Successional dynamics of *Cynosurus* pasture after abandonment in Podkrkonoší

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ABSTRACT

Between 1996–2002, successional dynamics on an abandoned pasture in Přední Ždírnice (lat. 50°32′N, long. 15°40′E) was examined. A 7-year study was performed on the abandoned mesotrophic pasture classified as *Cynosurion* Tüxen 1947 at the start of the study. Two permanent plots (100 m^2) were established and sampled three times a year; changes in plant species composition (species cover) and plant species diversity (species number) were studied. Species assemblages of the *Cynosurus* pasture were described, E1 (herb layer) and E2 (shrub layer) covers were calculated and a secondary succession in the plant community was evaluated. Abandonment caused the decrease in the cover of the species sensitive to shading – e.g. *Taraxacum* sect. *Ruderalia*, *Trifolium repens*, *Lathyrus pratensis*, *Plantago major*, *Stellaria graminea*, *Vicia cracca*. Contrary to this, the cover of *Calamagrostis epigejos*, *Rubus* sp., *Galium album*, *Galium verum*, *Knautia arvensis*, *Veronica chamaedrys* increased, probably due to their ability to spread by clonal growth and as a result of the competitive relationships in the plant community. A big production of *Calamagrostis epigejos* litter may be the outcome of a significant decrease (by 9%) in E1 cover ($P = 0.04$). Although the grassland was invaded by ruderal and weedy species (*Apera spica-venti*, *Myosotis arvensis*, *Veronica arvensis*) and by shrubs *Crataegus* sp. and *Rosa* sp. (an increase by 16%), an increase in species number was not significant. Phytosociologically, the *Cynosurion* Tüxen 1947 community came closer to the *Arrhenatherion* Koch 1926 alliance.

Keywords: grassland; successional dynamics; *Cynosurus* pastures; land use; abandoned meadows; Podkrkonoší

Mountain and submountain meadows and pastures changed significantly in the course of the 20th century. Semi-natural grasslands in Podkrkonoší were regularly managed, cut once or twice a year, livestock grazed or partly grazed by sheep. The traditional management changed after WW2 in relation to the removal of the German population inhabiting frontier areas. During the communist era, there was an intensive land use supported by excessive application of fertilizers. There was a radical change after 1989, the fodder demand decreased and the low productive grasslands were set aside in many cases.

Many contemporary studies were focused on the influence of livestock grazing or sheep grazing and mowing on hay meadows (e.g. Krkonoše-related studies – see Kettnerová et al. 1995, Krahulec et al. 2001). However, fewer studies dealt with grassland dynamics and succession following the abandonment from agriculture.

The botanical composition of grassland vegetation is a reflection of many factors, and there are two levels on which we can describe secondary successional changes after abandonment – the species level and the community level. Begon et al. (1996) and Burrows (1990) describe the secondary succession as a sequential or directional change in species number, species composition, community structure, or community site. Abandonment of regularly managed grasslands resulted in the degradation processes of the ecosystem characterised by predomination of several species or by decrease in species diversity. As is generally known, it can cause irreversible processes and changes in the plant community.

Pecháčková and Krahulec (1995) state that hay meadows may turn into degradation phases of tall grasses and forbs and that the final phase of the degradation process is marked by its extension to the woodland (Krahulec et al. 1996). Huhta (1996) states that a temporary increase in species diversity caused by arriving immigrants after abandonment may be regarded as an indicator of ongoing succession. Some colonizing species may be present in the soil bank, and on the other hand, abandoned stands can be invaded by species from neighbouring vegetation. In various experiments carried out by Clément and Touffet (1990), it was found out that except for the persistence of the seed bank the species cover can also be affected by the regeneration ability of the vegetation.

The possibility of an increase in the cover of strongly competitive species, especially with rapid vegetative growth and those forming tussocks, e.g. grasses, is related to the above-mentioned trend (Huhta and Rautio 1998). Generally, early successional dynamics brings about a change in the proportion between plants of different life histories and plant strategies. The proportion of defoliation tolerant plants occurs to be larger in managed grasslands, and correspondingly, pastures and meadows after abandonment are occupied by K-strategists. After abandonment, most species are able to persist in a stand but on the other hand the cover and richness of those species dependent on regular defoliation may rapidly decrease (Bakker 1989).

