Preslia, Praha, 65:1-20, 1993

What do we know about *Calamagrostis villosa*? - A review of the species behaviour in secondary habitats

Co víme o chování druhu *Calamagrostis villosa* na druhotných stanovištích?

Petr Pyšek

Institute of Applied Ecology, University of Agriculture Prague, CZ-281 63 Kostelec nad Černými lesy, Czech Republic

Pyšek P. (1993): What do we know about *Calamagrostis villosa*? - A review of the species behaviour in secondary habitats. - Preslia, Praha, 65:1-20.

Keywords: *Calamagrostis villosa*, biology, population characteristics, phytosociology, response to environmental factors, succession, deforested areas, air pollution, Krušné hory Mts., Czech Republic

Air pollution-caused deforestation in central European mountain regions created a new ecological situation. Vast areas were, after spruce forest damage, colonized by an expansive rhizomatous grass, *Calamagrostis villosa*. Not surprisingly, this species attracted considerable research attention, especially at the turn of the eighties and nineties. This paper summarizes the results achieved so far by studies focused upon the autecology of *C. villosa* and the vegetation of deforested spots. The current state of knowledge on phytosociology, population biology (plant dry mass production, reproductive characteristics, response to perturbations), response to environmental factors, competitive relationships with other species, and succession is reviewed, and outputs for the forest management authorities and possible directions of future research are recommended.

Introduction

In central Europe, atmospheric SO_2 pollution has caused considerable changes in landscape, especially in regions affected by winds coming from coal mining areas (e.g. Krause 1989, Fuhrer 1990). The northern part of the Czech Republic has been suffering from the strong air pollution for last several decades and the damage caused there is extremely striking as this region represents an otherwise relatively undisturbed mountain environment. Forest decline and subsequent timber extraction have lead to the creation of new habitats available for colonization. Some species have adapted to the changing environment better than the others; among the most successful is *Calamagrostis villosa*, an expansive perennial grass (Samek 1988, Jakrlová 1989a, Pyšek 1990, 1993a). This species' success is determined by two kinds of processes running simultaneously in the present central European mountain landscape:

(a) Increase in vigour and cover in existing sites. *C. villosa* is a dominant understorey species of natural spruce forests, and is being favoured by the locally changed conditions following the forest dieback (Samek 1988, Pyšek 1991).

(b) Simultaneously, the species is expanding into new habitats (Jakrlová 1989a,b).

Vol. 64 No. 4 (p. 289-384) editum 22 February 1993

This large-scale "experiment" unintentionally carried out by man in the central European mountains provided us with a unique opportunity to follow the expansion of a native species into secondary habitats and compare its behaviour with that in the primary habitats in close vicinity. Not surprisingly, there has been and still is an extraordinary research effort directed at *C. villosa* (Table 1), especially in the Czech Republic whose mountain areas have been locally affected by air pollution to a critical extent. This research was triggered by two stimuli, (a) practically motivated effort to assess the effect of grass cover on tree saplings used for replantations, and (b) scientific interest in the natural situation providing nearly monospecific clonal stands of a species with considerable expansive potential and internal population dynamics.

This paper represents an attempt to summarize what the research in *C. villosa* has brought so far and how this "ecological challenge" was faced. Finally, not only what we do know but also what we do not know will be discussed. As the author is one of those involved in the research, the question being addressed here, i.e. whether the results obtained up to now are worthy of the time and energy spent on the problem, is to be answered by the reader.

Study species - description and characteristics

Calamagrostis villosa (Chaix) J. F. Gmelin (*Poaceae*) is a rhizomatous grass perennial (Fig. 1) with flowering shoots reaching up to 50-100 (-150) cm in height, dark-green leaves, 3-8 mm wide (Conert 1989, see Grulich 1986 for determination characters). The species forms dense system of rhizomes occupying soil profile up to the depth of 15-20 cm. Roots arise at nodes of both horizontal and vertical rhizomes, most of which possess lateral branches and fibrous roots. The underground organs thus form an extremely compact

Table 1. Overview of studies on *Calamagrostis villosa* in secondary habitats. Only studies based on original data are included. Thorough analysis of the given area of interest is indicated by ++, problems that were only touched are indicated by +. 1 - phytosociology, 2 - population characteristics, 3 - response to environmental factors, 4 - relationships with other species, 5 - succession (number of years for which the succession was studied or inferred is given), 6 - response to perturbations, 7 - practical management.

