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The influence of *Calamagrostis villosa* on the species diversity of deforested sites in the Krušné hory Mts.

Vliv *Calamagrostis villosa* na druhovou diverzitu odlesněných stanovišť v Krušných horách

Petr Pyšek

Dedicated to Professor Zdeněk Černohorský on his 80th birthday

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The effect of *Calamagrostis villosa* on the performance of the other species present in the community was studied in the Krušné hory Mts. Higher species richness was found in the moist meadow invaded by *C. villosa* than in the deforested site completely dominated by this species. Log-series distribution of species abundances was the best fit, especially in the deforested site. The diversity indices used (α, H') were able to discriminate significantly ($P < 0.001$) between sites. In the moist meadow, the relationships were studied on the within-community level. Number and total biomass of the other species decrease with the biomass of *C. villosa*, both being more closely related to its litter ($P < 0.01$) than to its living biomass ($P < 0.05$). Linear increase of evenness J' of the other species with *C. villosa* total biomass was recorded. The species diversity H' showed no significant relation to the *C. villosa* productivity. Performances of all but two species are significantly negatively correlated with *C. villosa* biomass. Differentiated relationships of the other species to *C. villosa* litter and live biomass may be interpreted with respect to their growth forms and life strategies.

Na Dlážděnce 2096, 182 00 Praha 8, Czechoslovakia

INTRODUCTION

Forest decline linked with human activities has been reported from various parts of the world. The most severe instances of forest dieback are those reported from Eastern Europe (PITELKA et RAYNAL 1989, STOUT 1989). Mortality is mostly attributed to high sulphur dioxide concentrations from point sources of industrial activity (VAVROUŠEK et MOLDAN 1989). Deforested sites with changed soil chemistry due to acidic deposition (VAVROUŠEK et MOLDAN l.c.) are occupied by invasive plant species.

At higher altitudes of the Krušné hory Mts., original Norway spruce forests have been mostly replaced by the vast stands of *Calamagrostis villosa* (CHAIX) J. F. GMEL. This species is clearly resistant against acidic deposition and herbivore attack. Moreover, because of its light requirements, its spreading is supported by deforestation (SAMEK 1988, PYŠEK 1991). The competitive ability of the species has been ascribed to a high production of both aboveground (FIALA et al. 1989) and underground (FIALA 1989) biomass.

This paper aims at a comparison of the sites invaded by *C. villosa* to a

Table 1. — Performance of species in the sites I and II. Frequency values (%) are given.

	Site I	Site II
total number of species in 20 plots	39	19
mean number of species per plot	7.8	3.2
total species number in the site	63	25
mean cover of *Calamagrostis villosa* (%)	26.2	35.5
diversity index α	16.19	9.35
Senecio fuchsii	80	50
Epilobium angustifolium	70	100
Cirsium palustre	65	10
Equisetum sylvaticum	55	25
Galeopsis bifida	55	10
Juncus effusus	30	5
Rubus idaeus	25	10
Maianthemum bifolium	25	10
Urtica dioica	25	5
Rumex acetosa	10	10
Deschampsia flexuosa	5	20
Carex leporina	5	5
Myosotis laxiflora	45	—
Holcus mollis	30	—
Epilobium adenocaulon	30	—
Moehringia trinervia	30	—
Cirsium arvense	15	—
Ranunculus repens	15	—
Galium palustre	15	—
Epilobium palustre	15	—
Betula pendula	—	15

Other species:
Site I — 10 %: *Dactylis glomerata, Viola palustris, Galeopsis pubescens, Deschampsia caespitosa, Oxalis acetosella, Dryopteris austriaca, Cardamine pratensis.* — 5 %: *Stellaria media, Impatiens parviflora, Poa trivialis, Ajuga reptans, Carex flava* s.l., *Chrysosplenium alternifolium, Taraxacum officinale, Veronica serpyllifolia, Lychnis flos-cuculi, Brachythecium rutabulum, Plagiomnium elatum.* Site II — 10 %: *Vaccinium myrtillus, Galium harcynicum.* — 5 %: *Carex panicea, C. pallescens, Rumex obtusifolius, R. acetosella.*

various extent and addresses the following questions:

1. What is the performance of the other species present in the community with regard to the performance of *C. villosa*?
2. Is the occurrence of the other species influenced mainly by this-year living biomass or by accumulated litter of *C. villosa*?

STUDY SITE

The research was carried out in the Krušné hory Mts., Northern Bohemia. From the geological point of view, it is a part of the Krušné hory crystalline complex formed by meta-igneous and sedimentary rocks (Bárta et al. 1973). The area belongs to the district of a moderately cold climate. Mean annual temperature is 5.0 °C, annual precipitation is 984 mm (Fláje meteorological station, 50-years average, 1901—50). Woodrush beech forests (*Luzulo-Fagion*) and waterlogged spruce forests (*Bazzanio-Piceetum*) represent the units of the reconstructed natural vegetation (Mikyška et al. 1972).

The study site was located 1 km SW from the westernmost shore of the Fláje reservoir, district of Litvínov (50.36 N, 13.37 E), at the altitude of 840 m.

