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ORIGINAL RESEARCH PAPER

The influence of *Calamagrostis epigejos* expansion on the species composition and soil properties of mountain mesic meadows

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Abstract

Due to social and economic changes which have occurred in the last decades, many meadows located in mountain regions have ceased to be used. Abandonment of meadows leads to the degradation of their species composition. An example of degradation may be seen in the development of patches dominated by *Calamagrostis epigejos*. The aim of this research was to determine the influence of *C. epigejos* in its consecutive expansion stages on qualitative properties of meadow sward and on selected physico-chemical properties of soils. The study revealed strong degradation of mountain meadows due to the expansion of *C. epigejos*. The degradation manifested in a decrease in species diversity, a decline of species typical for mesic meadows, and an increased proportion of synanthropic species. The increase in aboveground biomass of *C. epigejos* strongly reduced the biomass of other species, while underground biomass had no effect on accompanying species. However, only a small impact of *C. epigejos* expansion on soil degradation was detected. The cumulating plant necromass dominated by this species caused a decrease in diversity indices and, at the same time, an increase in exchangeable forms of potassium and phosphorus in the soil.

Keywords

Arrhenatheretalia grasslands; wood small-reed; degradation of vegetation; biodiversity

Introduction

Grasslands, a characteristic element of agrarian landscapes in Europe, are among the semi-natural plant communities with the highest species richness [1–3]. They owe their existence to systematic mowing and grazing, which have shaped their floristic composition for centuries [4,5]. However, in the last decades we have observed a decline in diversity of meadow and pasture communities as well as a decrease of the area of semi-natural grassland in many regions of Europe. This is a result of fragmentation and changes in traditional meadow management [6–8]. The cessation of traditional management methods and the abandonment of grassland are the main problems, which concern especially mountain regions, where the traditional agricultural economy has become unprofitable in the last decades [5,9].

The abandonment of grasslands leads to degradation processes touching their vegetation. We define the degradation of meadow vegetation following Prach [10] and Krahulec et al. [11]. They have described processes initiated by the abandonment of grasslands, which consist in an expansion of some species leading to their domination in a community, followed by the decrease of species richness and diversity. The growing abundance of an expansive species may strongly change the quantitative proportions between species as well as spatial properties of the sward. In Central Europe, one such species is *Calamagrostis epigejos* (wood small-reed), whose expansion often leads to the degradation of vegetation of abandoned or irregularly managed meadows [9,13–17].

Calamagrostis epigejos is a fast-growing perennial grass, which is one of the strongest competitors, and therefore is able to degrade various plant communities in Europe [9,12,13,16] and North America [18]. This species possesses various features of an expansive plant, such as high morphological and physiological plasticity, long rhizomes [19,20], and a high growth rate [13]. It is able to produce large amounts of biomass and to outcompete other species, particularly small and light-demanding forbs [21]. It also produces a particularly dense and thick litter, which prevents the germination of other species [21,22]. Intense intake of nitrogen from the soil, the ability to store it in the roots and shoot base, and its translocation from dying organs [19,23,24] are also very advantageous. Moreover, *C. epigejos* is highly tolerant to abiotic stress factors [17]. Stands dominated by *Calamagrostis epigejos* form long-lasting stable grassland communities, what means stopping the course of succession [25,26].

There are many publications about the physiology and ecology of *Calamagrostis epigejos* [13,19,27,28]. However, its expansion mechanism and the dynamics of changes it causes in grassland communities and habitats still remain relatively poorly explained. Both aspects of the issue can be studied when developing *Calamagrostis epigejos* patches come into contact with meadow vegetation. We studied the growth of *C. epigejos* in successive stages of its expansion. Our intention was to test the hypothesis that the development of patches dominated by *C. epigejos* influences both qualitative properties of meadow vegetation and physico-chemical characteristics of the soil. The aim of this research was to determine the influence of *C. epigejos* in its consecutive expansion stages in meadows on (***i***) species composition, species diversity, biomass production, and accumulation of plant necromass; and (***ii***) selected physico-chemical properties of soils.

