.016
K	–0.217	–0.418	0.772	–2.607	0.014
Organic matter	0.182	0.370	0.757	2.254	0.031
Cover of *C. epigejos*					
Light	0.859	0.792	0.322	7.458	<0.001
pH	–1.109	–0.659	0.815	–5.031	<0.001
Share of silt	–0.585	–0.463	0.763	–3.003	0.005
Organic matter	–0.584	–0.412	0.822	–2.598	0.014

The cover of *C. epigejos* was positively correlated with light level. Negative correlations were noted for pH, percentage fraction of silt, and organic matter.

Light is one of the main factors stimulating the size of aboveground and underground biomass of *C. epigejos*. Long-term survival in the understory layer would not be possible without adaptation allowing the effective use of sun energy. The morphological and physiological adaptation of the species to low light enabled it to survive under a dense cover of coniferous trees, where the maximal size of photosynthetic photon flux rarely exceeds the lower limit (20 µmol g m^{-2}) of sciophyte vascular plants (Gloser and Gloser, 1996). On open surfaces, absorption of light energy causes an increase in the growth rate (Gloser and Gloser, 1996) and enables generative multiplication of *C. epigejos* (Lehmann and Rebele, 1994). The significant influence of light on the size of the biomass is relative. Along with the increase of sunlight availability, photosynthesis intensification takes place, which in turn leads to the storage of substances in underground parts and their increased growth.

Apart from its flexibility towards light, *C. epigejos* is characterized by a high tolerance to nutrients in soil (Gloser and Gloser, 1999). In their research, Lehmann and Rebele (2005), Tůma et al. (2005), and van der Berg et al. (2005) recorded an increase in *C. epigejos* biomass caused by nitrogen fertilization. Meanwhile, Süß et al. (2004) noted a positive, linear correlation between *C. epigejos* coverage and humidity index, soil nitrogen, potassium, and phosphorus. On the other hand, Heinsdorf (1984) found no influence of potassium and phosphorus on *C. epigejos* aboveground biomass. Additionally, Brünn (1999) recorded low potassium requirements in *C. epigejos*. This observation was not, however, confirmed in our research. One of the main factors influencing the size of aboveground and underground *C. epigejos* biomass was the concentration of exchangeable forms of phosphorus in soil. The negative relation between potassium and underground biomass is not found in other researchers' studies. A positive relation between organic matter content and aboveground biomass and a negative one with *C. epigejos* cover should be regarded as related to the availability of nutrients that reach the species as a result of dead organic matter decomposition.

In research carried out by Heinsdorf (1984), calcium was one of the elements that had a decisive influence on the size of aboveground *C. epigejos* biomass. Our research did not confirm that finding. We observed no significant influence of exchangeable calcium forms. However, our results showed a negative correlation between aboveground biomass and *C. epigejos* and the pH of soil. Rebele and Lehmann (2001) noted that high calcium concentrations may indirectly influence the increase of pH in acidic soils, which may lead to the limitation of macrocomponent assimilation, above all magnesium and nitrate ions (Gloser and Gloser, 2000), which directly influence the growth and development of the studied species, thus explaining the results of our research.

According to Jańczyk-Węglarska (1996), *Calamagrostis epigejos* inhabits soils without any relation to their granulometric contents. It occurs on sandy, sandy-clay, and even clay soils. However, the results of our studies show that soils with dominating sand or silt inhibit the expansive properties of *C. epigejos*.

Apart from factors connected with the physicochemical properties of soil, our research showed a significant positive correlation between the thickness of soil and aboveground biomass and a negative one with the underground biomass of *C. epigejos*. Wood small-reed is one of the species whose rhizomes occur at 3–35 cm depth. Most of the root growth is within 0–40 cm (Burschel, 1958). On shallow soils root densification occurs (with regard to units per volume), which explains the results obtained in this research.

