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Long-term changes in species diversity in abandoned calcareous grasslands in Latvia

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Abstract

The aim of this study is to assess the development of plant species diversity and species composition over a seven-year period in two calcareous grasslands abandoned for nearly 20 years and to find out which factors influence vegetation dynamics. In the Abava River valley, Latvia, different calcareous grasslands were studied, one on the south-west facing slope and another on the north-east facing slope. Vegetation analyses on permanent plots showed that dry calcareous grasslands can be resistant to deterioration for a long period of time – succession was slower than reported in many cases for Central and Western Europe. None of the studied communities showed a decrease neither in total species number recorded per community nor in average species richness per plot. Vascular plant species richness even increased by 3–4 species per 1-m² plot in the grassland on the south-west facing slope. An unexpected result of the research was that *Calamagrostis epigeios* did not expand in this grassland. This fact can be explained by the influence of disturbances (drought, tree cutting) and local differences in soil parameters and topography. In parts of the north-east exposed grassland, with deeper soils and better water availability, species diversity (Shannon index) decreased significantly in areas overgrown by *Aegopodium podagraria.*

Zusammenfassung: Langfristige Veränderungen der Artendiversität in brachgefallenen Kalktrockenrasen in Lettland

In der vorliegenden Untersuchung wird die Entwicklung der Artenvielfalt und Artenzusammensetzung in zwei seit 20 Jahren brachliegenden Kalkmagerrasen über einen Zeitraum von sieben Jahren analysiert. Die Untersuchungsflächen liegen im Tal des Flusses Abava, Lettland, an einem südwestlich und einem nordöstlich exponierten Hang. Die Ergebnisse von Dauerflächenuntersuchungen zeigen, dass die typische Artenzusammensetzung und Artenvielfalt von Kalkmagerrasen unter bestimmten Bedingungen auch bei langjähriger Brache überdauern kann. Dies steht im Gegensatz zu Ergebnissen anderer Untersuchungen aus Mittel- und Westeuropa. In den Dauerflächen der südwestlich exponierten Hänge wurde sogar ein Anstieg von drei bis vier Arten pro 1 m²-Dauerfläche registriert. Entgegen den Erwartungen wurde an den südwestlich exponierten Hängen keine Ausbreitung von *Calamagrostis epigeios* beobachtet. Dies lässt sich mit Störungen (Trockenperioden, Entbuschung) und lokalen edaphischen und topographischen Unterschieden erklären. Die Diversität (Shannon-Index) nahm nur in einigen Bereichen der nordöstlich ausgerichteten Hängen signifikant ab, an denen sich *Aegopodium podagraria* auf tiefgründigeren Böden mit besserer Wasserverfügbarkeit ausbreitete.

Keywords: *Calamagrostis epigeios,* monitoring, overgrowing, secondary succession, topography, vegetation dynamics, permanent plot.

1. Introduction

Calcareous grasslands are among the most diverse vegetation types in Europe (DENGLER 2005). They have developed in ancient cultural landscapes during centuries of traditional land use by grazing or mowing (POSCHLOD & WALLISDEVRIES 2002). Numerous studies indicate that species richness decreases continuously in abandoned grasslands (e.g. WILLEMS 2001, LUOTO et al. 2003). However, the rate at which plant species richness decreases is very variable. For example, studies of calcareous grasslands in Western Europe have shown that 40 to 70% of the plant species disappeared during 10 years of abandonment (WILLEMS 1990, 2001), but there was no significant decrease in species richness after 5–10 years of abandonment of grasslands in Sweden (ÖCKINGER et al. 2006) and in Romania (BAUR et al. 2006). Such great differences are due to a huge number of factors influencing the course of succession. Important factors are management history, edaphic and topographic variables, as well as disturbances, fragmentation etc. (e. g. ELLENBERG 1996, LÖBEL et al. 2006, ENYEDI et al. 2008, RUPRECHT et al. 2009, SCHRAUTZER et al. 2009).

Calcareous grasslands are diminishing continuously in Latvia, mainly because of land use abandonment. However, there are no data available concerning the rate at which plant species diversity decreases. Furthermore, experiences from Central and Western Europe are not applicable to the Latvian situation in most cases because grassland fragmentation, the impact of intensive agriculture, and the amount of atmospheric N deposits are less pronounced in Latvia (RŪSIŅA 2007).

The aim of this study was to analyse the development of vegetation, species composition and plant species diversity (species richness, Shannon index and evenness) over a period of seven years in two (dry and mesic) calcareous grasslands abandoned for nearly 20 years and to find out which factors influence the observed dynamics.

2. Material and methods

2.1. Study site

Latvia is located at the eastern coast of the Baltic Sea. Forests cover about 45% of the country, mires 6%, and arable fields 38%, while semi-natural grasslands occupy only about 0.4% of the territory (KABUCIS et al. 2003).

The investigations were carried out in two calcareous grasslands (referred to in the text as Drubazas and Priednieki, respectively) located in Western Latvia in the Abava River valley (57° 02 25 N latitude and 22° 35 09 E longitude), the most spectacular calcareous grassland territory in Latvia (nature park "The Abava River Valley"). At the European level, the calcareous grasslands in this region are protected as Natura 2000 habitats (Natura 2000 code: 6210).The climate in this region is relatively mild and moist. The mean annual temperature is 6.2 °C. The coldest month is February with –4.6 °C, the warmest August with +17.1 °C. The mean annual precipitation is 650 mm. The vegetation period lasts about 180–200 days (VEINBERGS 1994).

The two sites differed in aspect: Drubazas was located on the south-west facing slope, Priednieki on the north-east facing slope (Figs. 1–3). The slope inclination in both sites ranged from 15° to 20°. Vegetation history was the same for both sites: the grasslands had been mown and grazed for decades until they were abandoned about 20 years ago. Occasional management (cutting of pines and mowing in winter in Drubazas; sheep grazing in Priednieki) took place in the late 1990s.

2.2. Sampling design

Both sites included grassland patches with typical structure and species composition as well as patches overgrown by expansive grasses and tall herbs (Fig. 1). These patches were treated as separate communities. Communities were defined as physionomically uniform zones, where the dominant species were the same and overall species composition was similar. Detailed syntaxonomical analyses of the grassland vegetation of the study area have never been done. That is why no syntaxonomical units were used in the current study. Instead, plant communities were named according to dominant species, and all analyses were done separately for each community. Results of the detrended correspondence analysis (DCA) and species cover changes over time (see below) indicated that there were changes in species composition and cover, but no community turned into another community in the analysed period of time.