Material and methods

Data collection

The research was conducted in the Central Sudetes (SW Poland), in the Sowie Mountains region and in the hills in their SW foreground. Eight *Arrhenatheretalia* meadows were chosen for the study, all with the presence of patches dominated by *Calamagrostis epigejos*. In those patches, saplings of trees and shrubs were noticed only sporadically. Three 20-m-long transects were set on each meadow, crossing perpendicularly the border between vegetation degraded with *C. epigejos* and non-degraded, where *C. epigejos* was not recorded. Along the transects, 1-m^2 plots were marked 1, 2, 3, 4, 5, and 10 meters from the border on both sides of vegetation patches. The border of the degraded meadows was outlined by the patches in which the *Calamagrostis epigejos* occurred. In total, 288 relevés were taken from these plots. The species cover was expressed on a percentage scale. Five random samples of *C. epigejos* aboveground biomass were collected on the plots using a 100-cm^2 frame, and underground biomass samples were collected from the depth of 0–15 cm. The underground biomass represented only stolons of *C. epigejos*, which were prepared during sampling. Another five randomly established subplots (100 cm^2) were used to collect samples of biomass of accompanying species and samples of plant necromass. Samples of accompanying species' aboveground biomass were taken with distinction of graminoids and broadleaf forbs. Underground biomass samples of *C. epigejos* were collected from the depth of 0–15 cm. The upper layers containing undecomposed plant remnants were collected as necromass samples. In the laboratory, samples from each subplot were combined into a bulk sample and dried at 85°C to a constant weight.

In order to study the changes in habitat properties caused by *C. epigejos* expansion, we collected soil samples in five replications from places determined by the regular pattern: four corners and midpoint of the plot. The samples were collected with a metal cylinder (10 cm diameter, 15 cm height). The top layer of undecomposed organic matter was removed from the sample core. Five individual samples of equal volume were then merged into a collective sample. The samples were later dried at room temperature and, after a constant mass was obtained, it was sifted through a sieve with 2-mm mesh. Afterwards, the following characteristics of the samples were measured: (***i***) pH in water (w/v), (***ii***) organic matter contents after heating 2 g of soil in a muffle furnace at 600°C for 6 hours, (***iii***) total nitrogen content using the Kjeldahl method, (***iv***) 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 of ammonium acetate (pH 7.0). A Varian SpectrAA 200 spectrometer was used for all the determinations. It was set in emission measurement mode for calcium and potassium and in atomic absorption mode for magnesium [29,30].

Statistical analyses

One-way analysis of variance (ANOVA) or Kruskal–Wallis analysis of variance by rank were used to test differences between mean coverage of *C. epigejos* and the size of its aboveground and underground biomass, mean values of diversity index (H') and Shannon–Wiener evenness index (J'), number of species (S), plant necromass as well as aboveground biomass of accompanying forb and grass species on degraded and non-degraded parts of meadows. Pearson (r) or Spearman (r_s) correlations were calculated between coverage, the size of aboveground and underground *C. epigejos* biomass and the number of species (S), diversity index (H'), Shannon–Wiener evenness index (J'), accompanying herbs and grasses biomass, plant necromass as well as habitat properties. The Shapiro–Wilk test was used to check the normal distribution. Levene's test was used to check for homogeneity of variances. Because of the lack of normal distribution and/or homogeneity of variances, data were tested using nonparametric methods: Spearman rank correlation, Kruskal–Wallis analysis of variance by rank, or Spearman (r_s) correlation. The data for which a normal distribution was obtained were studied using parametric methods: Pearson correlation (r) and one-way ANOVA followed by post-hoc testing of significance of differences with the HSD Tukey test. All statistical analyses were performed using STATISTICA v. 12 software [31].

To determine the variability of plant species composition and reveal the main environmental gradients on the basis of the species composition of vegetation, detrended correspondence analysis (DCA) using the CANOCO v. 5.03 package was performed [32]. The length of the gradient represented by the first DCA canonical axis was 4.900 *SD*; therefore, canonical correspondence analysis (CCA) was chosen to assess the impact of *Calamagrostis epigejos* expansion on the vegetation. The environmental variables represent distance on the transect, above- and underground biomass of *C. epigejos*, and necromass. The square root transformed vegetation data were used in both analyses. The significance of the variables was tested with the Monte Carlo permutation test with stepwise variable selection.