Source	1	2	3	4	5	6	7
Huml 1970		+		++			
Lokvenc 1971	+	+					++
Sýkora 1983	++						
Šrůtek et Samek 1987	+				++50		
Fiala, Jakrlová et Zelená 1989		++	+				
Jakrlová 1989		+					+
Fiala 1989		++					
Pyšek 1990		+		++			
Pyšek 1991		++	+				
Morávková-Lipnická 1991	+	++		+	+3	++	+
Pyšek 1992a		++	+	++	++15		+
Pyšek 1993a	+		++	++			
Pyšek 1993b			++	++	+15		

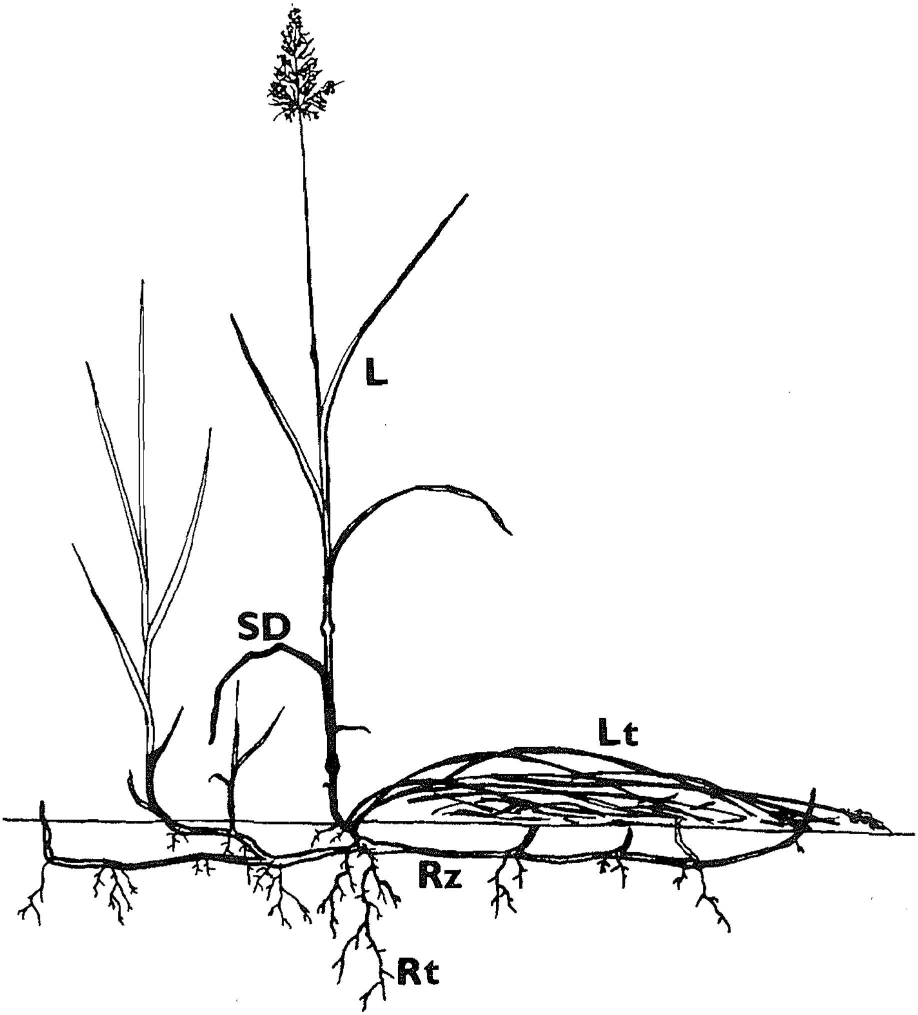

Fig. 1. *Calamagrostis villosa* (Chaix) J. F. Gmelin. L - living above-ground plant mass, SD - standing dead, Lt - litter, Rz - rhizomes, Rt - roots (redrawn from Morávková-Lipnická 1991).

± 5 cm thick turf at the soil surface (Söyrinki 1954-56, Fiala 1989).

In mountain areas of the Czech Republic, young shoots emerge in April and May, flowering occurs between June and August, and shoots die-off from September on, forming a litter layer accumulated on the soil surface.

Intraspecific taxa, mostly evaluated at the variety level, have been distinguished on the basis of leaf characters and spikelet features (Heine et Leuschner 1972). Several cytotypes (2n = 28, 42, 56, 70) have been reported (Májovský, Murín et al. 1987).