However, several vegetation relevés from the study sites have been included in the regional study of dry and mesic grassland vegetation syntaxonomy of Latvia (RŪSIŅA 2003, RŪSIŅA 2007). According to these publications, the *Filipendula vulgaris-Helictotrichon pratense* community of the Drubazas site (Fig. 4) and the *Carex flacca-Helictotrichon pratense* community as well as the transition community from the *Carex flacca-Helictotrichon pratense* to the *Aegopodium podagraria* community of the Priednieki site (Figs. 6 and 7) belonged to the provisionally delimited association *Filipendulo-Helictotrichetum* ass. prov. *typicum* subass. prov. (Drubazas) or *caricetosum flaccae* subass. prov. (Priednieki), respectively. The *Calamagrostis epigeios* community of the Drubazas site (Fig. 5) could still be assigned to the same association although the spread and dominance of *Calamagrostis epigeios* had impoverished the species

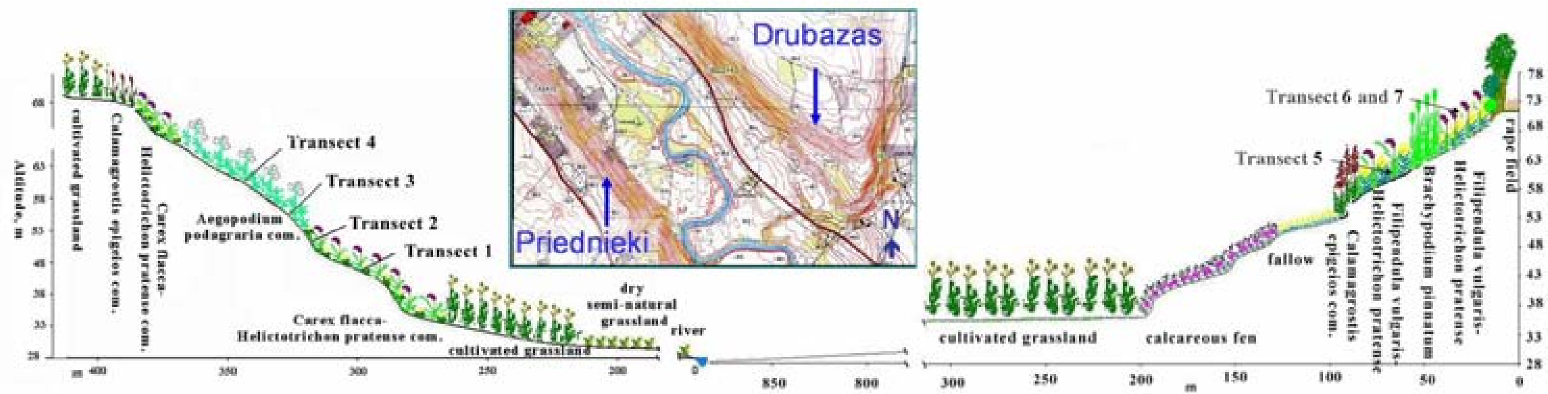

Fig. 1: Location of the monitoring transects in the vegetation profile.

Abb. 1: Lage der Untersuchungstransekte entlang von Vegetationsprofilen

Fig. 2: Calcareous grasslands of Priednieki in 2007. The transects are located in the grassland on the slope between the two lines of shrubs (behind the fenced area with cultivated grassland).

Abb. 2: Kalkmagerrasen von Priednieki im Jahr 2007. Die Transekte befinden sich im Grasland am Hang zwischen den Buschreihen (hinter dem eingezäunten Grünland).

Fig. 3: Calcareous grasslands of Drubazas in 2006. Transects are located in open patches of grassland on the upper part of the slope.

Abb. 3: Kalkmagerrasen von Drubazas im Jahr 2006. Die Transekte befinden sich auf offenen Graslandflächen im oberen Bereich des Hanges.

composition. This association belongs to the North European alliance *Filipendulo vulgaris-Helictotrichion pratensis* Dengler & Löbel in Dengler & al. 2003 of the class *Festuco-Brometea* Br.-Bl. & Tx. ex Klika & Hadač 1944. The association is not validly described, and according to preliminary results of the Working Group on Dry Grasslands in the Nordic and Baltic Region, it can be merged into the association *Fragario viridis-Helictotrichetum pratensis* Hallberg 1971 described from Scandinavia (DENGLER et al. 2009).

The *Aegopodium podagraria* community of the Priednieki site was clearly a derivate community of the class *Galio-Urticetea* as no species of the class *Festuco-Brometea* and the alliance *Filipendulo-Helictotrichion* remained.

Permanent plots (1 m²) were established both in patches with the typical structure of low-productive calcareous grasslands and in patches overgrown by tall herbs and expansive grasses. Percentage cover of all vascular plant species was recorded each year in July and August from 2001 to 2007 on these plots, established along transects parallel to the river located on the terrace slopes (Fig. 1). The distance between the plots on a transect was 2 m. Fifteen plots were monitored in Drubazas: ten replicate plots along transects 6 and 7 in the most diverse part of the grassland in the *Filipendula vulgaris-Helictotrichon pratense* (FvHp) community and five plots on transect 5 in a part overgrown by *Calamagrostis epigeios* (Calepi). In total, 20 plots were monitored in Priednieki: Ten replicate plots were established in the *Carex flacca-Helictotrichon pratense* community (CfHp), which was the most diverse part of the grassland (transects 1 and 2 in Fig. 1), six plots on transect 4 in a part overgrown by *Aegopodium podagraria (*Aegpod), and four replicate plots on transect 3 in a transition from CfHp to Aegpod (Tc).

2.3. Soil samples

Soil profiles were investigated in each plant community in order to classify the soil type according to the Latvian soil classification (KĀRKLIŅŠ et al. 2009). Four soil samples were taken in 2006 for soil chemical analyses. One sample from the upper soil layer was taken in each community. Each sample was obtained by sampling soil at five random points in a 1 m × 2 m plot situated between vegetation sampling plots to a depth of 10 cm by a soil auger with 5 cm diameter. Soil pH was determined in 1 *M* KCl solution, the sum of exchangeable basic cations by extraction with 0.1 *M* HCl (method of Kappen-Gilkovich), the plant-available P and K by the Egner-Riem (DL) method, the exchangeable Mg and Ca by flame photometry (extractant 0.1 *M* KCl), soil organic carbon by the method of Tyurin (oxidation by $K_2Cr_2O_7 + H_2SO_4$), and total nitrogen by the Kjeldahl method (SKUJĀNS & MEŽALS, 1964, JĒKABSONE et al. 1997). The grain size distribution of the soil was analysed by the sedimentation and pipette method after KATCHINSKY (1958).

2.4. Data analysis

Vegetation data were stored in a database using the software program TURBOVEG (HENNEKENS & SCHAMINÉE 2001). In total, 245 relevés were collected during seven years. Tree and shrub species were not included in the analysis as there were only seedlings, which could often not be identified to the species level. Bryophytes and lichens were also excluded from the analysis as they were not recorded each year. To analyse species diversity, species richness, Shannon's diversity index (*H*') and Pielou's evenness index (*H*'/ln *S*, with *S* = species richness) were calculated (KENT & COKER 1994). Vegetation dynamic patterns were analysed by detrended correspondence analysis (DCA, HILL & GAUSCH 1980) using the program PC-ORD 5 (MCCUNE & MEFFORD 1999). The DCA was calculated with presence-absence data because in a previous DCA with square-root transformed covers, results for axes 2 and 3 had been unstable with low orthogonality values for axis 1 vs. axis 3. An after-the-fact evaluation of the quality of the analysis was done by calculating the coefficient of determination between the Euclidean distance in the ordination space and the relative Euclidean distance in the original multidimensional space (MCCUNE & MEFFORD 1999).