The Shannon–Wiener diversity index H' was calculated according to the formula: $H' = -\Sigma (p_i \ln p_i)$, and the Shannon–Wiener evenness index J' was calculated as follows: $J' = H' / \ln S$, where $p_i = n_i/N$, n_i = the abundance of the species i expressed as its cover, N = the sum of abundances of all species, and S = the total number of species. The MVSP v. 3.131 package [33] was used for calculations of all diversity indices.

Diagnostic species for classes and orders of vegetation were taken from Matuszkiewicz [34] and Hájková et al. [35].

Results

Mean *C. epigejos* coverage within the degraded areas was between 53% and 88% (Fig. 1). The lowest values were noted 1 m within the degraded areas. In the 2 to 10 m range there was a significant increase in *C. epigejos* coverage (H = 39 249; p < 0.0001) as compared to the first plot (1 m) within the degraded patch. Progressing *C. epigejos* expansion was associated with its aboveground biomass increase (H = 13 160;

$p = 0.0219$), but no differences were observed in its underground biomass ($H = 8345$; $p = 0.1382$; Fig. 1).

The lowest values of species number per plot were noted 10 m within the patches of degraded meadows (Fig. 2). However, only plots located within a distance of 4–10 m inside degraded patches had a significantly lower species number as compared to the richest ones occurring at the ends of transects in non-degraded parts of meadows. The analysis of vegetation accompanying *C. epigejos* in that section showed a drop in biomass of other grass species ($H = 83\,445$; $p < 0.0001$) and biomass increase in forbs ($H = 46\,936$; $p < 0.0001$). Plots established within degraded patches had greater amount of plant necromass ($H = 66\,448$; $p < 0.0001$) dominated mainly by the remnants of *C. epigejos*.

The results of CCA showed that the habitat gradient was related to the first two axes of the CCA, which had a decisive influence on the grassland composition (Fig. 3). The eigenvalues for axes one and two were 0.381 and 0.04, respectively. Cumulative percentage variance of species data for those axes were 4.49 and 4.98, respectively. All axes explained 5.7% of the total variance of the data for vegetation. The results of the Monte Carlo permutation test with stepwise variable selection showed that only the *C. epigejos* aboveground biomass ($F = 10.8$; $p = 0.002$), whose contribution to the total variation was only 3.6%, and distance on the transect ($F = 3.6$; $p = 0.002$), whose contribution to the total variation was 1.2%, had a significant impact on the species composition. Species typical for *Arrhenatheretalia* meadows (e.g., *Arrhenatherum elatius*, *Agrostis capillaris*, *Cynosurus cristatus*, *Galium mollugo*, *Plantago lanceolata*) were gathered within the distance between 1 and 10 m within the non-degraded areas. With an increasing level of degradation (from 1 to 10 m) the study showed a 22% decrease of the total number of *Molinio-Arrhenatheretea* class species, whereas the proportion of synanthropic species belonging to classes *Epilobietea angustifolii* and *Stellarietea mediae* increased by 15.3% and 7.6%, respectively (Fig. 3).