In my experiment, I observed the successional dynamics of the abandoned mesotrophic pasture for over 7 years. Two replicate plots were observed and temporal changes monitored by repeated sampling. Objectives of this study were twofold: (i) to investigate the changes in plant species diversity and in plant species composition on the species level; (ii) to describe species assemblages on the pasture, to calculate the E1 (herb layer) and E2 (shrub layer) cover, and to evaluate the plant community during the secondary succession on the community level.

For nomenclature see Kubát et al. (2002). Moss species were not determined.

MATERIAL AND METHODS

Description of the locality

The study site is a mesotrophic pasture in Přední Ždírnice (lat. 50°32′N, long. 15°40′E), 15 km southwest of Hostinné in the upland of the Krkonoše. The altitude of the study site is 430 m a.s.l. (ranging from 420 to 440 m a.s.l.). Diversification of the pasture is simple with mostly southern exposition, the slope is 35°. Precipitation is 732 mm (Čistá meteorological station). Soil substrate is cambisol.

The study site is based on two permanent plots. In summer 1996, permanent plot 1 was dominated by *Alchemilla* sp. (8% cover), *Anthoxanthum odoratum* (7%), *Cynosurus cristatus* (7%), *Festuca rubra* (7%), *Leondodon autumnalis* (7%), *Leontodon hispidus* (28%), *Prunella vulgaris* (6%), *Taraxacum* sect. *Ruderalia* (8%), *Trifolium repens* (5%), and other 50 vascular plants. *Alopecurus pratensis* (15%), *Rubus* sp. (10%), and *Calamagrostis epigejos* (6%) were dominant in permanent plot 2, followed by *Trifolium repens* (6%), *Taraxacum* sect. *Ruderalia* (5%), *Poa pratensis* (5%), and other 41 species. In addition to this, plot 2 included shrub layer E2 composed of *Crataegus* sp. (3%) and *Rosa* sp. (5%). According to the phytosociological nomenclature (Moravec et al. 1995), both communities were classified as *Cynosurion* Tüxen 1947 at the beginning of the experiment.

Between 1952–1992, grassland management consisted of livestock grazing (Czech Red Pied cattle). It was a rotational grazing with three grazing cycles per year. The stand was not chemically treated against weeds. Between 1992–1996, an extensive livestock grazing (four grazing cycles per year), combined with mowing and mass removal once a year, was applied. In 1996, the management was stopped and the pasture was left aside.

Experimental design, sampling

In 1996, two permanent plots (each of 100 m^2) were established on the experimental pasture. They varied in the species richness and presence of the shrub layer (see Description of the locality). The count of all vascular species (including the shrub layer), their percentage cover on each plot, and E1 and E2 cover were visually estimated. Plots were sampled three times during the vegetation season – at the beginning of May, July and September. The 7-year study consists of the set of 42 phytosociological relevés including the initial sampling in the starting year (1996).

Statistical analyses

Statistical programme Canoco for Windows 4.5 (Ter Braak and Šmilauer 1998) and Statistika software package were used to evaluate the data set. Redundancy Analysis (RDA) was used to evaluate the plant species composition data. Temporal changes of selected species were evaluated by the Repeated Measures ANOVA after obtaining significant results from RDA. Ordination diagram showing reaction of the plant species to environmental variable was constructed by CanoDraw for Windows 4.0 programme (Ter Braak and Šmilauer 2002).

RESULTS AND DISCUSSION

As mentioned above herein, the measurements were carried out on two levels. On the species level, the plant species composition (species number) and plant species diversity (species cover) were estimated, on the community level, the E1 and E2 covers were estimated.