Two different habitats were investigated:

a) A moist meadow with a small brook flowing through (further referred to as site I). — Locally wet soil prevented the habitat from being absolutely dominated by *C. villosa* cover of which varied from 0 to 100 % within the site (estimated in 0.25 m^2 plots). The floristic composition of the community was similar to that of *Junco effusi-Calamagrostietum villosae* Sýkora 1983.

b) The deforested site completely dominated by *C. villosa* (site II). — The cover of green tillers varied from 5 to 70 %, being thus mostly lower than the cover of litter accumulated on the soil surface.

METHODS

The research was conducted in the period of full vegetation development (June-July 1989). Each site (I, II) was sampled by 20 randomly located quadrats of 0.25 m^2. In order to obtain data on frequency, total species composition was recorded in each plot. The relationships between *C. villosa* and the performance of the other species were further studied in the site I. Fifteen quadrats of 0.25 m^2 located at random were harvested for biomass assesment.

Plant material was dried for 48 hours at 85 °C. For each plot, the following characteristics were recorded: the aboveground living biomass, litter, and the total aboveground biomass of *C. villosa*, the number of the other species, and biomass of each species present.

The species diversity H' (log base e) was computed using the Shannon formula (Peet 1974, Magurran 1988). Data on biomass were used as relative importance values. Evenness J' was expressed according to Pielou's formula (Pielou 1966). Sites I, II were compared using the analysis of species abundance distribution (May 1975, Magurran 1988).

The data were analysed using linear regression. The relationships of individual species to the performance of *C. villosa* were evaluated by Spearman's rank correlation coefficient (Sokal et Rohlf 1981).

The nomenclature follows Rothmaler (1986).

RESULTS

Comparison of sites

The data on species occurrence are summarized in Table 1. There is obviously higher species richness in the moist meadow (site I), whether expressed in terms of the total number of species or mean species number per plot.

Rank abundance plots (May 1975, Begon et al. 1986, Van der Maarel 1988) for both sites are presented on Fig. 1. For the estimation of species abundances, the data on frequency were used. Small number of abundant species and the large proportion of rare species in site II indicate the log-series distribution of species abundance. However, the discrimination between models based on the shape of the rank-abundance plots only is difficult. To be certain it is necessary to formally test mathematical fit (Magurran 1988). The chi^2 test revealed that there was no significant difference between the observed and expected distribution with $P < 0.70$. It can, nevertheless, be concluded that the log-series is the better fit than the other distribution models. However, this is not the case of site I which may represent a transition to the log-normal distribution.

Diversity index α obtained from the log series (Williams 1964) is considered the best discriminator between sites when comparisons of species

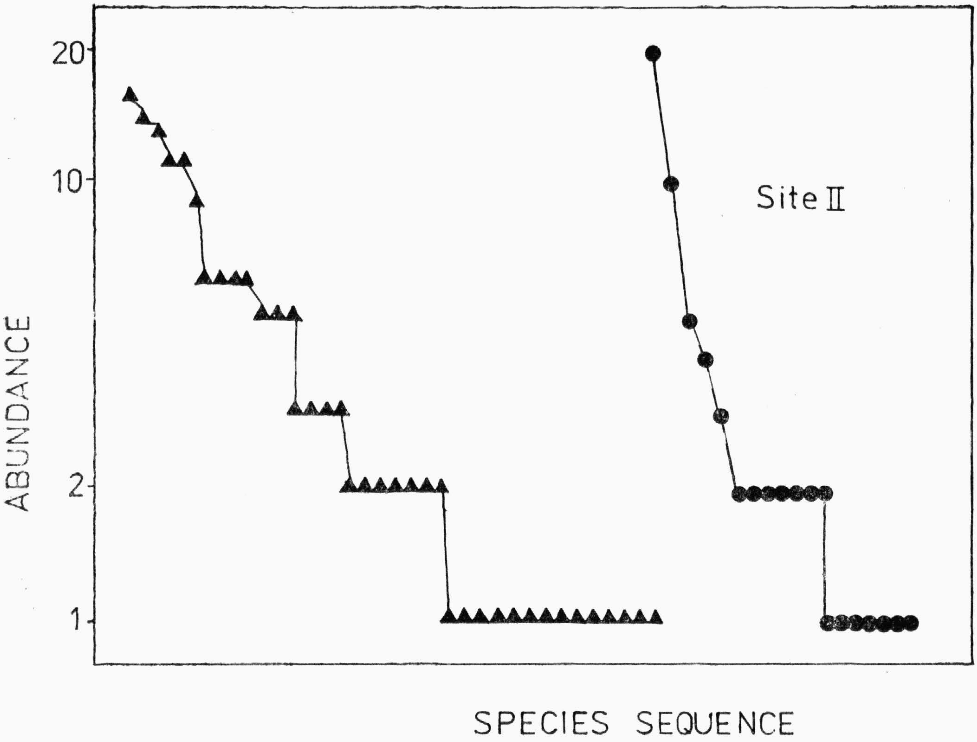

Fig. 1. — Rank abundance plots of the species in the moist meadow (I) and deforested site (II)

diversity are to be made (KEMPTON et TAYLOR 1974). Index α computed for site I (16.19) is clearly different from that obtained for site II (9.35). However, the Shannon index H' calculated on the basis of species frequency also revealed that the sites are significantly different in terms of the diversity (H' = 3.22 and 2.40, respectively, $P < 0.001$, *t* test).