Ellenberg indicator values for light, moisture, reaction and nitrogen (ELLENBERG et al. 1992), vegetation structure, and species diversity data were used to analyse vegetation changes. Ellenberg indicator values were calculated as weighted means using the program JUICE (TICHY 2002). Rank correlations between these values and the DCA ordination axes were calculated by PC-ORD 5 using the Kendall rank correlation coefficient. Data of soil properties were not used to interpret ordination as soil samples were not collected for each plot, but as one mixed sample per plant community.

Significance of differences between the first and the last year of observation with respect to species richness, Shannon index, evenness and species cover was evaluated by the non-parametric Wilcoxon test using the software package SPSS for Windows, version 17.0 (SPSS 2008). Nomenclature for vascular plants follows GAVRILOVA & ŠULCS (1999).

Fig. 4: *Filipendula vulgaris-Helictotrichon pratense* community in July 2007, Drubazas.
Abb. 4: *Filipendula vulgaris-Helictotrichon pratense*-Gesellschaft im Juli 2007, Drubazas.

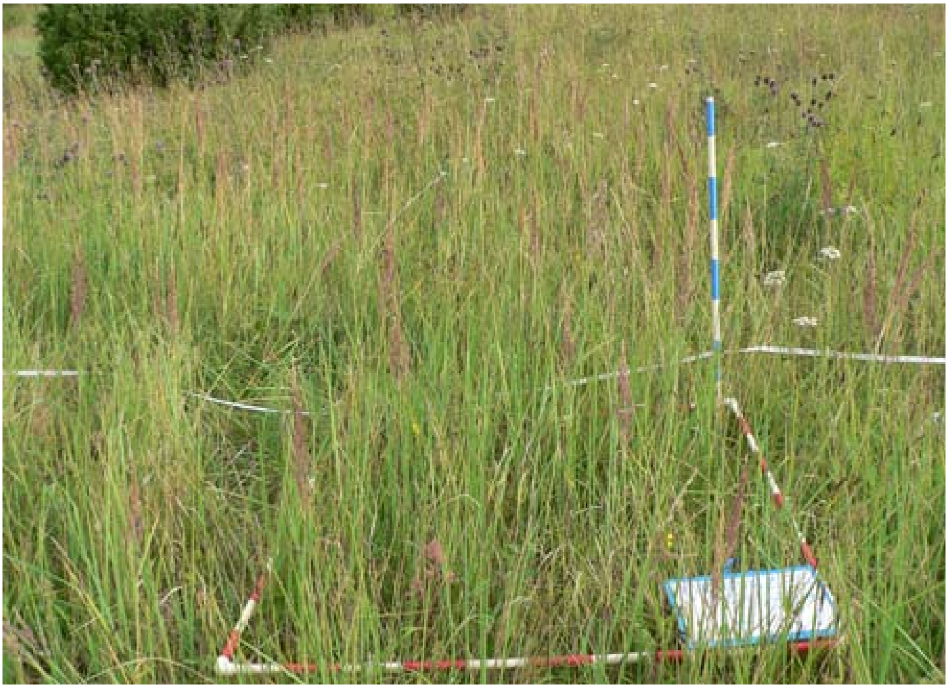

Fig. 5: *Calamagrostis epigeios* community in July 2006, Drubazas.
Abb. 5: *Calamagrostis epigeios*-Gesellschaft im Juli 2006, Drubazas.

Fig. 6: *Carex flacca-Helictotrichon pratense* community in July 2005, Priednieki.

Abb. 6: *Carex flacca-Helictotrichon pratense*-Gesellschaft im Juli 2005, Priednieki.

Fig. 7: Transition community from the *Carex flacca-Helictotrichon pratense* to the *Aegopodium podagraria* community (background) in 2005, Priednieki.

Abb. 7: Übergangsgesellschaft von der *Carex flacca-Helictotrichon pratense*- zur *Aegopodium podagraria*-Gesellschaft (Hintergrund) im Jahr 2005, Priednieki.

3. Results

3.1. Soil properties

The soil under the *Filipendula vulgaris-Helictotrichon pratense* community in Drubazas was classified as rendzina according to the taxonomy of Latvian soils (KĀRKLIŅŠ et al. 2009). It was rather shallow with a partly weathered dolomite layer in 40–65 cm depth (Table 1). The soil of the *Calamagrostis epigeios* community at Drubazas was classified as typical sod calcareous soil (automorphic soil class). It was deep, and only few small dolomite rock fragments were present (less than 3–5% of soil volume) in upper horizons (from 0 to 50 cm).

In Priednieki, both plant communities (the *Carex flacca-Helictotrichon pratense* community and the *Aegopodium podagraria* community) were developed on deep sod-gley soil with distinct gleyic properties (gley soil type, semihydromorphic soil class). Gleyic properties were more pronounced in the *Carex-Helictotrichon* community (gley horizon, Br, was present in 48–85 cm depth) than in the *Aegopodium* community (no gley horizon, but only Bg horizon with gleyic properties). Partly weathered fragments of dolomite (3–5% of soil volume) were observed throughout all soil profiles in both plant communities.

Physical properties of the upper soil layer were quite similar for all communities except for the *Carex-Helictotrichon* community, where the proportion of sand was higher (Table 1). For the majority of the measured soil chemical parameters, the values were quite similar among the plant communities. In total, soils of Priednieki were richer in elements responsible for soil fertility (N, C, P, and K) than soils at Drubazas. The highest values were

Table 1: Physical and chemical properties of the upper soil layer, and soil horizons (according to the FAO soil classification; Kārkliņš et al. 2009). FvHp – *Filipendula vulgaris-Helictotrichon pratense* community; Calepi – *Calamagrostis epigeios* community; CfHp – *Carex flacca-Helictotrichon pratense* community; Aegpod – *Aegopodium podagraria* community.

Tabelle 1: Physikalische und chemische Eigenschaften des Oberbodens und Darstellung der Bodenhorizonte (gemäß der FAO-Bodenklassifikation; Kārkliņš et al. 2009). FvHp – *Filipendula vulgaris-Helictotrichon pratense*-Gesellschaft; Calepi – *Calamagrostis epigeios*-Gesellschaft; CfHp – *Carex flacca-Helictotrichon pratense*–Gesellschaft; Aegpod – *Aegopodium podagraria*-Gesellschaft.