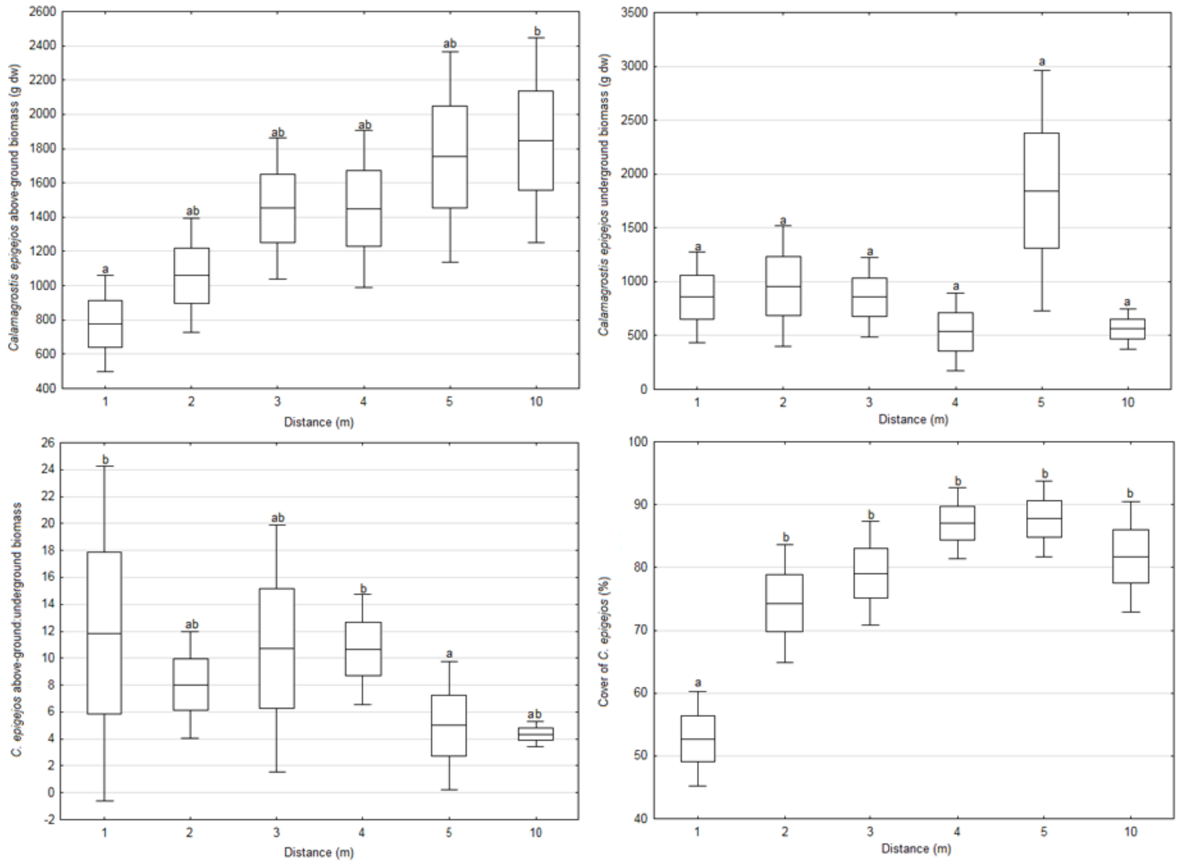

Fig. 1 Mean coverage of *C. epigejos* and the size of its aboveground and underground biomass in degraded patches. Means with standard error values (boxes) and confidence intervals (whiskers) for plots are given. Different letters indicate significant differences obtained in the Kruskal–Wallis test ($p \leq 0.05$).