Performance of the other species in *Calamagrostis villosa* stands

The biomass values found are presented in Table 2. The number of the other species plotted against the total biomass of *C. villosa* shows an obvious decrease. On the contrary, evenness J' of the other species increases with the *C. villosa* total biomass (Fig. 2). Thus, the stronger the dominance of *C. villosa*, the lower the probability that a strong dominant appears among the other species.

The decrease in species number is compensated by the increase of species evenness. This is reflected by the pattern of species diversity H' which does not show any significant relation to the performance of *C. villosa* (Fig. 3).

The biomass of the other species is negatively correlated with the biomass of *C. villosa* (Fig. 3). The relation is similar to that found between species number and the *C. villosa* biomass (Fig. 2).

The proportion of litter increases with the *C. villosa* total aboveground biomass (Fig. 4). Table 3 presents an attempt to separate the effect of litter

Table 2. Biomass values (g) of *Calamagrostis villosa* and the other species recorded in harvested plots in the site I

Plot no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Calamagrostis villosa:															
living aboveground biomass	1.9	17.8	16.6	20.5	25.2	47.8	71.3	67.5	65.9	50.0	51.0	97.0	155.3	88.5	150.6
litter	0.5	—	3.1	8.2	35.4	32.1	31.1	70.4	98.7	125.8	169.9	183.8	136.7	234.0	179.8
total aboveground biomass	2.4	17.8	19.7	28.7	60.6	99.9	102.4	137.9	164.6	175.8	220.9	280.8	292.0	322.5	330.4
other species:															
total biomass	55.5	76.1	62.6	68.3	90.1	25.3	47.9	25.8	15.2	5.1	27.0	3.9	16.5	15.5	24.5
number of species	20	9	14	12	14	6	8	5	4	4	7	2	6	3	7
species diversity H'	2.11	1.08	1.44	1.36	1.50	0.85	1.08	1.07	0.57	1.17	1.26	0.68	1.23	0.75	1.55
species evenness J'	0.70	0.49	0.54	0.55	0.56	0.47	0.52	0.66	0.41	0.84	0.64	0.98	0.68	0.68	0.79
Senecio fuchsii	2.1	0.1	1.3	1.9	<0.1	19.5	30.2	14.1	0.4	2.2	5.8	2.2	4.8	6.4	4.6
Epilobium angustifolium	3.1	—	4.5	3.2	52.3	2.6	5.9	—	2.3	—	0.9	—	0.5	—	1.3
Cirsium palustre	2.7	1.0	—	—	6.5	0.4	0.1	3.7	—	0.6	—	—	6.4	8.8	4.1
Myosotis laxiflora	0.7	0.1	—	0.7	0.4	—	—	0.4	—	0.4	—	—	—	—	7.7
Holcus mollis	7.2	35.0	37.3	39.5	—	1.4	—	—	—	—	12.4	—	—	—	—
Juncus effusus	4.7	7.7	6.6	9.7	1.2	0.6	—	—	—	—	—	—	—	—	—
Galeopsis bifida	0.1	1.0	—	—	3.8	—	1.0	—	—	—	0.4	—	—	—	<0.1
Moehringia trinervia	0.2	<0.1	0.3	<0.1	5.0	—	9.1	—	—	—	—	—	—	—	—
Epilobium adenocaulon	2.0	<0.1	0.5	0.4	—	—	<0.1	—	—	—	—	—	0.1	—	—
Equisetum sylvaticum	1.5	—	—	1.1	0.9	—	—	7.4	12.4	—	—	—	—	—	6.5
Deschampsia caespitosa	—	31.1	5.1	10.4	—	0.9	—	—	—	—	—	—	—	—	—
Rubus idaeus	—	—	—	—	—	—	0.1	—	—	—	7.2	1.7	—	—	
Cardamine pratensis	<0.1	—	0.3	—	0.1	—	—	—	—	—	—	—	—	—	—
Urtica dioica	1.2	—	—	0.6	10.1	—	—	—	—	—	—	—	—	—	—
Maianthemum bifolium	—	—	—	—	0.4	—	—	—	—	—	0.1	—	—	—	—
Oxalis acetosella	—	—	—	—	—	—	—	—	0.1	—	—	—	<0.1	—	—
Galium palustre	—	—	—	—	—	—	—	—	—	—	—	—	—	0.3	0.4
Dryopteris austriaca	—	—	—	—	1.2	—	—	—	—	—	—	—	4.8	—	—
Veronica serpyllifolia	0.1	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—
Ranunculus repens	21.6	—	5.1	—	—	—	—	—	—	—	—	—	—	—	—
Epilobium palustre	0.3	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—
E_0: *Brachythecium rutabulum*	0.6	—	0.4	0.7	7.9	—	—	—	—	—	—	—	—	—	—
Plagiomnium elatum	0.1	—	0.4	0.1	—	—	—	—	—	—	—	—	—	—	—

Present in one plot only: *Dactylis glomerata* 0.1 (No. 1), *Lychnis flos-cuculi* 3.1 (1), *Cirsium arvense* 4.2 (1), *Taraxacum officinale* 0.3 (5), *Deschampsia flexuosa* 1.6 (7), *Galeopsis pubescens* 1.9 (10), *Trientalis europaea* 0.2 (11).