Plant species composition

It was found out that plant species composition (species cover) was strongly dependent on the time

Table 1. Results of RDA analyses of cover estimates in 10 × 10 m plots

Expl. var.	Covar.	Standard.	% ax 1 (all)	*F* ax 1 (all)	*P* ax 1 (all)
Spring	PlotID	N	37.1	6.48	0.008
Summer	PlotID	N	45.3	9.11	0.008
Autumn	PlotID	N	50.0	10.98	0.008
Sp, Su, Au	PlotID	N	48.0 (50.3)	35.1 (19.2)	0.18 (0.18)

Expl. var. = explanatory variables; Covar. = covariables; Standard. N = standardization was not used; % ax 1 (all) = % species variability explained by 1-st axis (all axes); *F* ax 1 (all) = *F*-ratio statistics for the test (1-st, all axes); *P* ax 1 (all) = corresponding probability value obtained by the Monte Carlo permutation test (499 permutations, i.e. Type I error probability in testing the hypothesis that the effect of all explanatory variables is zero); Sp, Su, Au = analysis of measurements in spring, summer and autumn; PlotID = identifier of each plot

during the season when the measurements took place. The temporal effect of the measurement in autumn was the most significant one. The results of RDA ordination (Table 1, Figure 1) indicate that the species responded differently to abandonment. Species promoted after abandonment were *Calamagrostis epigejos*, *Galium album*, *Galium verum*, *Knautia arvensis*, *Rubus* sp., and *Veronica chamaedrys*. Figure 1 also shows the species the cover of which was 0% when the experiment was launched (i.e. the species were not recorded in the baseline) and which invaded the plot – *Apera spica-venti* (0.5% cover in 2002), *Carex muricata* (3%), *Geranium dissectum* (1%), *Myosotis arvensis* (2%), *Veronica arvensis* (1%), the juvenile shrub individuals of *Crataegus* sp. (1%), and *Rosa* sp. (1%). Consequently, this resulted in an increase in species diversity (see below).

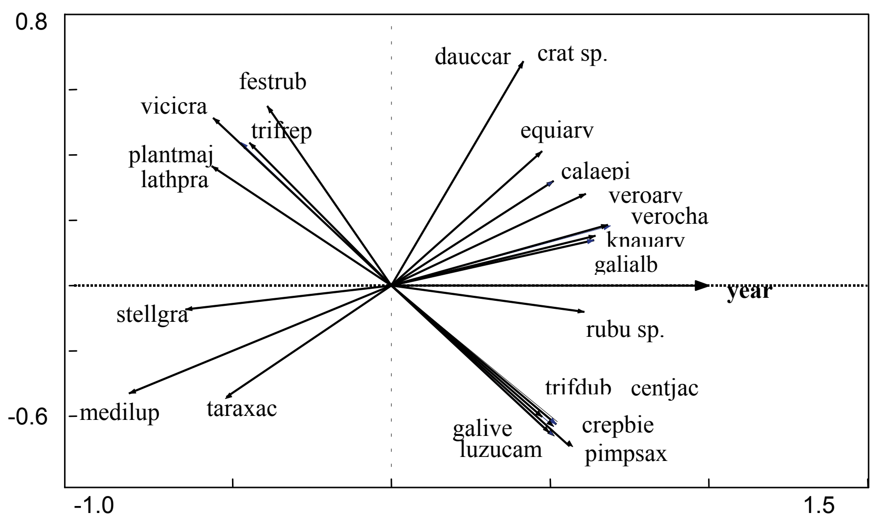

Figure 1. Biplot ordination diagram showing results of RDA analysis of plant species composition in 10 × 10 m plots (autumn measurements)

year – serial year number, calaepi – *Calamagrostis epigejos*, centjac – *Centaurea jacea*, crat sp. – *Crataegus* sp., crepbie – *Crepis biennis*, dauccar – *Daucus carota*, equiarv – *Equisetum arvense*, festrub – *Festuca rubra*, galialb – *Galium album*, galiver – *Galium verum*, knauarv – *Knautia arvensis*, lathpra – *Lathyrus pratensis*, luzucam – *Luzula campestris*, medilup – *Medicago lupulina*, pimpsax – *Pimpinella saxifraga*, plantmaj – *Plantago major*, rubu sp. – *Rubus* sp., stellgra – *Stellaria graminea*, taraxac – *Taraxacum* sect. *Ruderalia*, trifdub – *Trifolium dubium*, trifrep – *Trifolium repens*, veroarv – *Veronica arvensis*, verocha – *Veronica chamaedrys*, vicicra – *Vicia cracca*

Table 2. Results of repeated measures ANOVA of cover estimates, plant species diversity, and E1 cover in 10 × 10 m plots; H_0: time (abandonment) has no effect on variables tested