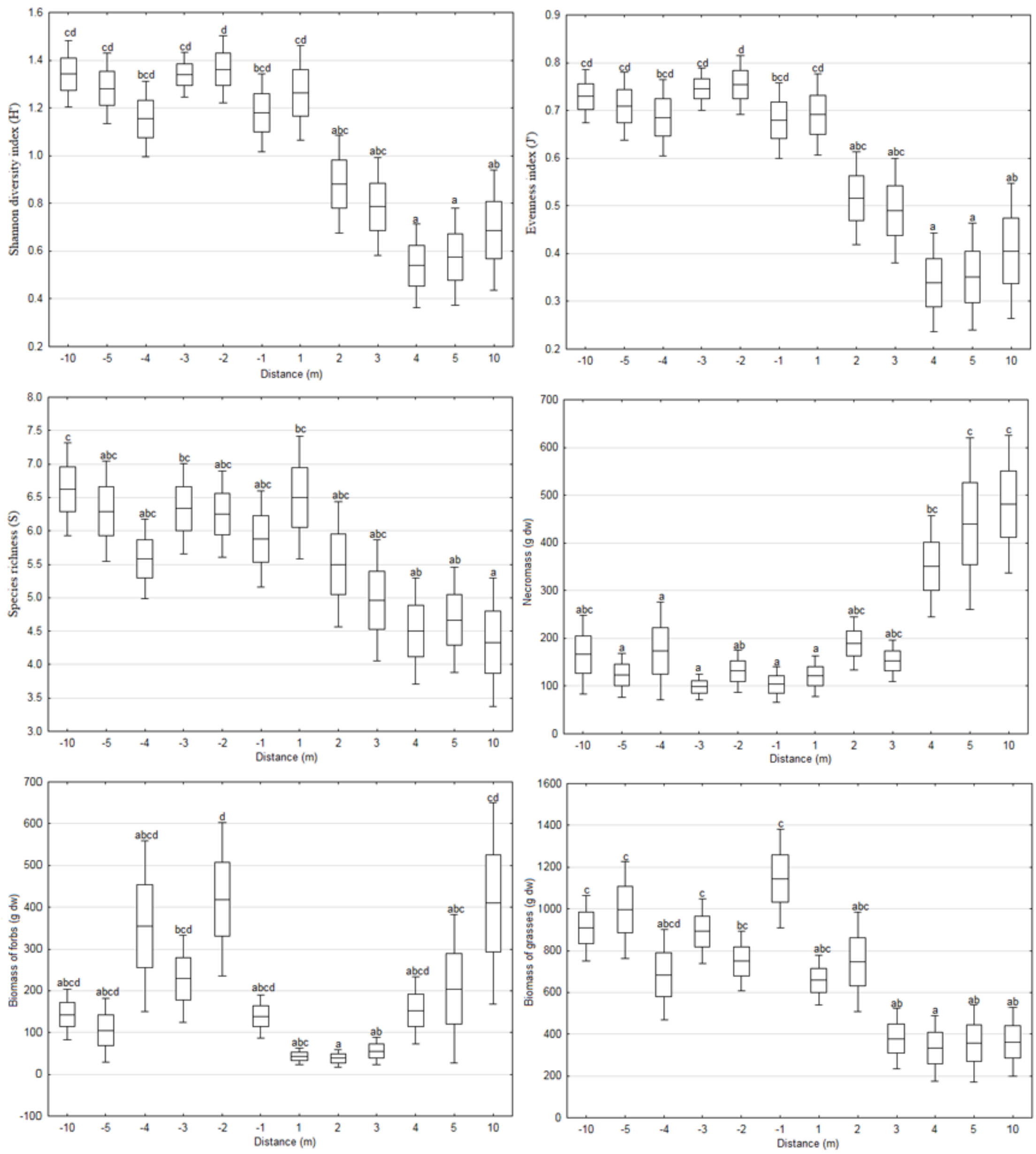

Fig. 2 Mean values of diversity index (H') and Shannon–Wiener evenness index (J'), number of species (S), plant necromass as well as aboveground biomass of accompanying forb and grass species on degraded (1–10 m) and non-degraded (between −1 and −10 m) parts of meadows. Means with standard error values (boxes) and confidence intervals (whiskers) for plots are given. Different letters indicate significant differences obtained after the Kruskal–Wallis test ($p \leq 0.05$).

The parts of transects running through degraded meadow patches did not significantly differ in organic matter content (mean 6.16%, range 3.43–10.21%, $H = 7.59$; $p = 0.1803$), soil pH (mean 5.06, range 4.74–5.79, $H = 9.34$; $p = 0.0962$), total nitrogen concentration (mean 0.30%, range 0.06–0.50%, $H = 9.08$; $p = 0.1061$), phosphorus (mean 29.65 mg kg^{-1}, range 15.18–40.48 mg kg^{-1}, $H = 4.59$; $p = 0.4680$), calcium (mean 803.04 mg kg^{-1}, range 482–1219.60 mg kg^{-1}, $H = 10.96$; $p = 0.0522$), or magnesium (mean 116.03 mg kg^{-1}, range 37.08–200.16 mg kg^{-1}, $H = 10.79$; $p = 0.0557$). Only the concentration of total exchangeable potassium showed significant differences (mean 96.81 mg kg^{-1}, range 61.16–218.16 mg kg^{-1}, $H = 11.43$; $p = 0.0434$). The highest concentrations were recorded 4 m deep within the degraded patches, whereas the lowest ones were found 10 m deep.

Significant negative correlations were found between *C. epigejos* coverage (and the magnitude of its aboveground biomass) and species number, Shannon–Wiener species diversity and evenness indices and biomass of accompanying grasses and herbs