	Drubazas		Priednieki	
	FvHp	Calepi	CfHp	Aegpod
Physical and chemical parameters of the upper soil layer (0–10 cm)				
Clay [%]	6.0	10.3	10.8	12.8
Silt [%]	74.5	76.6	42.1	62.7
Sand [%]	19.5	13.0	47.1	24.5
pH_{KCl} (0–10 cm)	6.9	7.1	7.1	7.1
pH_{KCl} (50 cm)	7.5	6.9	7.6	7.5
Exch.bases [meq/100 g]	43.3	49.7	49.6	52.8
Organic C [%]	4.1	4.5	5.0	5.0
N [g/kg]	2.1	2.2	2.5	3.2
P_2O_5 [mg/100 g]	1.9	2.5	2.6	3.8
K_2O [mg/100 g]	5.6	8.4	31.1	37.0
CaO [mg/100 g]	145.5	128.7	346.9	213.3
MgO [mg/100 g]	107.5	71.9	49.0	142.2
Description of exemplary soil profiles (horizon, depth, texture)				
	ApB 9–26 silty clay	Ap 13–49 sandy loam	Ap 0–23 loam	Ap 0–56 loam
	Bg 26–40 clay	ApB 49–80 fine sand	Bg 23–48 loam	Bg 56–81 loam
	Bk 40–65 clay, dolomite	BC >80 fine sand	Br 48–65 silt loam	BC 81–97 loam
	Bt >65 very fine sand		Cg 65–70 very fine sand	
			Br 70–85 loam	

observed in the *Aegopodium* community, indicating that the soil of this plant community was the most fertile among all. The amount of K_2O was also considerably higher in the *Carex-Helictotrichon* community in Priednieki than in any of the two plant communities in Drubazas (Table 1).

3.2. Species diversity

During the research period, vascular plant species richness increased significantly in two communities. In the *Calamagrostis epigeios* community in Drubazas (SW slope) it increased by 4 species per 1 m², and in the *Carex-Helictotrichon* community in Priednieki (NE slope) it increased by 3 species per 1 m² (Table 2).

Shannon's diversity index and Pielou's evenness index increased significantly in both communities of Drubazas, while they decreased in Priednieki; however, only for the *Aegopodium* community the decrease was significant (Fig. 8, Table 2).

3.3. Vegetation dynamics

The grassland vegetation was more dynamic at Priednieki than at Drubazas. In Drubazas, only 8% of all species experienced significant changes in cover and constancy (7 species out of 86), compared to 19% in Priednieki (24 species out of 127).

In Drubazas, the overall species composition was stable in the *Calamagrostis epigeios* community, but the mean cover of *Calamagrostis epigeios* decreased significantly from 37% in 2001 to 17% in 2007, and two species newly appeared in this plant community (*Aegopodium podagraria* and *Campanula rapunculoides*, see Table 3). The mean total cover of the herb layer decreased steadily from 92% in 2001 to 57% in 2007, while the litter cover increased.

In the *Filipendula vulgaris-Helictotrichon pratense* community of Drubazas, similar changes occurred. Among the four species with significant changes (Table 3), only the cover of *Helictotrichon pratense* decreased considerably (from 36% in 2001 to 8% in 2007). The total cover of the herb layer decreased from 72% in 2001 to 57% in 2007, and the litter cover increased.

Table 2: Differences in species richness, evenness and Shannon diversity index between 2001 and 2007, tested by Wilcoxon test. Significant p-values are in bold ($\alpha = 0.05$).

Tabelle 2: Unterschiede der Artenzahl, der Evenness und des Shannon-Index zwischen 2001 und 2007. Signifikante p-Werte (Wilcoxon-Text; $\alpha = 0.05$) sind fett markiert.

Location	Plant community	Mean 2001	Mean 2007	*p*
Species richness (1 m²)				
Drubazas	FvHp (*n* = 10)	24.3	27.5	0.151
	Calepi (*n* = 5)	17.0	21.4	**0.041**
Priednieki	CfHp (*n* = 10)	32.1	35.4	**0.021**
	Tc (*n* = 4)	30.3	32.8	0.357
	Aegpod (*n* = 6)	13.0	13.7	0.336
Evenness				
Drubazas	FvHp (*n* = 10)	0.62	0.74	**0.007**
	Calepi (*n* = 5)	0.55	0.77	**0.043**
Priednieki	CfHp (*n* = 10)	0.79	0.74	0.139
	Tc (*n* = 4)	0.77	0.69	0.273
	Aegpod (*n* = 6)	0.64	0.43	**0.028**
Shannon index				
Drubazas	FvHp (*n* = 10)	1.96	2.45	**0.009**
	Calepi (*n* = 5)	1.58	2.35	**0.009**
Priednieki	CfHp (*n* = 10)	2.75	2.65	0.445
	Tc (*n* = 4)	2.63	2.41	0.273
	Aegpod (*n* = 6)	1.62	1.13	**0.028**