In conclusion, our study revealed that expansion of *Calamagrostis epigejos* and particularly its underground biomass significantly influenced the species diversity and composition of the surveyed communities. *C. epigejos* growing in various forest and nonforest communities significantly differed in its biometric features. The competitive strength of *C. epigejos* was stimulated by insolation and some physicochemical properties of the soils (proportion of sand and silt, organic matter, pH, P, K). In the forest communities development of *C. epigejos* patches was inhibited by light deficiency and soil infertility.

References

Allen SE (1989). Chemical Analysis of Ecological Materials. 2nd ed. Oxford, UK: Blackwell Scientific Publications.

Brünn S (1999). Untersuchungen zum Mineralstoffhaushalt von *Calamagrostis epigejos* (L.) Roth in stickstoffbelasteten Kiefernwäldern. Berichte des Forschungszentrums Waldökosysteme Universität Göttingen, Reihe A, Bd. 160. Göttingen, Germany: University of Göttingen (in German).

Burschel P (1958). Die Bewurzelung einiger forstlicher Bodenpflanzen. Forst- und Jagdzeitung 129: 89-94 (in German).

Dolečková H, Osbornová J (1990). Competition ability and plasticity of *Calamagrostis epigejos*. Zpr Čs Bot Společ 25: 35-38.

Gloser V (2002). Seasonal changes of nitrogen storage compounds in a rhizomatous grass *Calamagrostis epigejos*. Biol Plantarum 45: 563-568.

Gloser V (2005). The consequences of lower nitrogen availability in autumn for internal nitrogen reserves and spring growth of *Calamagrostis epigejos*. Plant Ecol 179:119-126.

Gloser V, Gloser J (1996). Acclimation capability of *Calamagrostis epigejos* and *C. arundinacea* to changes in radiation environment. Photosynthetica 32: 203-212.

Gloser V, Gloser J (1999). Production processes in a grass *Calamagrostis epigejos* grown at different soil nitrogen supply. In: Grassland Ecology V. Proceedings of the 5th Ecological Conference, pp. 69-76.

Gloser V, Gloser J (2000). Nitrogen and base cation uptake in seedlings of *Acer pseudoplatanus* and *Calamagrostis villosa* exposed to an acidified environment. Plant Soil 226: 71-77.

Gloser V, Košvancová M, Gloser J (2004). Changes in growth parameters and content of N-storage compounds in roots and rhizomes of *Calamagrostis epigejos* after repeated defoliation. Biologia Bratislava 59 (Suppl. 13): 179-184.

Házi J, Bartha S, Szentes S, Wichmann B, Penksza K (2011). Seminatural grassland management by mowing of *Calamagrostis epigejos* in Hungary. Plant Biosyst 145: 699-707.

Heinsdorf D (1984). Wirkung von Mineraldüngung auf Ernährung und Wachstum von Winterlinden (*Tilia cordata* Mill.) auf Kippenbodenformen der Niederlausitz. Beitr Forstwirtsch 18: 28-36 (in German).

Holub P, Sedláková I, Fiala K, Tůma I, Záhora J, Tesařová M (2004). Reasons and consequences of expansion of *Calamagrostis epigejos* in meadows of the Dyje river floodplain. Verhandlungen der Gesellschaft für Ökologie 34: 167.

Holub P, Tůma I, Záhor J, Fiala K (2012). Different nutrient use strategies of expansive grasses *Calamagrostis epigejos* and *Arrhenatherum elatius*. Biologia 67: 673-680.

Holub P, Záhora J (2008). Effects of nitrogen addition on nitrogen mineralization and nutrient content of expanding *Calamagrostis epigejos* in the Podyjí National Park, Czech. J Plant Nutr Soil Sci 171: 795-803.

Hultén E, Fries M (1986). Atlas of North European Vascular Plants. North of the Tropic of Cancer. Königstein, Germany: Koeltz Scientific Books.

Jańczyk-Węglarska J (1996). The strategy of *Calamagrostis epigejos* (L.) Roth individual development under ecological conditions of the valley ravine of the River Warta near Poznań. In: Ser. Biologia, 56. Poznan, Poland: Adam Mickiewicza University (in Polish with an abstract in English).