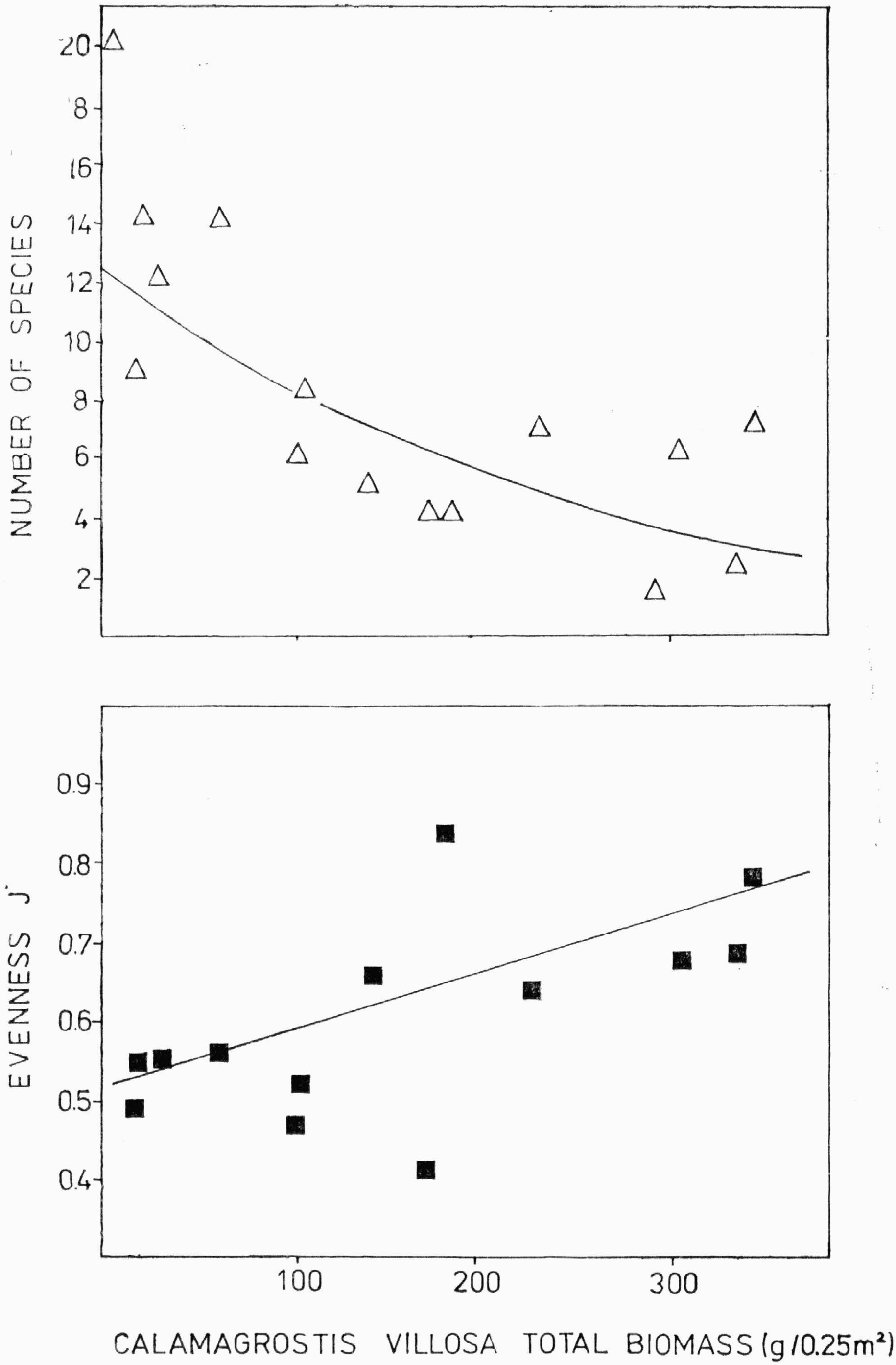

Fig. 2. — Number of species and evenness J' of the other species related to *C. villosa* biomass. △r = −0.74, P < 0.01, $y = e^{-0.0039x+2.512}$ (only exponential equation was used to fit the curve), ■ r = 0.57, P < 0.05, y = 0.0007x + 0.52.

Table 3. — Relationship between the performance of the other species and *Calamagrostis villosa* biomass expressed by correlation coefficients. $P < 0.05$, bold-faced types — $P < 0.01$, NS — non-significant

		Biomass of *Calamagrostis villosa*		
		total	living	litter
Performance of the other species	number of species	**−0.74**	−0.56	**−0.75**
	total biomass	**−0.71**	−0.53	**−0.73**
	species diversity	NS	NS	NS

from that of living biomass on the performance of the other species. Both the number of the other species and their total biomass are more closely related to the amount of *C. villosa* litter ($P < 0.01$) than to its living biomass ($P < 0.05$).