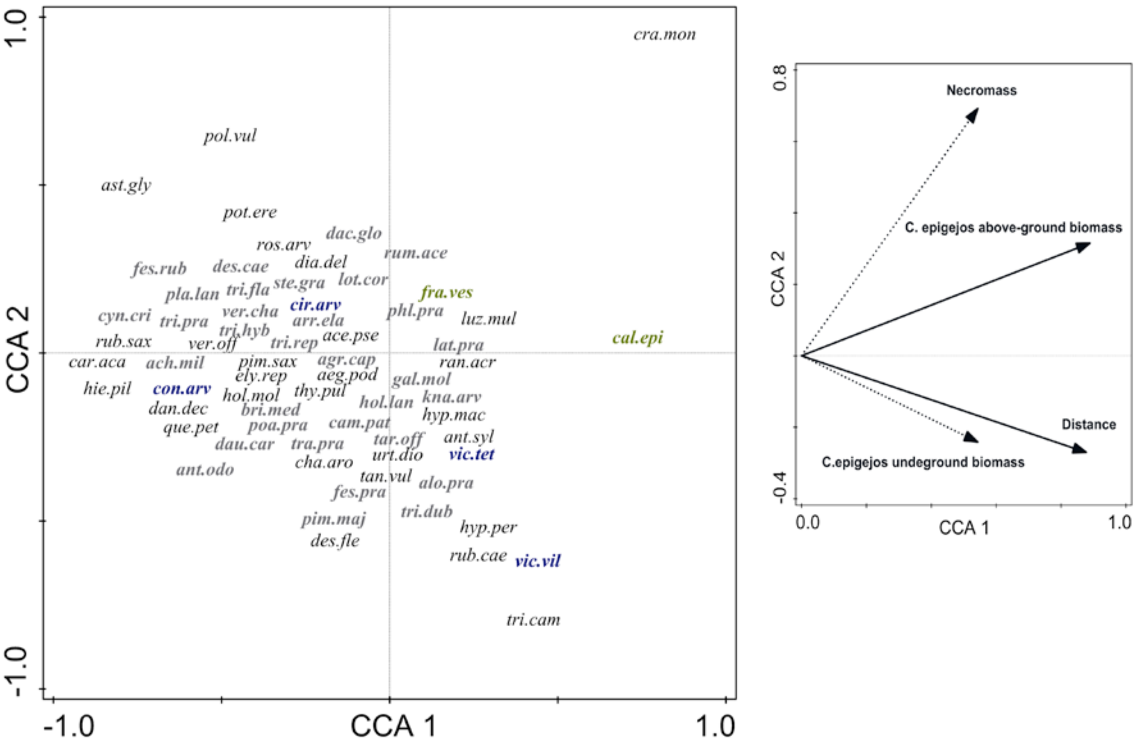

Fig. 3 Results of the canonical correspondence analysis (CCA) for the species. Vectors indicated by solid lines reflect the variables selected as significant ($p \leq 0.05$) by the Monte Carlo test. Gray text indicates species representing *Molinio-Arrhenatheretea* class species, blue those from *Epilobietea angustifolii* class species, and green species of *Stellarietea mediae* class according to Matuszkiewicz [34] and Hájková et al. [35]. Abbreviations of species names: ace.pse – *Acer pseudoplatanus*, ach.mil – *Achillea millefolium*, aeg.pod – *Aegopodium podagraria*, agr.cap – *Agrostis capillaris*, alo.pra – *Alopecurus pratensis*, ant.odo – *Anthoxanthum odoratum*, ant.syl – *Anthriscus sylvestris*, arr.ela – *Arrhenatherum elatius*, ast.gly – *Astragalus glycyphyllos*, bri.med – *Briza media*, cal.epi – *Calamagrostis epigejos*, cam.pat – *Campanula patula*, car.aca – *Carlina acaulis*, cha.aro – *Chaerophyllum aromaticum*, cir.arv – *Cirsium arvense*, con.arv – *Convolvulus arvensis*, cra.mon – *Crataegus monogyna*, cyn.cri – *Cynosurus cristatus*, dac.glo – *Dactylis glomerata*, dan.dec – *Danthonia decumbens*, dau.car – *Daucus carota*, des.cae – *Deschampsia caespitosa*, des.fle – *Deschampsia flexuosa*, dia.del – *Dianthus deltoides*, ely.rep – *Elymus repens*, fes.pra – Festuca pratensis, fes.rub – *Festuca rubra*, fra.ves – *Fragaria vesca*, gal.mol – *Galium mollugo*, hie.pil – *Hieracium pilosella*, hol.lan – *Holcus lanatus*, hol.mol – *Holcus mollis*, hyp.mac – *Hypericum maculatum*, hyp.per – *Hypericum perforatum*, kna.arv – *Knautia arvensis*, lat.pra – *Lathyrus pratensis*, lot.cor – *Lotus corniculatus*, luz.mul – *Luzula multiflora*, phl.pra – *Phleum pratense*, pim.maj – *Pimpinella major*, pim.sax – *Pimpinella saxifrage*, pla.lan – *Plantago lanceolata*, poa.pra – *Poa pratensis*, pol.vul – *Polygala vulgaris*, pot.ere – *Potentilla erecta*, que.pet – *Quercus petraea*, ran.acr – *Ranunculus acris*, ros.arv – *Rosa arvensis*, rub.cae – *Rubus caesius*, rub.sax – *Rubus saxatillis*, rum.ace – *Rumex acetosa*, ste.gra – *Stellaria graminea*, tan.vul – *Tanacetum vulgare*, tar.off – *Taraxacum officinale*, thy.pul – *Thymus pulegioides*, tra.pra – *Tragopogon pratensis*, tri.cam – *Trifolium campestre*, tri.dub – *Trifolium dubium*, tri.hyb – *Trifolium hybridum*, tri.pra – *Trifolium pratense*, tri.rep – *Trifolium repens*, tri.fla – *Trisetum flavescens*, urt.dio – *Urtica dioica*, ver.cha – *Veronica chamaedrys*, ver.off – *Veronica officinalis*, vic.tet – *Vicia tetrasperma*, vic.vil – *Vicia villosa*.