Plant geography, phytosociology

Distribution

Distribution area of *C. villosa* covers mountain ranges of central and southeastern Europe (the species occurs in France, Germany, Switzerland, Austria, Italy, Poland, Czech Republic, Slovakia, Romania, Bulgaria, former Yugoslavia) and the Carpathian region of the European part of the former Soviet Union (see Meusel et Buhl 1962, Conert 1989 for distribution maps). Its altitudinal range varies from less than 100 m (Lausitz, Germany) to more than 2500 m (localities in the Alps, Conert 1989). The northern and western boundaries of its distribution lie in central Europe (Conert 1989). For details on distribution in the Czech Republic see e.g. Mladý (1978), Sofron (1985), and Chrtek (1991); in this territory the species may be considered an Alpine migrant (Mladý 1978) whose distribution closely fits that of Norway spruce (*Picea abies*). *C. villosa* is very common both in the Sudeten and Carpathian mountain ranges. In the eastern part of the latter, however, there is a distribution gap which corresponds to the gap in the occurrence of Norway spruce. However, recent reports from the Biesczady Mountains, Poland, a mountain range located in this gap area, have shown that, although not having been mentioned from there in older reports, the species seems to be increasing its distribution and abundance and, at present occurs in a variety of species-poor communities there (Jeník 1984).

C. villosa prefers deep, humus-rich, well-drained, nutrient- and base- poor soils, loamy to clayey, it grows also on peat. It is tolerant of acid soils; on calcareous rocks it occurs only where raw humus exists (Conert 1989, Sofron 1981, Samek 1988).

In central Europe, it occurs as a dominant species forming closed stands or understorey cover (Hartmann et Jahn 1967, Mikyška 1968, 1972) in various habitat types; phytosociologically, these stands have been classified into several community types, mostly at the association level, names of which are given in the following survey:

A. More or less natural occurrence above timberline

1. *Crepido-Calamagrostietum villosae* (Zlatník 1925) Jeník 1961
   [*Calamagrostion villosae, Calamagrostietalia villosae, Mulgedio-Aconitetea*] - the Krkonoše Mountains
2. *Sileno-Calamagrostietum villosae* Jeník, Bureš et Burešová 1980
   [*Calamagrostion villosae, Calamagrostietalia villosae, Mulgedio-Aconitetea*] - the Hrubý Jeseník Mts.
3. community *Veratrum lobelianum-Calamagrostis villosa* Sýkora 1983
   [*Calamagrostietalia villosae, Mulgedio-Aconitetea*] - community of forest margins and transitions between forests and mountain meadows

B. Natural (climax) forest communities

4. *Calamagrostio villosae-Piceetum* (Tüxen 1937) Hartmann 1953
   [*Piceion excelsae, Piceetalia excelsae, Vaccinio-Piceetea*]
5. *Calamagrostio villosae-Fagetum* Mikyška 1972
   [*Luzulo-Fagion, Fagetalia, Querco-Fagetea*]
6. *Calamagrostio villosae-Pinetum* Staszk. 1958
   [*Dicrano-Pinion, Piceetalia excelsae, Vaccinio-Piceetea*]
7. *Calamagrostio villosae-Quercetum* Passarge 1969
   [*Quercion robori-petraeae, Quercetalia robori-petraeae, Querco-Fagetea*]

C. Secondary occurrence after deforestation

8. *Junco effusi-Calamagrostietum villosae* Sýkora 1983
[*Epilobion angustifolii, Atropetalia, Epilobietea angustifolii*]
9. *Myrtillo-Avenelletum flexuosae* (Schlüter 1966) Passarge 1984, type with *Calamagrostis villosa* - community of forest clearings in central Europe

Floristic composition

Floristic composition of communities with predominating *C. villosa* is compared in Table 2 which includes the above mentioned habitat types in a variety of geographical regions. Only two species are accompanying *C. villosa* in each relevé set, regardless of community type and region: *Vaccinium myrtillus* and *Deschampsia flexuosa*. The forest species occurring in the spruce understorey together with *C. villosa* may be divided into 2 groups:

(a) Those that do not occur in deforested sites originating after forest die-back, e.g. *Homogyne alpina, Trientalis europaea, Blechnum spicant, Luzula pilosa.*