The species performance of which, expressed in terms of biomass, shows a significant relation to some of the *C. villosa* parameters are listed in Table 4. Negative correlations with both litter and living biomass of *C. villosa* were also apparent in most of the remaining species but these were not statistically significant. With respect to the growth forms the following conclusions may be drawn:

All the creeping and prostrate plant species (with the exception of *Ranunculus repens*, the relation of which to the litter was non-significant) are negatively correlated with the *C. villosa* biomass. Graminoids provided similar results; moreover, most relations within this group are significant at the

Table 4. — Relationship of the species to the biomass of *Calamagrostis villosa* expressed by the values of Spearman's rank correlation coefficient. $P < 0.05$, bold-faced types — $P < 0.01$, NS — non-significant. Only the species performance of which shows significant relation to *C. villosa* were included.

	Biomass of *Calamagrostis villosa*		
	living	litter	total
a) erect herbs, lianes:			
Senecio fuchsii	0.54	NS	NS
Galium palustre	NS	0.54	0.59
Epilobium adenocaulon	NS	**−0.65**	−0.58
Urtica dioica	−0.53	NS	−.53
Epilobium palustre	−0.59	NS	−0.55
Veronica serpyllifolia	−0.58	NS	−0.54
b) graminoids:			
Holcus mollis	**−0.75**	−0.64	**−0.66**
Juncus effusus	**−0.85**	**−0.81**	**−0.85**
Deschampsia caespitosa	−0.60	**−0.65**	−0.61
c) prostrate plants:			
Moehringia trinervia	−0.58	**−0.73**	**−0.73**
Ranunculus repens	−0.59	NS	−0.55
Brachythecium rutabulum	**−0.66**	−0.52	−0.63
Plagiomnium elatum	**−0.65**	−0.58	−0.61

probability level of $P < 0.01$. The values of Spearman's rank correlation coefficient computed for *Juncus effusus* and *Holcus mollis* indicate the strongest negative correlation with *C. villosa* of all the species investigated.

Erect forbs clearly escape from the influence of the *C. villosa* litter which is reflected by mostly non-significant relations. In addition, this is the only group where positive correlations were revealed (*Senecio fuchsii*, *Galium palustre*). However, even within erect forbs 70 % of the species are negatively correlated with the *C. villosa* total biomass.

DISCUSSION

Despite frequent criticism (HURLBERT 1971, PEET 1974), diversity measures are considered a convenient tool in ecological research (MAGURRAN 1988). Diversity indices calculation of which is based on species richness (α, H') are appropriate for discrimination between sites (TAYLOR 1978 cited by MAGURRAN 1988). Evenness and dominance are less sensitive for these purposes. Whereas sites I and II were significantly discriminated using H', the differences in evenness J' were small (0.88 vs. 0.82).

Comparison of sites I and II was based on the species frequency which is a common technique for estimating species abundance (MAGURRAN 1988). The number of plots that a species occupied was summed to obtain its total abundance. Generally, this approach must be treated with caution for it will often lead to an underestimation of the abundance of the commonest species. However, for the purposes of this study, *C. villosa* was excluded from the comparison and understood as a part of the environment of the other species. Moreover, no other species present in the community reached remarkable dominance. Frequency may thus be used as a measure of species abundance.

The shape and slope of rank-abundance curves can be interpreted with the help of different distribution functions (MAY 1975, VAN DER MAAREL 1988). The species abundance distribution found in the deforested site dominated by *C. villosa* is comparable to the log-series distribution. It is expected to occur in simple stressed environments where one or few factors are important in determining the number and abundance of species present (MAY 1975). The dominance of *C. villosa* may thus be considered the factor decisive for occurrence of the other species in the deforested site.

MAGURRAN (1981 cited in 1988) showed that the plant species abundances in a conifer plantation in which light was a limiting factor followed a log-series distribution. KEMPTON et TAYLOR (1974) concluded that insect samples from stable environment were best fitted by the log-series whereas in changing environment the log-normal distribution was preferred. From the viewpoint of the other species, *Calamagrostis villosa* stands represent a stable environment.

According to VAN DER MAAREL (1988) the log-series distributions are the most realistic distribution types for plant communities. On the other hand, some results available from insect communities suggest that species-abundance relationships are of relatively little practical importance for studying community ecology (JAROŠÍK 1990).