(Tab. 1). Together with the growth in aboveground biomass of *C. epigejos*, the study revealed an increased concentration of exchangeable phosphorus in the soil and a slight increase in exchangeable potassium (Tab. 1). The research also showed that the growth in *C. epigejos* percentage was positively correlated with the presence of plant necromass, which was at the same time negatively correlated with the number of species ($r_s = -0.482$; $p < 0.001$), Shannon–Wiener diversity ($r_s = -0.544$; $p < 0.001$), and evenness indices ($r_s = -0.521$; $p < 0.001$), as well as with the biomass of accompanying grasses ($r_s = -0.320$; $p < 0.001$). The increase in plant necromass was also associated with the increase of exchangeable potassium ($r_s = 0.268$; $p = 0.002$) and phosphorus ($r_s = 0.238$; $p < 0.007$) concentrations in the soil.

Tab. 1 Spearman's rank correlation coefficient between coverage, the size of aboveground and underground *C. epigejos* biomass and the number of species (S), diversity index (*H'*), Shannon–Wiener evenness index (*J'*), accompanying forbs and grasses biomass, plant necromass, and habitat properties. Analyses were only conducted for degraded areas.

	Cover of *C. epigejos*	*C. epigejos* aboveground biomass	*C. epigejos* undeground biomass
Number of species (S)	−0.608***	−0.510***	−0.113
Diversity index (*H'*)	−0.839***	−0.580***	−0.219**
Evenness index (*J'*)	−0.827***	−0.549***	−0.221**
Biomass of forbs	−0.198*	−0.317***	−0.102
Biomass of grasses	−0.218*	−0.517***	0.009
Plant necromass	0.530***	0.604***	0.092
Organic matter	−0.328***	0.022	−0.380***
pH	0.160	0.123	0.173*
N	−0.033	−0.085	−0.153
P	0.199*	0.526***	0.233**
K	0.102	0.235**	−0.089
Ca	0.044	0.016	0.071
Mg	−0.021	0.116	0.087

Asterisks denote correlation coefficients significant at $p \leq 0.05$ (*), $p \leq 0.01$ (**), and $p \leq 0.001$ (***).