(b) However, the majority of these species are more or less able to persist in *Calamagrostis*-invaded stands after timber removal and/or to spread with expanding *C. villosa* into neighbouring areas: *Vaccinium myrtillus, Deschampsia flexuosa, Oxalis acetosella, Athyrium filix-femina, Senecio fuchsii, Dryopteris dilatata, Galium harcynicum.*

The latter group of species is completed by those species that persist in deforested spots as remnants of originally present vegetation or migrate from surrounding habitats (*Nardus stricta, Polygonum bistorta, Potentilla erecta, Chamerion angustifolium, Juncus effusus, Deschampsia caespitosa, Rubus idaeus*) or occur as a consequence of disturbances (*Urtica dioica, Rumex acetosella*).

The moss layer is obviously richer in forest habitats (Table 2). However, it may happen that it is ignored by some phytosociologists, especially by those not familiar with bryophytes, so that the data given in Table 2 should be treated with caution. Nevertheless, comparison of spruce forest with deforested sites carried out by the same author in the Šumava Mountains (Sofron 1981, 1985, columns E vs. J in Table 2) shows a striking decrease in both frequency and cover of bryophytes in deforested areas compared to the forest understorey.

Table 2. Comparison of communities with predominating *Calamagrostis villosa* from various regions and different habitat types. Constancy (expressed as a percentage of relevés in which the species occurred: V 81-100 %, IV 61-80 %, III 41-60% , II 21-40%, I 1-21%) and the range of values in the original relevé scale (7 ... Braun-Blanquet scale, 11 - Domin scale). Habitat types are indicated: ? above timberline, * spruce forests, ! deforested areas. Sources and the community phytosociological classification, if given by the original author: A: Burešová 1976, *Crepidi-Calamagrostietum villosae,* Krkonoše Mts., B: Berciková 1976, *Crepidi-Calamagrostietum villosae molinietosum caerulae* var. typicum, Krkonoše Mts., C - Jeník 1984, various community types, Biesczady Mts., D - Hartmann et Jahn (1967), *Calamagrostio villosae-Piceetum,* Harz, Sudeten Mountains, E - Sofron 1981, *Calamagrostio villosae-Piceetum,* Šumava Mts., Krušné hory Mts., Slavkovský les; F - Šrůtek et Samek 1987, Jizerské hory Mts., G - Pyšek 1993a, Krušné hory Mts., H - Andresová 1979, eastern Bohemia; I - Sýkora 1983, community *Veratrum lobelianum-Calamagrostis villosa,* Jizerské hory Mts., J - Sofron 1985, *Calamagrostietum villosae,* Šumava Mts.; K - Sýkora 1983, *Junco effusi-Calamagrostietum villosae,* Jizerské hory Mts.; L - Pyšek 1993a, Krušné hory Mts. Nomenclature follows Neuhäuslová et Kolbek (1982); n.g. - not given.