Species richness is related to productivity with maximum richness occurring at moderate levels of productivity (GRIME 1979, TILMAN 1982). The study

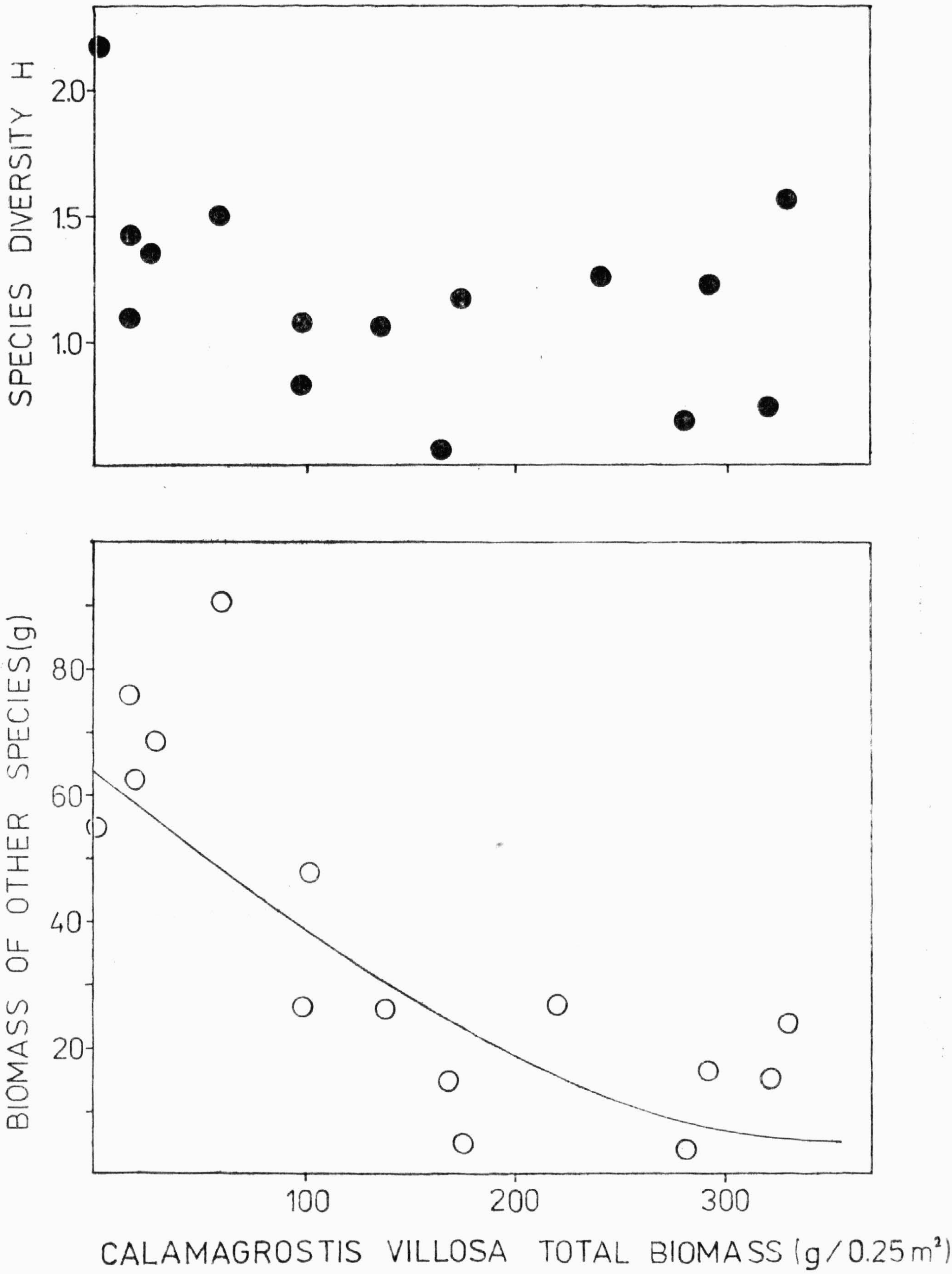

Fig. 3. — Diversity H' and biomass of the other species plotted against *Calamagrostis villosa* total biomass. ● NS, ○ $r = -0.71$, $P < 0.01$, $y = e^{-0.057x+4.148}$ (only exponential equation was used to fit the curve).