Dependent variable	*DF*	*MS*	*F*-ratio	*P*-value
Calamagrostis epigejos	6	2.30	1.00	0.47
Rubus sp.	6	6.67	1.92	0.16
Taraxacum* sect. *Ruderalia	**6**	**5.17**	**11.42**	**0.01**
Trifolium repens	**6**	**4.74**	**10.47**	**0.01**
E1 cover	**6**	**33.50**	**3.09**	**0.04**
Plant species diversity	6	26.32	1.14	0.39

DF = degrees of freedom, *MS* = mean square, *F*-ratio = statistics for the test, *P*-value = corresponding probability value; significant effects ($P < 0.05$) are written in bold

The results of repeated measurements ANOVA for *Calamagrostis epigejos* and *Rubus* sp. cover are shown in Table 2. Although an average *Calamagrostis* cover increased from 3 to 12% and *Rubus* cover from 7.5 to 22.5% (Figure 2), the most pronounced effect of the increase in their cover was not significant probably due to the lack of data collected in two replications with a relatively different variability of plant species composition.

Species which were negatively influenced by the abandonment and the cover of which decreased were *Lathyrus pratensis*, *Plantago major*, *Stellaria graminea*, *Vicia cracca*, and others (Figure 1). Significant response and cover changes of *Taraxacum* sect. *Ruderalia* ($P = 0.01$) and *Trifolium repens* ($P = 0.01$) between 1996–2002 were revealed (Table 2, Figure 2).

A remarkable increase in the cover of *Calamagrostis epigejos* and *Rubus* sp. may be explained predominantly by their wide phenotypic plasticity and clonal growth. The species composition (or fine-scale dynamics on the stand) is regarded to be a result of clonal growth and competitive interactions among species. Some authors (e.g. Rebele 2000, Rebele and Lehmann 2001) concentrated on the guerrilla growth strategy of *Calamagrostis* and on the interference competition which was enabled by a dense cover of aboveground biomass and litter. Lehman (1997) found out that the clonal diversity of this vegetatively propagating grass was higher on abandoned grasslands and on habitats polluted with heavy metals. On the other hand, stressful conditions favour the coexistence of a great number of clones and decrease the role of competition.

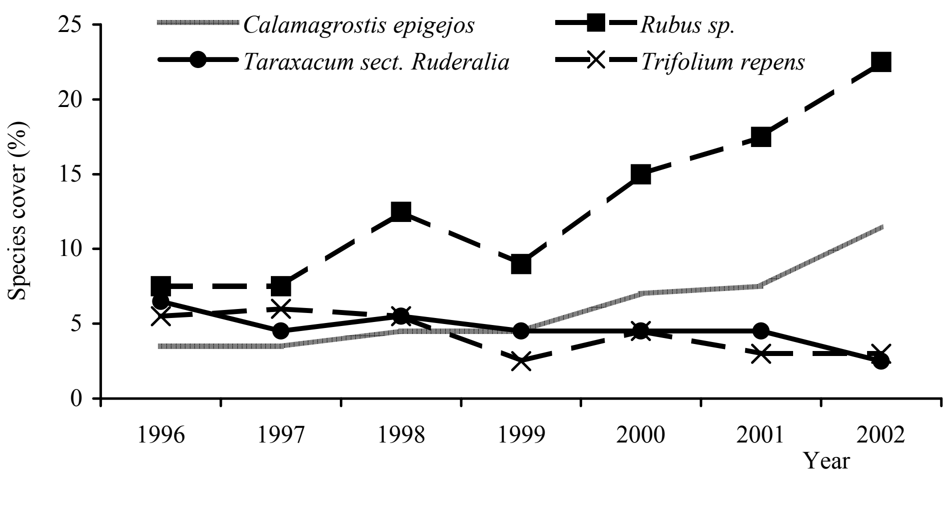

Figure 2. Cover of *Calamagrostis epigejos*, *Rubus* sp., *Taraxacum* sect. *Ruderalia* and *Trifolium repens* between 1996–2002 (autumn measurements)

Furthermore, Lehmann and Rebele (1994) state that despite large numbers of sexually produced seeds, its reproductive effort is comparably low. *Calamagrostis epigejos* frequently occurs on natural and man-made habitats. Its appearance is often connected with temporary final stages which are considered to be much resistant to invasions of woody species and can not develop to scrublands and open forest (Wiegleb and Birgit 2001). However, the results of the experiment I concluded do not corroborate this high environmental resistance of *Calamagrostis* stands.