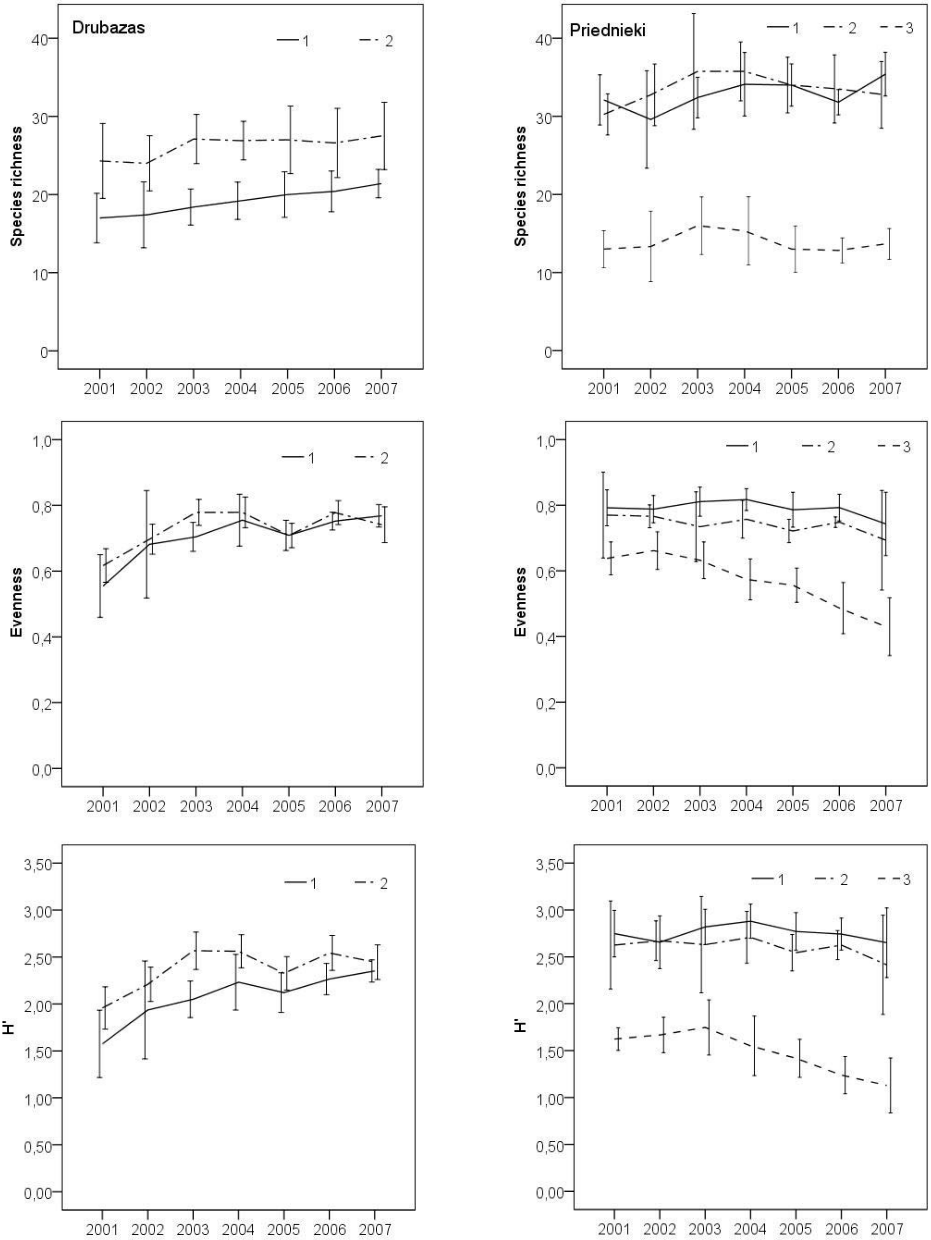

Fig. 8: Changes in species richness, evenness and Shannon diversity index (*H'*) in the course of time. Drubazas: 1 – *Calamagrostis epigeios* community, 2 – *Filipendula vulgaris-Helictotrichon pratense* community; Priednieki: 1 – *Carex flacca-Helictotrichon pratense* community, 2 – Transition community, 3 – *Aegopodium podagraria* community. For significance of changes between the first and the last year, see Table 2.

Abb. 8: Veränderung der Artenzahl, der Evenness und des Shannon-Diversitätsindex während der Untersuchungsperiode. Drubazas: 1 – *Calamagrostis epigeios*-Gesellschaft, 2 – *Filipendula vulgaris-Helictotrichon pratense*-Gesellschaft; Priednieki: 1 – *Carex flacca-Helictotrichon pratense*-Gesellschaft, 2 – Übergangsgesellschaft, 3 – *Aegopodium podagraria*-Gesellschaft. Signifikante Unterschiede zwischen den Werten des ersten und letzten Untersuchungsjahrs sind in Tabelle 2 dargestellt.

In Priednieki, the most dynamic vegetation type was the *Carex flacca-Helictotrichon pratense* community, where 21 species changed significantly in cover (Table 3). In total, 11 species increased, but only *Aegopodium podagraria* increased strongly (10% to 38%). A decrease was observed for 10 species, with *Briza media* (12% to 3%), *Festuca rubra* (8% to 3%), and *Medicago lupulina* (8 to 0.5%) showing a particularly strong decrease.

A change in dominant species was detected in the *Aegopodium podagraria* community during the observation period. *Aegopodium podagraria* and *Dactylis glomerata* decreased from 29% to 17% and from 31% to 3%, respectively, but *Chaerophyllum aromaticum* increased from 29% to 90%.

In the transition community, changes in species cover indicated a gradual turn into the *Aegopodium* community. *Chaerophyllum aromaticum* and *Aegopodium podagraria* doubled their cover (25% to 52%, and 12% to 23%, respectively), and *Phleum pratense* increased

Table 3: Comparison of species cover (in %) in 2001 and 2007. Only species with significant changes are shown. Significant decrease (Wilcoxon test; $\alpha = 0.05$) is marked by boldface, and significant increase is shaded in grey. Calepi – *Calamagrostis epigeios* community; FvHp – *Filipendula vulgaris-Helictotrichon pratense* community; Aegpod – *Aegopodium podagraria* community; Tc – transition community from CfHp to Aegpod; CfHp – *Carex flacca-Helictotrichon pratense* community.

Tabelle 3: Vergleich der Deckungsgrade (in %) in den Jahren 2001 und 2007 für Arten mit signifikanten Veränderungen. Signifikante Abnahmen sind fett und signifikante Zunahmen (Wilcoxon-Test; $\alpha = 0.05$) durch graue Schattierung markiert. Calepi – *Calamagrostis epigeios*-Gesellschaft; FvHp – *Filipendula vulgaris-Helictotrichon pratense*-Gesellschaft; Aegpod – *Aegopodium podagraria*-Gesellschaft; Tc – Übergangsgesellschaft von CfHp zu Aegpod; CfHp – *Carex flacca-Helictotrichon pratense*-Gesellschaft.

Site	Drubazas				Priednieki					
Plant community	Calepi ($n = 5$)		FvHp ($n = 10$)		Aegpod ($n = 6$)		Tc ($n = 4$)		CfHp ($n = 10$)	
Year	2001	2007	2001	2007	2001	2007	2001	2007	2001	2007
Aegopodium podagraria	0.0	4.4	0.0	0.0	**29.2**	**17.5**	11.5	22.5	9.8	37.8
Briza media	0.1	0.1	2.7	6.8	0.0	0.0	1.3	1.4	**11.6**	**3.3**
Calamagrostis epigeios	**37.0**	**17.4**	0.2	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Campanula rapunculoides	0.0	0.8	0.0	0.1	0.0	0.0	0.0	0.3	0.3	0.5
Carex caryophyllea	0.0	0.2	0.1	0.5	0.0	0.0	0.5	0.0	0.2	0.2
Carex ornithopoda	0.0	0.0	0.1	2.2	0.0	0.0	0.0	0.0	0.0	0.4
Centaurea jacea	0.2	0.2	0.6	0.6	0.0	0.0	0.1	0.5	0.6	1.8
Chaerophyllum aromaticum	0.0	0.0	0.0	0.0	29.2	90.8	24.5	51.5	0.2	2.1
Dactylis glomerata	0.1	0.3	0.1	0.1	**30.9**	**3.2**	13.5	9.0	15.5	7.5
Daucus carota	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	**0.4**	**0.1**
Festuca rubra	0.8	1.9	0.8	0.6	0.1	0.0	2.4	1.0	**7.8**	**2.9**
Geum rivale	0.0	0.0	0.0	0.0	0.1	0.2	2.1	3.1	0.4	1.1
Helictotrichon pratense	4.8	2.5	**36.0**	**7.5**	0.0	0.0	0.0	0.0	0.1	1.3
Knautia arvensis	0.7	0.8	0.2	0.4	0.0	0.0	0.1	0.0	0.3	0.8
Lathyrus pratensis	0.0	0.0	0.0	0.0	0.1	0.0	1.5	0.4	0.4	0.6
Leontodon danubialis	0.1	0.1	0.3	0.1	0.0	0.0	1.5	0.3	**2.7**	**0.5**
Leontodon hispidus	0.0	0.0	0.3	0.2	0.0	0.0	2.1	0.3	**1.0**	**0.4**
Medicago lupulina	0.0	0.0	0.7	0.3	0.0	0.0	0.3	0.0	**7.5**	**0.4**
Phleum pratense	0.0	0.0	0.0	0.1	1.3	1.2	0.8	4.1	0.2	0.7
Picris hieracioides	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.2	0.9
Poa pratensis	0.0	0.0	0.0	0.0	**0.3**	**0.0**	**0.5**	**0.0**	**0.5**	**0.0**
Potentilla reptans	0.3	0.4	0.1	0.3	0.3	0.0	2.0	4.3	0.7	3.5
Primula veris	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.4	1.9
Prunella vulgaris	0.0	0.1	0.2	0.2	0.0	0.0	4.1	0.1	**1.0**	**0.2**
Tragopogon pratensis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.1	0.4
Trifolium pratense	0.0	0.0	3.7	0.3	0.0	0.0	0.3	0.0	**2.3**	**0.2**
Trifolium repens	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0	**3.0**	**0.0**