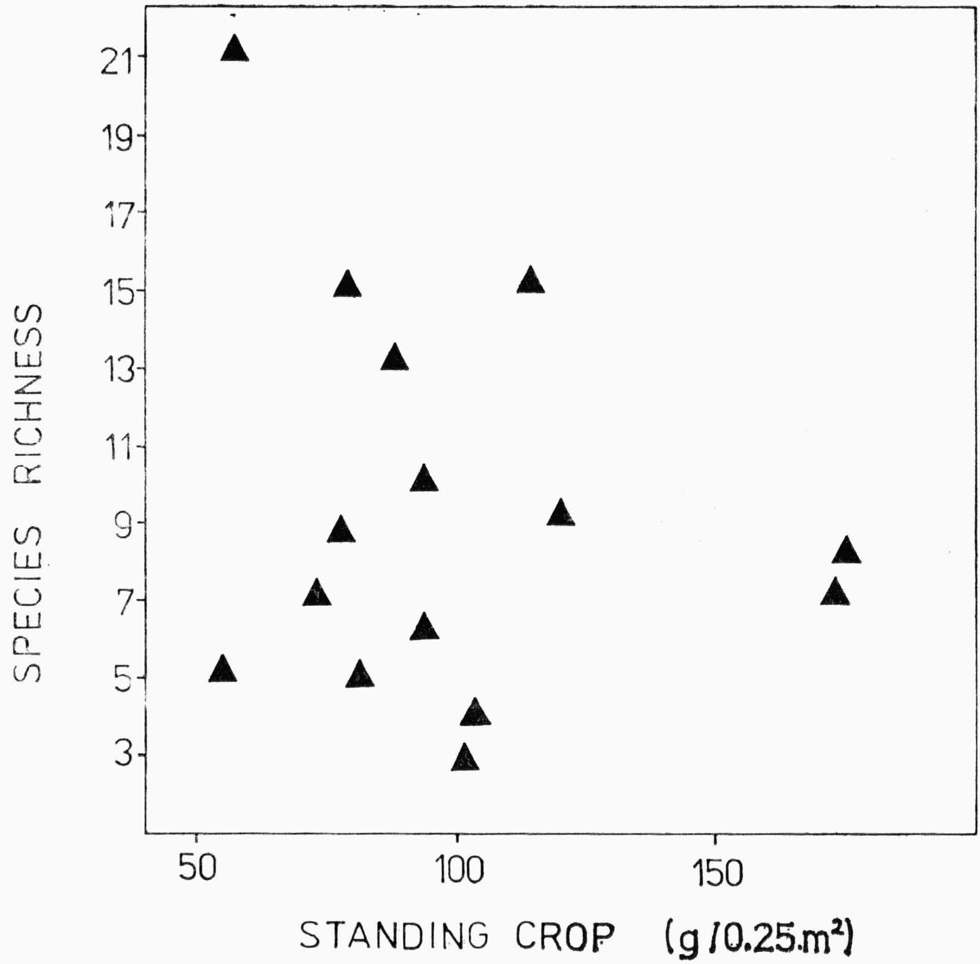

Fig. 4. — Total species richness of the community related to its standing crop (the living biomass of *Calamagrostis villosa* and the total biomass of the other species).

of Moore et Keddy (1989), conducted at wetlands, confirmed this model only at a coarse level of organization — among vegetation types. Within vegetation types, no significant relation between species richness and standing crop was found. Fig. 4 presents the same relationship in the *Calamagrostis villosa* stand. The results are directly comparable with that of Moore et Keddy (l.c.) because of the same sampling methods used (biomass analysis in 15 plots of 0.5 × 0.5 m). At higher levels of productivity, the number of species is reduced. It is unfortunately not possible to decide unequivocally whether it reaches maximum value at moderate level of productivity. The results obtained in the *C. villosa* community do not confirm the hypothesis of Moore et Keddy (1989). It seems necessary to seek further evidence in different types of environment.

The importance of the scale used in an ecological study (Krahulec et Lepš 1989, Moore et Keddy 1989) may, however, be demonstrated. At

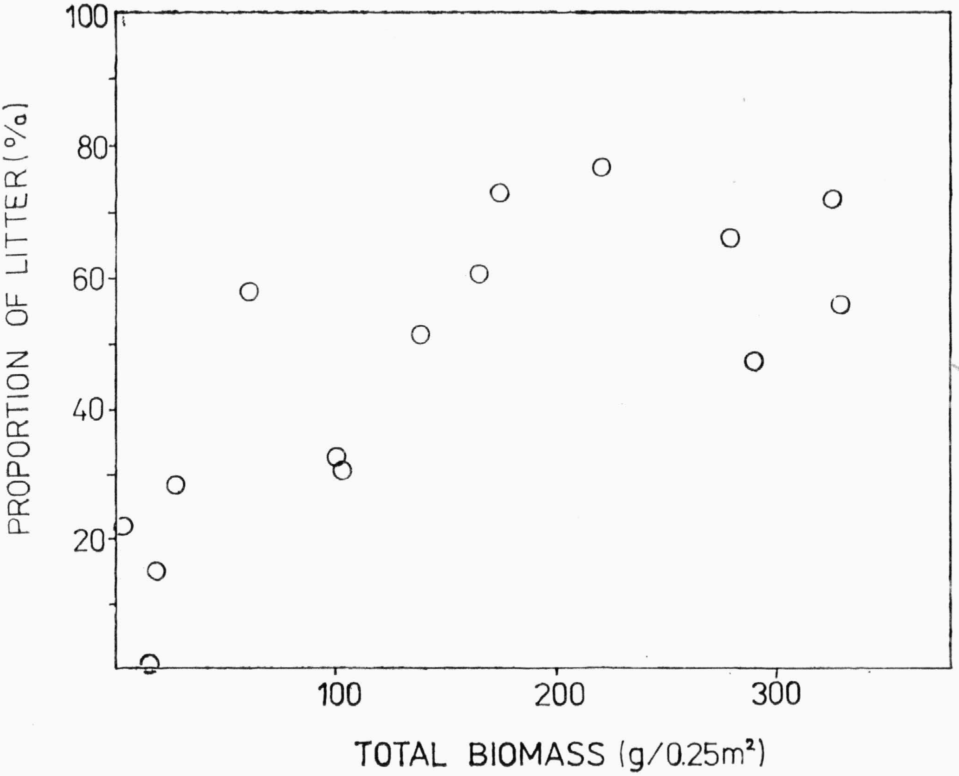

Fig. 5. — Proportion of *Calamatrostis villosa* litter related to its total aboveground biomass.