As opposed to the positive response to abandonment mentioned above, the cover of *Trifolium repens*, *Taraxacum* sect. *Ruderalia*, and others decreased. The impact of abandonment on these defoliation sensitive species is apparent. Previous grazing system involved repeated and frequent defoliation, manuring, and trampling of the pasture during the vegetative plant growth, whereas during the 7-year abandonment the vegetation was not exposed to this regular disturbance. Laidlaw et al. (1995) determined a *Trifolium repens* content in a continuously stocked sward. He pointed out that the presence of *Trifolium* depends on regular defoliation and grazing pressure; he explained the changes in the canopy structure under different grazing techniques and defoliation intervals. Defoliation during the vegetation period favours the growth of *Trifolium* over tall grasses because of reduced competition from grasses (Singh et al. 1997), and it stimulates tillering, forward prostrate growth forms, and rosette plants.

Plant species diversity

Plant species diversity, or, as the case may be, species number or species richness, was higher in the abandoned meadow than on a regularly grazed pasture. General increase in plant species diversity was not statistically significant (Table 2) as a result of only two replications. In plot 1, the species diversity varied from 50 to 68 species (increase by 36%), whereas in plot 2, the average increase was 2.4%. A general trend of increasing species diversity or up-and-down effect reported by Pietsch (1998) can not be confirmed.

Species diversity in plot 2 was more or less constant between 1996–2002. This can be explained by the already mentioned expansion of *Calamagrostis* in plot 2 and by high production of litter related thereto. Its persistence affects and, in particular, reduces species diversity. Contrary to this, Jakob et al. (1996) reported that a positive influence of *Calamagrostis* on soil development can be a precondition to the colonizability by nongraminoid species. This trend was described by Butler and Briske (1988) who argued that the cessation of unrestricted selective grazing of specific plant species, which often leads to reduction in species richness, brings about an increase in species diversity. High frequency of tiller defoliation is assumed to be a prerequisite for a production of patches (creation gaps in vegetation) resulting from selective grazing. The development of these long-term patches can be an early sign of a weed invasion or of an impending land degradation (Taylor et al. 1984, Lütge et al. 1998). This theory entirely corresponds to the results obtained in my experiment, and as was showed, the open patches in plot 1 were colonized by *Apera spica-venti*, *Carex muricata*, *Geranium dissectum*, *Myosotis arvensis*, and *Veronica arvensis*. It seems that the vacant space was filled up by weedy and ruderal species and by species with variable life-history strategies.

E1 and E2 cover

Statistically significant influence of time on E1 cover is presented in Table 2. Figure 3 indicates temporal changes in E1 and E2 cover between 1996–2002. E1 cover significantly declined ($P = 0.04$) from 91.5 to 82.5%, E2 cover consisting of *Crataegu*s sp. and *Rosa* sp. increased from 8 to 25%.

As has already been mentioned above herein, regular defoliation by mowing or grazing increases species diversity, but there also occur opposite tendencies during intensive continuous grazing. After abandonment, the impact of defoliation, which is a very beneficial process for the vegetation since it reduces litter build-up, vanishes and competitive relationships in a grassland change radically (Butler and Briske 1988). The decrease in E1 cover may be explained by the above-mentioned cessation of former livestock grazing and by the absence of the removal of above-ground biomass, which resulted in an increase in C*alamagrostis* and *Rubus* cover. It is probable that a high production of *Calamagrostis* litter caused the decrease in E1 cover which became more patchy with coarser grain in vegetation structure. In the regularly grazed pasture, the number and cover of grasses stayed relatively constant while the cover decreased in the course of years following abandonment. Stampfli and Zeiter (1999) gloss this effect by extensive rhizome systems of grasses which are typical and also remain on abandoned grasslands.