Table 4: Kendall rank correlation coefficients for correlations of site scores of the DCA axes with vegetation structure and diversity data, and weighted means of Ellenberg indicator values. Correlation coefficients > 0.50 are printed in bold face.

Tabelle 4: Kendall-Rangkorrelationskoeffizienten für Korrelationen zwischen den Aufnahme-scores der DCA-Achsen und Daten zur Vegetationsstruktur und Artenvielfalt sowie den gewichteten Mittelwerten der Ellenberg-Zeigerwerte. Korrelationskoeffizienten > 0,50 sind fett gedruckt.

Parameter	Drubazas			Priednieki		
	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
Year	0.13	–0.16	–0.07	0.04	**0.70**	–0.09
Herb layer	–0.32	0.19	0.06	0.29	–0.20	0.10
Moss layer	–0.42	–0.27	0.13	–0.14	0.08	0.11
Litter layer	**0.54**	–0.13	–0.05	–0.14	**0.69**	–0.10
Species richness	**–0.56**	–0.20	–0.03	**–0.51**	0.03	–0.15
Shannon index	–0.24	–0.20	–0.07	**–0.58**	–0.16	0.01
Evenness	–0.02	–0.10	–0.04	–0.48	–0.23	0.06
Light value	–0.35	0.10	0.16	**–0.66**	–0.18	0.12
Moisture value	0.21	–0.01	–0.05	**0.63**	–0.02	0.12
Reaction value	–0.04	0.05	–0.08	–0.50	0.10	0.03
Nutrient value	**0.56**	–0.13	–0.18	**0.82**	–0.07	0.02

from 1% to 4%. Nevertheless, the changes in cover were significant only for these three species and for one species that showed a significant decrease (*Poa pratensis* from 1% to 0%). Therefore, it can be concluded that the total species composition was still more similar to the *Carex-Helictotrichon* community than to the *Aegopodium* community.

The DCA ordination of the plant species data recorded in 2001 and 2007 revealed similar processes as the analysis of cover values of single species. For Drubazas, the gradient length of axis 1 was 2.19 standard deviations (SD). The after-the-fact evaluation showed that 43% of the variance in the dataset can be explained by axis 1, 8% by axis 2, and 7% by axis 3, respectively. Along axis 1, the *Calamagrostis* (Calepi) and the *Filipendula-Helictotrichon* plots (FvHp) were clearly separated from each other. Both communities changed their position along axis 1 and 2, but in different directions without a clear successional trend (Fig. 9). Based on correlations of DCA axes scores with weighted means of Ellenberg indicator values, vegetation structure, and diversity parameters (Table 4), axis 1 can be interpreted as soil fertility gradient. Along this axis, litter cover and the Ellenberg indicator value for nutrients increased, and species richness decreased. Axis 2 and axis 3 showed only weak correlations with weighted means of Ellenberg indicator values or other vegetation parameters. With their low proportion of explained variance they could not be interpreted ecologically.

For Priednieki, the gradient length of the DCA axis 1 was 3.3 SD units. Axis 1 explained 83% of the variance, axis 2 explained 2%, and axis 3 another 2%. All three plant communities (Aegpod, Tc and CfHp) were clearly separated along axis 1, and their plots showed a clear movement along axis 2 (Fig. 10). The mean Ellenberg indicator values for nutrients and moisture increased, and the indicator values for light and the Shannon index decreased along axis 1, which means that this axis can be interpreted as soil fertility and moisture gradient. For axis 2, positive correlations with litter cover and with the year of observation were found (Table 4), which can be interpreted as a successional gradient. The low proportion of explained variance of axes 2 and 3, however, indicates that these axes are only of minor importance.

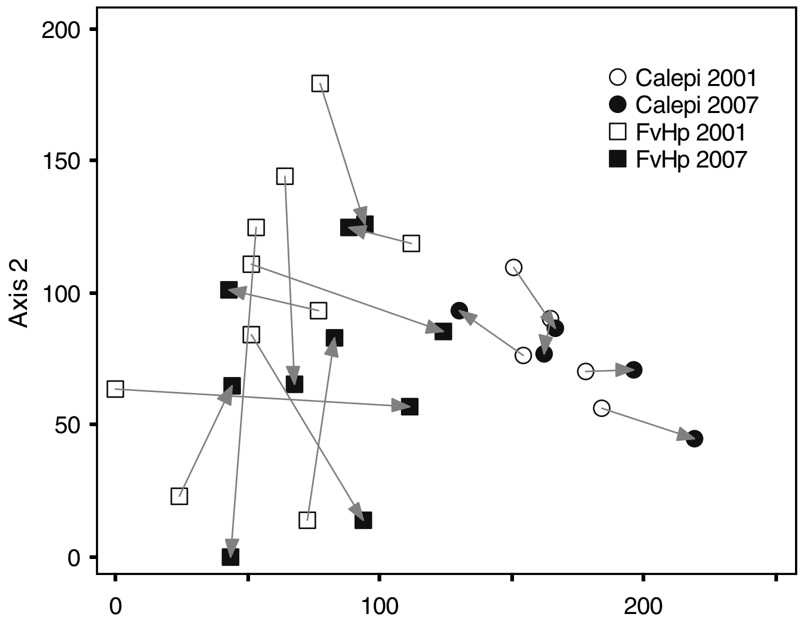

Fig. 9: DCA ordination of vegetation relevés (presence/absence transformed) for the grasslands of Drubazas. Vegetation relevés of the same plots in 2001 and 2007 are connected by arrows. Rare species present in < 5% of the plots were excluded from the analysis. FvHp – *Filipendula vulgaris-Helictotrichon pratense* community; Calepi – *Calamagrostis epigeios* community.