the level of sites, the dominance of *C. villosa* obviously reduced the diversity of the other species. On the other hand, at the within-community level it was not possible to relate species diversity to the performance of *C. villosa.*

Litter accumulation was found to be probably responsible for the decrease of the species number in the abandoned chalk grasslands (WILLEMS 1984). The amount of litter gradually increased to about 60 % of the total aboveground biomass, the value which is comparable to 50—80 % observed in *C. villosa* stands (Fig. 5). Litter prevents germination and/or establishment of many plant species (SILVERTOWN 1980 cited by WILLEMS 1984).

In a number of investigations (WATT 1970 cited by SYDES et GRIME 1981a, GRIME 1973, AL-MUFTI et al. 1977) persistent litter has been suggested to have damaging effect upon vegetation. A negative correlation between total shoot biomass of the woodland floor plants and the amount of tree litter was reported by SYDES et GRIME (1981a).

In general, the following species showed successful performance in the communities invaded by *C. villosa*: (a) tall forbs escaping from the influence of litter by its easier penetration and/or fast growth and being capable of successful competition for light (*Senecio fuchsii*, *Epilobium angustifolium*), (b) species which are able to spread vegetatively and produce their own litter (*Holcus mollis*), and (c) species, the occurrence of which is made possible by ecological factors of the habitat, especially the moisture (*Juncus effusus, Deschampsia caespitosa, Cirsium palustre*).

SYDES et GRIME (1981a) consider two factors of particular importance in determining the distribution of plants on the woodland floor, the first being the influence of topography upon the distribution of the litter, and the second one the different ability of species to penetrate through the persisting litter. Those species that remained relatively abundant in plots containing large amount of litter showed clear adaptations of shoot structure for penetrating through litter (*Galeobdolon luteum, Anemone nemorosa*). On the other hand, there was an abrupt decline in the biomass with the increasing mass of tree litter among grasses (*Holcus mollis, Poa trivialis, Milium effusum*). This has been ascribed to straggling growth-form and weak mesophytic leaves in the grasses, which make the emergence more difficult (SYDES et GRIME 1981b). Clearly, these conclusions are in accordance with those presented in this paper: The strongest negative correlations between species performance and the amount of litter were typical of graminoids whereas all but one erect herbs were not significantly supressed by the litter.

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SOUHRN

Vliv dominance *Calamagrostis villosa* na ostatní druhy přítomné ve společenstvech imisních holin byl studován v Krušných horách. Na dvou odlišných stanovištích byly zjištěny hodnoty frekvence přítomných druhů v náhodně rozmístěných ploškách 0,5 × 0,5 m. Vlhká louka s protékajícím potokem, na níž se pokryvnost *C. villosa* pohybuje v rozmezí 0—100 %, má vyšší druhovou diverzitu než odlesněné stanoviště kompletně zarostlé *C. villosa*. Použité indexy druhové diverzity (α, H') umožnily statisticky vysoce průkazné rozlišení stanovišť. Distribuce druhové početnosti se blíží logaritmické řadě; výrazněji patrné je to u odlesněného stanoviště, kde je několik málo hojných druhů doprovázeno větším počtem druhů vzácných.

Na vlhké louce byla sledována úroveň uvnitř společenstva. Z 15 náhodně rozmístěných čtverců 0,5 × 0,5 m byla odebrána biomasa *C. villosa* a ostatních druhů. Počet ostatních druhů i jejich celková biomasa klesá s biomasou *C. villosa*, přičemž obě charakteristiky vykazují průkazně užší vztah ke stařině *C. villosa* ($P < 0{,}01$) než k její živé biomase ($P < 0{,}05$). Druhová vyrovnanost J' naopak lineárně stoupá s narůstající biomasou třtiny. Mezi druhovou diverzitou H' ostatních druhů a biomasou třtiny nebyl nalezen žádný vztah. Na tom lze demonstrovat důležitost zvolené úrovně studia — na úrovni mezi společenstvy přítomnost *C. villosa* výrazně snižuje diverzitu ostatních druhů, zatímco na úrovni uvnitř společenstva nikoli; pokles v počtu druhů je tu kompenzován zvýšením vyrovnanosti.

Výskyt většiny druhů je negativně korelován s *C. villosa*. Pouze ve skupině vysokých bylin, schopných uniknout vlivu stařiny adaptacemi k jejímu proražení, rychlým růstem a následně obstát v kompetici o světlo, byla u některých druhů zjištěna pozitivní korelace (např. *Senecio fuchsii*). Kromě takových druhů jsou v porostech *C. villosa* schopny se uplatnit druhy intenzivně se vegetativně šířící a vytvářející vlastní stařinu (*Holcus mollis*) nebo ty, jejichž výskyt je umožněn lokálním působením ekologických faktorů, zejména vlhkosti (*Juncus effusus, Deschampsia caespitosa, Cirsium palustre*).

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