From the phytosociologic point of view, the *Cynosurion* Tüxen 1947 plant community came closer to the *Arrhenatherion* Koch 1926 alliance during the 7-year abandonment. It is related to a decrease in grazing-tolerant species typical for *Cynosurus* pastures, e.g. *Bellis perennis*, *Cynosurus cristatus*, *Euphrasia rostkoviana*, *Leontodon autumnalis*, *L. hispidus*, *Lolium*

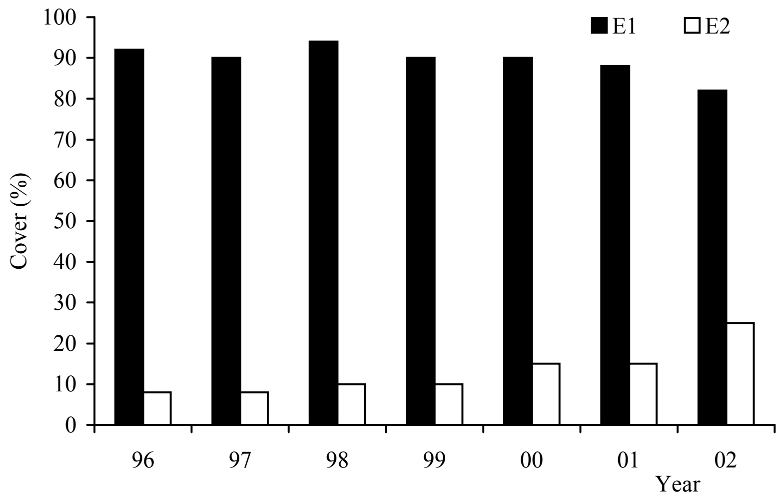

Figure 3. Temporal changes in E1 and E2 cover between 1996–2002 (autumn measurements)

perenne, *Rumex obtusifolius*, *Taraxacum* sect. *Ruderalia*, and *Trifolium repens*. Furthermore, the abandoned pasture was enriched by tall-herb vegetation with higher degree of coverage of grasses (*Anthoxanthum odoratum*, *Arrhenatherum elatius*, *Festuca rubra*, and *Festuca pratensis*) and herbs (*Campanula patula*, *Crepis biennis*, *Daucus carota*, *Galium album*, *Knautia arvensis*, and others).

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ABSTRAKT

Sukcesní dynamika neobhospodařované poháňkové pastviny v Podkrkonoší

Způsob obhospodařování je jedním z důležitých faktorů pro udržení produkčních funkcí a diverzity porostu. V roce 1996 byly na opuštěné pastvině svazu *Cynosurion* Tüxen 1947 v obci Přední Ždírnice v Podkrkonoší (50° 32′ s. š., 15° 40′ v. d.) založeny dvě trvalé plochy, na kterých byla v letech 1996–2002 třikrát ročně sledována sukcesní dynamika mezofilního travního porostu. K hodnocení vlivu času (opuštění) na druhovou pokryvnost, počet druhů a pokryvnost bylinného (E1) a keřového patra (E2) byla použita metoda RDA (program Canoco for Windows 4.5) a Repeated Measures Analysis (ANOVA) ze statistického programu Statistika. Průkazné snížení pokryvnosti bylo zaznamenáno především u defoliačně citlivých druhů, například u *Taraxacu*m sect. *Ruderalia*, *Trifolium repens*, dále u *Lathyrus pratensis*, *Plantago major*, *Stellaria graminea*, *Vicia cracca*. *Calamagrostis epigejos*, *Rubus* sp., *Galium album*, *Galium verum*, *Knautia arvensis*, *Veronica chamaedrys* pokryvnost zvýšily. Tvorba a hromadění odumřelé biomasy *Calamagrostis epigejos* byly pravděpodobně příčinou snížení pokryvnosti E1 o 9 %. Zvýšení počtu druhů, typický fenomén pro opuštěné porosty, nebylo statisticky průkazné, přestože na pastvinu invadovaly některé plevelné a ruderální druhy – *Apera spica-venti*, *Carex muricata*, *Geranium dissectum*, *Myosotis arvensis*, *Veronica arvensis* aj. Z fytocenologického hlediska lze studovanou neobhodpodařovanou pastvinu hodnotit jako degradační fázi poháňkových pastvin s přechodem k mezofilním loukám svazu *Arrhenatherion* Koch 1926.

Klíčová slova: luční porost; sukcesní dynamika; poháňkové pastviny; systém obhospodařování; opuštěné louky; Podkrkonoší

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