Kavanová M, Gloser V (2005). The use of internal nitrogen stores in the rhizomatous grass *Calamagrostis epigejos* during regrowth after defoliation. Ann Bot-London 95: 457-463.

Kovach Computing Services (2004). MVSP v3.131. Pentraeth, UK: Kovach Computing Services.

Lehmann C, Rebele F (1994). Zum Potential sexueller Fortpflanzung bei *Calamagrostis epigejos* (L.) Roth. Verh Ges f Ökol Bd 23: 445-450 (in German).

Lehmann C, Rebele F (2005). Phenotypic plasticity in *Calamagrostis epigejos* (Poaceae): response capacities of genotypes from different populations of contrasting habitats to a range of soil fertility. Acta Oecol 28: 127-140.

Mudrák O, Frouz J, Velichová V (2010). Understory vegetation in reclaimed and unreclaimed post-mining forest stands. Ecol Eng 36: 783-790.

Olędzki JR (2007). Regiony geograficzne Polski. Teledetekcja Środowiska 38: 1-337 (in Polish).

Pruchniewicz D, Żołnierz L (2014). The influence of environmental factors and management methods on the vegetation of mesic grasslands in a central European mountain range. Flora 209: 687-692.

Pruchniewicz D, Żołnierz L (2017). The influence of *Calamagrostis epigejos* expansion on the species composition and soil properties of mountain mesic meadows. Acta Soc Bot Pol 86: 3516.

Radojević M, Bashkin VN (2006). Practical Environmental Analysis. Cambridge, UK: The Royal Society of Chemistry.

Rebele F, Lehmann C (2001). Biological flora of Central Europe: *Calamagrostis epigejos* (L.) Roth. Flora 196: 325-344.

Rothmaler W (1988). Exkursionflora für die Gebiete der DDR und der BRD. B.II. Gefässpflanzen. Berlin, Germany: Volk und Wiessen Volkseigener Verlag.

Somodi I, Virágh K, János P (2008). The effect of expansion of the clonal grass *Calamagrostis epigejos* on the species turnover of a semi-arid grassland. Appl Veg Sci 11: 187-192.

StatSoft (2014). STATISTICA (Data Analysis Software System), Version 12. Tulsa, OK, USA: StatSoft.

Stránská M (2004). Successional dynamics of *Cynosurus* pasture after abandonment in Podkrkonoší. Plant Soil Environ 40: 364-370.

Sultan SE (1987). Evolutionary implications of phenotypic plasticity in plants. Evol Biol 21: 127-178.

Süß K, Storm C, Zehm A, Schwabe A (2004). Succession in inland sand ecosystems: which factors determine the occurrence of the tall grass species *Calamagrostis epigejos* (L.) Roth and *Stippa capillata* L.? Plant Biol 6: 465-476.

ter Braak, CJF, Šmilauer P (2012). CANOCO Reference Manual and User's Guide: Software for Ordination, Version 5.0. Ithaca, NY, USA: Microcomputer Power.

Tůma I, Holub P, Fiala K (2009). Soil nutrient heterogeneity and competitive ability of three grass species (*Festuca ovina*, *Arrhenatherum elatius* and *Calamagrostis epigejos*) in experimental conditions. Biologia 64: 694-704.

van der Berg LJL, Tomassen HBM, Roelofs JGM, Bobbink R (2005). Effects of nitrogen enrichment on coastal dune grassland: a mesocosm study. Environ Pollut 138: 77-85.

WBO (2005). Ecophysiographic study for the Lower Silesian Voivodeship. Wrocław, Poland: Wojewódzkie Biuro Urbanistyczne we Wrocławiu.

Appendix. Photographs showing the studied plant communities.

Photo 1. Mountain beech forest (*Luzulo luzuloidis-Fagetum*).

Photo 2. Patch of *Calamagrostis epigejos* in an artificial Norway spruce stand.

Photo 3. Clearing community (*Epilobietea angustifolii*).

Photo 4. Mesic mountain meadow community of the *Arrhenatheretalia* order.