Abb. 9: DCA-Ordination mit Präsenz/Absenz-transformierten Vegetationsaufnahmen aus Drubazas. Vegetationsaufnahmen derselben Flächen aus den Jahren 2001 und 2007 sind durch Pfeile verbunden. Seltene Arten, die in weniger als 5 % der Aufnahmen vorkamen, wurden aus der Analyse ausgeschlossen. FvHp – *Filipendula vulgaris-Helictotrichon pratense*-Gesellschaft; Calepi – *Calamagrostis epigeios*-Gesellschaft.

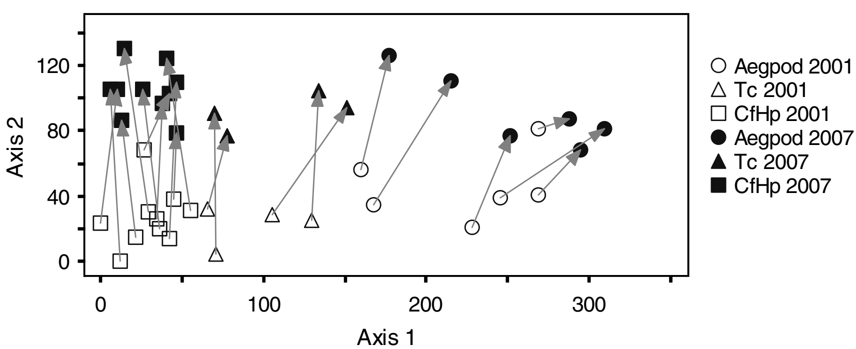

Fig. 10: DCA ordination of vegetation relevés (presence/absence transformed) for the grasslands of Priednieki. Vegetation relevés of the same plots in 2001 and 2007 are connected by arrows. Rare species present in < 5% of the plots were excluded from the analysis. CfHp – *Carex flacca-Helictotrichon pratense* community; Aegpod – *Aegopodium podagraria* community; Tc – transition community fro CfHp to Aegpod.

Abb. 10: DCA-Ordination mit Präsenz/Absenz-transformierten Vegetationsaufnahmen aus Drubazas. Vegetationsaufnahmen derselben Flächen aus den Jahren 2001 und 2007 sind durch Pfeile verbunden. Seltene Arten, die in weniger als 5 % der Aufnahmen vorkamen, wurden aus der Analyse ausgeschlossen. CfHp – *Carex flacca-Helictotrichon pratense*-Gesellschaft; Aegpod – *Aegopodium podagraria*-Gesellschaft; Tc – Übergangsgesellschaft von CfHp zu Aegpod.

4. Discussion

4.1. Succession

Several successional stages of dry grassland vegetation after abandonment have been described in the literature. Species richness may increase in the first years after abandonment due to cessation of mechanical disturbances by grazing or cutting. The next stage is characterised by stabilisation of species richness, but after a comparatively short time, species richness starts to decline, firstly because of the expansion of clonally growing species and dominant grasses, and secondly because of tree and shrub invasion (WARD 1990, ELLENBERG 1996, HUHTA & RAUTIO 1998, SOMODI et al. 2008).

During the observation period, the grassland of Drubazas was to some extent still in the second successional stage with aggressive grasses already abundant in patches, but most parts of the grassland were still diverse. Some parts of the grassland had been overgrown by *Pinus sylvestris,* but trees had been cut down in the late 1990s. Thus, during the monitoring period no effect of shading took place. The grassland of Priednieki was in the mid-successional stage, when tall nitrophilous herbs (*Aegopodium podagraria*, *Chaerophyllum aromaticum*) were expanding and cover and number of low-growing species were in decline.

In most parts of our dry calcareous grasslands (apart from the *Aegopodium* community), species richness did not suffer from abandonment for a comparatively long period of time. The observed succession of calcareous grassland vegetation was slower than reported in many cases in Central and Western Europe. For example, in the Netherlands, BOKDAM & GLEICHMAN (2000) found an initial increase in plant species richness in the first five years after abandonment of grazing and no changes during the next five years, and WILLEMS (2001) reported that *Brachypodium pinnatum* took over calcareous grassland in 10 years, and after 17 years, only 15% of all calcareous grassland plant species remained.

In our case, large parts of the calcareous grasslands still showed a typical species composition and high diversity even after nearly 20 years of abandonment. An increase of "aggressive" grasses and tall herbs was observed only in mesic, but not in dry grasslands. Our data show more similarities in succession rate with Northern and Southeastern Europe. In Southern Sweden, no decrease in species richness was observed in grasslands abandoned for 5–10 years (ÖCKINGER et al. 2006). A very slow decrease of diversity has also been reported from abandoned steppe-like calcareous grasslands in Romania, where grasslands were still very diverse after 30–50 years of abandonment (RUPRECHT et al. 2009). In Estonia, alvar grasslands overgrown with pine were still very species-rich after 40 years of abandonment (PÄRTEL & ZOBEL 1995, PÄRTEL et al. 1999).

One reason explaining the slow rate of succession in comparison to Central and Northwestern Europe could be the lower amount of aerial nitrogen deposition in Latvia (6–7.8 kg/ha per year, ANON. 2008). In Central and Northwestern Europe, N deposition rates are much higher, and the critical load of nitrogen for dry calcareous grasslands is 14–25 kg/ha per year (BOBBINK et al. 2003). Several studies have shown that the rate of succession is accelerated by nitrogen additions (WILSON et al. 1995, BOBBINK & WILLEMS 2001, DORLAND et al. 2003, SMART et al. 2003).

4.2. Comparison of vegetation dynamics at the two study sites

The vegetation analysis indicated that grassland vegetation on the south-west facing slope (Drubazas) was more stable over time than at the north-east facing slope (Priednieki). In Priednieki, the encroachment of *Aegopodium podagraria* and *Chaerophyllum aromaticum* in the *Carex flacca-Helictotrichon pratense* community and especially in the transition community from the *Carex-Helictotrichon* to the *Aegopodium* community was obvious, and more species experienced significant changes in cover than at Drubazas. An unexpected result of the research was that the grassland of Drubazas did not show an expansion of *Calamagrostis epigeios*, although this species was partly dominant in 2001. The species is reported to very aggressively encroach grasslands shortly after abandonment (REBELE &

LEHMANN 2001, SOMODI et al. 2008) as it can spread vegetatively at about 1 m per year (SCHUHMACHER & DENGLER, 2008). In Drubazas, the cover (in the *Calamagrostis epigeios* community) and the constancy (in the *Filipendula-Helictotrichon* community) of *Calamagrostis epigeios* decreased strongly, and at the same time, the total species richness per plot even increased significantly in the *Calamagrostis* community.