Discussion

Our survey confirms that expanding *Calamagrostis epigejos* is capable of strong degradation of *Arrhenatheretalia* type grassland vegetation. The degradation of the mesic meadows involves a decline of species diversity as well as decreasing percentage representation of species characteristic for mesic meadows. The expansion mechanism of *C. epigejos* and the nature of its influence on the species composition are still poorly explained. According to Pyšek et al. [36], intensity of the influence on biodiversity as well as productivity depend on the growth stage and height of the competitive species. Species taller than 120 cm exert a significant influence on shorter plants. *Calamagrostis epigejos*, which grows up to 200 cm tall [13], is one such species. Its main property conducive to its expansion in hay meadows [9,15,19,37] and pastures [38] is a high rate of growth [13]. According to Holub et al. [39], the success of *Calamagrostis epigejos* expansion is based on the ability to shadow slower growing species, the capacity to mineralize nitrogen on the covered patches, and the creation of a thick layer of slowly degrading litter. Dolečková and Osbornová [40] claimed that the expansion mechanism of *C. epigejos* relies mostly on forming a vast system of rhizomes, aggressive spread, and very high production of aboveground biomass, which, by forming a thick layer of non-degraded litter, prevents other species from emerging. However, in our study, we did not observe significant diversity in the amount of *C. epigejos* underground biomass along the marked transects, nor its strong influence on species diversity parameters. In the case of aboveground biomass, the highest values were recorded up to 10 m deep in the degraded areas. The mean value of *C. epigejos* aboveground biomass production at that distance was 1848.9 g m^{-2}, exceeding the values given for dry grassland sward eight-fold [41] and exceeding the values given for *Cnidion* and *Molinion* meadows two-fold [15]. Our research indicated that the ratio between the underground and aboveground biomass of *C. epigejos* was typical for meadows rich in nutrients [13]. An analysis of functional group proportions of accompanying species showed a decrease in grass and dicot herb biomass correlated with the increase in *C. epigejos* growth. An abundant growth of *C. epigejos* aboveground biomass is also related to a decrease in species diversity of the studied grassland communities. Additionally, it is important to note the drop in *Molinio-Arrhenatheretea* class species number in favor of species belonging to the classes *Epilobietea angustifolii* and *Stellarietea mediae*, which suggests progressing synanthropization of the studied meadows. According to Rebele [21], on degraded meadows *C. epigejos* competes more strongly for light than for resources in the soil, which leads to the decline of meadow species. Likewise, Sedláková and Fiala [22] and Somodi et al. [16] assert that degradation of grassland communities is caused mainly by shadowing due to the growth of *C. epigejos*. We also observed a negative influence on the species diversity caused by the litter, which is dominated by the *C. epigejos* remains. This observation corresponds with the findings of Holub et al. [39] and Somodi et al. [16]. A thick layer of non-decomposed plant necromass makes seedling recruitment impossible [42], quickly leading to a decrease in the species diversity of grassland communities. This issue, however, requires further study.

According to Fiala et al. [37], effective use of water and nutrients enables *C. epigejos* to successfully compete with other species but also leads to the deterioration of soil properties in the degraded patches. However, our research did not confirm that observation. Despite results showing a positive correlation between aboveground biomass and the amount of cumulating plant necromass which is dominated by this species with the exchangeable phosphorus and potassium concentrations in the soil, significant differences between plots along the transects occur only in the case of potassium. On the other hand, our results are in line with the observations of Süß et al. [26] regarding non-degraded dry grasslands. They recorded weak positive correlations between *C. epigejos* coverage and soil richness in potassium and phosphorus. *Calamagrostis epigejos* is a species with low requirements for both phosphorus and – like other grasses – potassium [43]. Nevertheless, according to Rebele [44] and Lammerts et al. [45], the availability of phosphorus and potassium facilitates the growth of *C. epigejos*. Süß et al. [26] observed that in some cases scarcity of nutrients might prevent vast coverage by *C. epigejos*. The species' growth and expansion are physiologically aided by ecological succession, the corresponding increased nitrogen content in the soil, and the eutrophication of habitats as a result of increased phosphorus and potassium concentrations. Our research supports this observation.

Conclusions

Our study confirms strong degradation of mesic meadows as a result of *C. epigejos* expansion. The degradation manifests as a decrease in species diversity, a decline of species typical for mesic meadows, and an increased percentage of synanthropic species. Significant correlations between *C. epigejos* aboveground biomass and the decrease of accompanying species number and their biomass were observed, while there was not found such a relation for the underground biomass. Despite a strong impact of *C. epigejos* expansion on vegetation, no significant direct influence on the physico-chemical properties of the soil was found. However, the study revealed an indirect influence of *C. epigejos* on vegetation and the elemental composition of soil. The cumulating plant necromass dominated by this species caused a decrease in diversity indices and, at the same time, an increase in exchangeable forms of potassium and phosphorus in the soil.

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