➡

Source	A	B	C	D	E	F	G	H	I	J	K	L
Habitat type	?	?	?	*	*	*	*	*	*/!	!	!	!
Number of relevés	10	10	8	52	20	18	6	10	8	7	10	5
Mean relevé area (m^2)	15	16	20	n.g.	233	n.g.	25	160	9.8	22.4	80	25
Mean cover E_1	100	100	85.6	n.g.	83.2	n.g.	76.7	89.6	95	85.7	95	95
Mean species number/relevé	5.6	21.7	9.1	11.3	8.2	n.g.	8.2	9.8	11.5	5	8.5	7.6
Total number of species	11	44	26	33	27	17	19	13	28	15	19	24
Altitude (100 m)	1400-1500	1300-1400	1250-1320	n.g.	950-1320	n.g.	850	320-600	900-1000	1200-1320	750-1040	800
Scale	11	7	7	7	11	cover	7	7	11	11	11	7
E_3												
Picea abies				V 2-5	V 8	V 35.5	V 3-4	V 3-5				
Sorbus aucuparia				II +-1	II 2-4	I 0.3						
E_2												
Picea abies				II +-3	II 2-3	I 1.0		V 3-5				
Sorbus aucuparia				III +-2	I 2							
E_1												
Calamagrostis villosa	V 8-10	V +-4	V 3-4	V +-5	V 5-10	V 61.1	V 1-5	V 4-5	V 8-10	V 5-9	V 9-10	V 3-5
Vaccinium myrtillus	III 2-4	V +-3	V 2-4	V +-4	IV +-6	V 13.9	III r-1	V +-3	II 2	III +-1	III +-5	I 1
Vaccinium vitis-idaea	I 1	I +	II +	I +-1	I 1	I +				I +		
Nardus stricta	II 2-4	III +-1		I +-2						III 1-4		
Polygonum bistorta	III 2-4	V +-2							II 2			
Homogyne alpina	III 2-3	V +-2	V +-2	III+-2	III 1-5	III 1.8				I 1		
Solidago virgaurea subsp. *minuta*	V 2-4	V +-2										
Veratrum lobelianum	IV 1-4	III +							V 2-6			
Gentiana asclepiadea		IV 1-2	II +-1									
Rumex alpestris		II +	II +	I +-2								
Senecio nemorensis		II +			I 4				III 1-4			
Polygonatum verticillatum			I +	I +	II +-2	I 1						
Allium victorialis		I +	I +									
Deschampsia flexuosa		V +-2		V +-4	V +-10	V 32.6	III r-2	IV 1-2	II 4-6	V 1-9	V 2-5	II 1-2
Silene vulgaris		V +-1	I +									
Luzula luzuloides		IV +-1	V +-1						II 1-2		I 2	
Potentilla erecta	I 2-4	IV +-1	III +-1						II 2-4	I +		
Trientalis europaea		III +-2		IV +-2	III 1-2	IV 1.4		I 1				
Melampyrum sylvaticum		III +-1		I +-1					IV +-3			
Calamagrostis arundinacea		II 1-2	IV +	I +-5							I +-4	
Maianthemum bifolium		II +-2		III +-2	III +-2	III 1.7			II 5-6			
Campanula rotundifolia		I+					I r					
Picea abies		I r	I +	II +-2	III +-2			I 1			I 2-3	
Phegopteris connectilis			II +-1	I +-1					II 1-4			
Sorbus aucuparia			II +	II +-1	II +-1		I r	I 1				
Huperzia selago			I +		I 1							
Rubus idaeus				I +-1	I 1	I +			III 1-5		IV 2-3	
Betula pendula								I 1	II +-2			II r
Anemone nemorosa					I 1				IV 3-4			
Athyrium filix-femina				I +-1	I 1	IV 1.7		I 2	II 2-3		II +-3	
Senecio fuchsii							IV r-2		II 2		I 1-2	II 3-4
Dryopteris dilatata				V +-2	V 1-4	V 4.1	V r-1	I 1-2		I 1	I 2-4	
Luzula sylvatica				III +-2	IV 1-7				I 2			
Oxalis acetosella				III +-2	IV 1-6	II 2.5	I +-1	I 1	III 4-6		II 1-6	
Blechnum spicant				III +-2	I 1	I +						
Fagus sylvatica					I 1		I r					
Galium saxatile				II +-1	I +-2	V 16.1	I +				III 2-5	I 1

Source	A	B	C	D	E	F	G	H	I	J	K	L
Luzula pilosa				I +	I 1	II 0.6						
Carex canescens				I +		II 0.6					II 1-3	
Deschampsia cespitosa						II +		I 1				III +-1
Juncus effusus						I +					V +-6	III r-+
Chamerion angustifolium				I +			IV r-+				IV 1-3	II 3
Rumex acetosa							I r					I r
Carex leporina							I r				II 1-4	I r
Luzula sudetica										I 2		I r
Luzula multiflora										I 1		I r
Athyrium distentifolium				II +-1	I 1-5							
Soldanella montana				I +-2	I 1-5							
Streptopus amplexifolius				II +-1	I +							
Lycopodium annotinum				II +-2	I 1-5							
Solidago virgaurea			IV +	I +-1								
Melampyrum pratense				I +-2						II 1		
E_0												
Rhytidiadelphus squarrosus	II 1-3	I +-1		I +-1	I +							
Polytrichum commune		I +-1		I +-3	II 1-5			I 2				
Polytrichum formosum			I 2	V +-3	III 1-8			IV r-1		I 1	II 3-6	
Dicranum scoparium				V +-3	IV 1-4			II +-2		I 1		
Sphagnum girgensohnii				II +-4	III 1-5			V 1-4		I 2		
Plagiothecium curvifolium				I +-1	II 1			I 1				
Barbilophozia lycopodioides				III +-2	II 1-2					I 1		
Barbilophozia barbata					I 1					I 5		
Plagiothecium undulatum				III +-2	I 3					I 1		
Pohlia nutans					I 1			II +-1				
Pleurozium schreberi				III +-2	I 1-5			II +-2		I 4		
Ptilidium ciliare				I +-1	I +					I 1		
Barbilophozia floerkei				II +-2	I 1							
Rhytidiadelphus loreus				II +-3	II 1-3							
Plagiochila asplenioides				I +-1				I 1				