As management history does not differ substantially between Priednieki and Drubazas, it can be assumed that the described differences are mainly due to topographic and edaphic factors. Firstly, different types of disturbances are very important to maintain the plant species diversity of semi-natural grasslands (e. g. DURING et al. 1988, KLEYER 1999, ZOBEL et al. 2000, KAHMEN & POSCHLOD 2008). Tree cutting and occasional mowing in winter (without removal of plant material) were anthropogenic disturbances in Drubazas, and the monitoring started at the same time as tree cutting took place. Vascular plant species richness can be negatively affected by shading of trees and shrubs, and species richness increases with decreasing tree and shrub cover (PYKÄLÄ et al. 2005). Therefore, it can be assumed that the increase in species richness on our permanent plots was the response to these disturbances.

During our study, natural disturbance by drought occurred in 2006, when only 24% of the mean precipitation was measured in July (LATVIJAS VIDES, ĢEOLOĢIJAS UN METEOROLOĢIJAS CENTRS). In this year, the percentage cover of the herb layer in the *Calamagrostis* community was lower than in all other observation years, and above-ground parts of many plants including *Calamagrostis epigeios* were brown and withered already in July.

In addition, the monitoring started only 13 years after abandonment, so the main decrease in species numbers might have happened before. Unfortunately, the average species richness per 1 m^2 is not known for these communities in Latvia, but there are on average 32 species per 9 m^2 in managed *Filipendula vulgaris-Helictotrichon pratense* grasslands (RŪSIŅA 2007) compared to 27.5 species per 1 m^2 in our *Filipendula-Helictotrichon* community and 21.4 species per 1 m^2 in our *Calamagrostis* community in 2007.

Like in other dry grassland studies (e.g. SÜSS et al. 2004, 2010), differences in soil properties and topography could explain the fact that the vegetation was more dynamic in Priednieki and increase of aggressive grass species (*Calamagrostis epigeios* and *Brachypodium pinnatum*) was not observed in the *Filipendula-Helictotrichon* community of the Drubazas site.

In the northern hemisphere and within the same parent material, soil moisture conditions and soil fertility are always better on north than on south facing slopes where higher insolation and extreme drought hamper biomass production and nutrient enrichment of soils (e. g. PERRING 1959, BENNIE et al. 2006, WILKINSON & HUMPHREYS 2006, ZELENÝ & CHYTRÝ 2007 and references therein). Succession is therefore slower on south than on north facing slopes (BENNIE et al. 2006).

Regarding the moisture regime, the gleyic properties of the soils in Priednieki indicated that moisture conditions were better than at Drubazas. It has been reported that uptake of potassium and phosphorus increases with increasing water content (DUNHAM & NYE 1976, KUCHENBUCH et al. 1986). Differences in plant nutrient availability of the soils at the two sites were not so clear. In total, the content of P_2O_5, N, and C in both study sites was similar to other dry calcareous grassland sites in Latvia (JERMACĀNE & LAIVIŅŠ 2002) and characteristic for infertile soils (BORUKS 2004). It was not higher than reported for dry calcareous grasslands from other European regions. For example, in Germany, in managed calcareous grasslands of the nature reserve Garchinger Heide, the amount of P_2O_5 in the upper soil layer was 1.6–4.6 mg/100g and that of K_2O 3.6–20.0 mg/100g, but in the upper soil layer of newly restored grasslands on former arable fields, these amounts were much higher with 45.4–47.6 mg/100 g and 52.0–53.1 mg/100 g, respectively (KIEHL & JESCHKE 2005). POSCHLOD et al. (2008) also found that soils in young grasslands (with residues of fertilisers from the former use as arable land) were richer in plant available P than ancient grasslands in Bavaria (38 mg/100 g versus 8.1 mg/100 g).

Nevertheless, there was a considerable difference in contents of K_2O between Drubazas and Priednieki (6–8 mg/100 g versus 31–37 mg/100 g). The amount of K_2O in the soil of Priednieki was within the limits of mean amounts for moderately fertile soils in Latvia, which is 20–30 mg/100 g (BORUKS 2004). The huge difference in K_2O contents between the grasslands of Drubazas and Priednieki together with differences in moisture regime could be responsible for better growth conditions for plants at the latter site.

The invasion process of *Calamagrostis epigeios* in the *Filipendula-Helictotrichon* community of Drubazas could also have been hampered because, in contrast to the *Calamagrostis* community, the subsoil of the *Filipendula-Helictotrichon* community consisted of a thick layer of partly weathered dolomite (in the depth of 40–65 cm), and the community was located higher on the slope promoting more rapid drying out than the soil of the *Calamagrostis* community. *Calamagrostis epigeios* is reported to be expansive in dry grasslands, but only at high (20–60 kg/ha per year) atmospheric N deposition rates (VAN DER BERG et al. 2005). It cannot survive and spread if stress factors, nutrient deficiency (total nitrogen, phosphate, and potassium), and drought are combined (SÜSS et al. 2004).

4.3. Implications for management of dry calcareous grasslands

In the Eastern Baltic region, biodiversity and cultural-historical values of semi-natural grasslands were assessed, and active protection started only recently (PAAL 1998, SENDŽIKAITĖ & PAKALNIS 2006, GAZENBEEK 2008, VELLAK et al. 2008). Although more than 85% of the semi-natural grasslands of Latvia are included in Natura 2000 sites, large areas are left unmanaged, and none of the habitat types fulfills the criteria of a favourable conservation status (ANON. 2007). The future of management activities depends totally on agri-environment subsidies (AUNIŅŠ 2008). The conditions for semi-natural grassland management to receive agri-environment subsidies as prescribed by the Rural Development Program of Latvia are in conflict with those management requirements that aim to preserve biodiversity, e. g. only late mowing (not before August) and mulching without hay removal are allowed. LĀRMANIS (2008) reported that processes that actually or potentially endanger the favorable conservation status of semi-natural grasslands occur in 22% to 72% of the total area of the grasslands of the European Natura 2000 network in Latvia.

These problems in grassland conservation are urgent also for the study sites and the whole nature protection area “Nature Park of the Abava River Valley”. Our results indicate that dry calcareous grasslands on southern and southwestern slopes of the Abava River Valley are quite resistant to abandonment and that their species diversity probably might last for some more decades without any management, but eventually the sites will turn into forest vegetation. Up to now, the original species richness and vegetation composition could still be easily restored. Grasslands on northern and northeastern slopes are not so resistant because of more mesic and fertile soil conditions favouring vegetation succession towards species-poor tall herb vegetation and further to shrub and forest vegetation. Active management of these grasslands is urgently needed.

The need for active conservation in the whole nature park is accentuated also by the decrease of semi-natural grasslands during the last 100 years from 28% to 18% of the nature park area (RUSKULE 2000), with only 15% in good condition (KABUCIS & JERMACĀNE 1998). It means that in future, grassland habitat fragmentation can appear as another important factor promoting local extinction of plant species and lowering restoration success as it has been reported from Central Europe (e.g., FISCHER & STÖCKLIN 1997, POSCHLOD et al. 1998, WILLEMS 2001, MAURER et al. 2003).

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