Species occurring only in one relevé set

E_3: E: *Abies alba* I 3-5; G: *Fagus sylvatica* I 2; H: *Larix decidua* II +-2, *Betula pendula* IV +-3, *Pinus sylvestris* I 1-2.

E_2: H: *Fagus sylvatica* I +, *Rubus fruticosus* I +, *Frangula alnus* I +.

E_1: A: *Anthoxanthum odoratum* I +-2, *Deschampsia* alpicola* III +-3; B: *Hypochoeris uniflora* IV +-1, *Ranunculus aconitifolius* II +-1, *Achillea sudetica* I +, *Potentilla aurea* III +-1, *Crepis conyzifolia* III +, *Molinia caerulea* V 3-4, *Anthoxanthum odoratum* IV +-1, *Pulsatilla alba* III +-1, *Hieracium alpinum* III +-1, *Galium pumilum* III +-2, *Calluna vulgaris* II +-1, *Anemone narcissiflora* II +-1, *Carex bigelowii* II +-1, *Geum montanum* I +-1, *Arnica montana* I +-1, *Vaccinium uliginosum* I +, *Hieracium* sp. I +, *Carex pallescens* I +, *Rhinanthus minor* I +, *Omalotheca norvegica* I +; C: *Melampyrum herbichii* II +, *Empetrum hermaphroditum* I +, *Angelica sylvestris* II +, *Laserpitium alpinum* I +, *Astrantia major* I +, *Stellaria holostea* I +, *Sedum argutum* I +, *Salix silesiaca* I +, *Rosa pendulina* I +; D: *Veratrum album* I +-1, *Oreopteris limbosperma* I +-2; E: *Hieracium laevigatum* I 1; G: *Circaea* x *intermedia* II r, *Rubus* sp. II +; H: *Calamagrostis epigeios* I 1, *Lysimachia vulgaris* I 2, *Quercus robur* I 1; I: *Ranunculus platanifolius* II +-3, *Cirsium heterophyllum* II 3-5, *Phyteuma spicatum* II 2-3, *Trollius europaeus* I 2, *Thalictrum aquilegiifolium* I 3, *Digitalis grandiflora* I 1, *Fragaria vesca* I 3, *Salix caprea* I 2, *Acer pseudoplatanus* I 2, *Equisetum sylvaticum* II 5, *Melandrium rubrum* II +-2; J: *Carex brizoides* III 2-3; K: *Rumex acetosella* II 2-3; L: *Cirsium palustre* II r-1, *Galeopsis bifida* II r, *Stellaria media* I r, *Holcus mollis* II 1-3, *Stellaria graminea* I r, *Urtica dioica* I r, *Cirsium arvense* I r, *Agrostis stolonifera* I 2, *Carex spicata* I +, *Scrophularia nodosa* I r.

E_0: B: A: *Polytrichum alpinum* I+; *Dicranum fuscescens* I +, *Cetraria islandica* I +; E: *Barbilophozia hatcheri* I 1, *Dicranodontium denudatum* I 2-3, *Sphagnum nemoreum* I 3-5, *Plagiothecium denticulatum* I 1-3, *Plagiothecium succulentum* I 1, *Brachythecium rutabulum* I 1, *Ptilium crista-castrensis* I 1, *Calypogeia meylanii* I 1, *Calypogeia trichomanis* I 1, *Lophocolea heterophylla* I 1, *Cladonia macilenta* I 1, *Cladonia uncialis* I 1; H: *Mnium hornum* I 2, *Pellia epiphylla* I 2, *Sphagnum squarrosum* I +; I: *Polytrichum* sp. II +-1, *Dicranum polysetum* I 1, *Sphagnum fimbriatum* I 1, *Plagiomnium affine* I 1.

Floristic richness, expressed as the total number of species in a given relevé set, was compared between forests and deforested sites with *C. villosa* for three regions of the Czech Republic from which data on both these habitat types were available (Table 3). Neither a clear geographical pattern nor any trend in differences between forest communities and those of deforested sites were found. Replacing the *C. villosa*-dominated spruce forest understorey by more vigorous *C. villosa* stands does not seem to reduce substantially the species diversity, understood in terms of the total species number occurring in a site, as some species are replaced by previously absent newcomers. Only a few species are common for both habitat types within each region; floristic similarity (expressed by Jaccard index) is rather low, varying from 0.19-0.38 according to the region (Table 3). These results indicate that the number of species able to coexist in *C. villosa* stand is rather limited. The richest in species are such stands of *C. villosa* that occur in those sites above the timberline that are less exposed to extreme climatic condititions, i.e. strong wind and frost (Bercikovà 1976, Table 2).

However, considering the possible differences between particular authors in choice of sampling plots, their size, number of relevés, and their approach, i.e. the factors affecting the resulting number of species in a given relevé set, these comparisons must be considered as having only an exploratory value.

Population characteristics

Biomass production

Biomass production has been repeatedly estimated by the majority of investigators involved in studying the species (Table 1). Due to the confusion with terming particular "plant mass categories", some data sets are not directly comparable with each other. For the purpose of the present review, the categories in Table 4 are understood as follows:

(a) Total above-ground plant mass consists of (1) living above-ground plant mass, and (2) standing dead; to the present author it does not make much sense to distinguish between these two categories in such a comparison, as the proportion of standing dead is principally affected by the sampling date.

Table 3. Comparison of floristic richness of communities with predominating *Calamagrostis villosa*. Capital letter given in each cell corresponds to the original source from which the data were extracted and which are referred to in Table 2. Total number of species/number of species occurring exclusively in a given area and habitat (i.e. in a given cell) are shown. Total/common numbers of species are given row-wise for habitats and column-wise for regions. Floristic similarity of the bare spot communities with those of the forest understorey is expressed for each region using Jaccard coefficient.

	Šumava	Krušné hory	Jizerské hory	Total/common
Forest	E: 25/10	G: 19/8	F: 17/5	37/5
Deforested sites	J: 15/7	L: 24/12	K: 19/7	39/3
Total/common	32/7	30/7	22/10	
Similarity (%)	0.21	0.19	0.38	

(b) Dead plant mass accumulated on the soil surface (mainly in the previous year but, if sampled at the end of growing period, the current year's production may contribute as well) is termed litter; although it does not correspond perfectly to the meaning in which the term is being used in forestry, its ecological effect is the same.
(c) Total underground plant mass consists of rhizomes and roots.
(d) Total plant mass is the sum of (1) total above-ground plant mass, (2) total underground plant mass, and (3) litter, i.e. the sum of all plant mass categories present concurrently in the site.

Despite the different number and size of sampling plots used by earlier authors, some rough generalizations may be inferred from the data summarized in Table 4: (1) Plant mass production is higher in deforested sites than in forest habitats, i.e. it increases with increasing available light (Pyšek 1991, Morávková-Lipnická 1991). (2) Aboveground plant mass decreases with slope steepness (Fiala, Jakrlová et Zelená 1989, Jakrlová 1989a); this decrease is compensated by increased underground production so that the resulting total plant mass does not differ between sites. (3) Root/shoot ratio varies considerably. It tends to be higher in more extreme conditions (shading, slope steepness - Fiala, Jakrlová et Zelená 1989, Pyšek 1991, Fiala, Zelená et Jakrlová 1993). Generally, its values correspond to those commonly found in unfertilized, extensively used mountain meadows (Rychnovská 1985).

Stands of *C. villosa* in deforested sites have been reported to reach their maximum biomass in July (Fiala, Zelená et Jakrlová 1993) or in August (Morávková-Lipnická 1991). Maximum root increment occurs in August whereas maximum rhizome increment was found in August and September (Fiala, Zelená et Jakrlová 1993).

The architecture of the rhizome/root system has been investigated in detail (Fiala 1989). The majority of rhizomes and roots (at least 50% and sometimes greater than 90% was reported by Morávková-Lipnická 1991) are located in the upper 5 cm of soil (Huml 1970,

Table 4. Plant mass production of *Calamagrostis villosa* reported from various areas and different habitats. Original data were recalculated to g of dry weight/m^2 and the size of sampling plots used by the respective author may be found in original papers. Values were rounded and their statistical characteristics omitted from the Table as they may be found, if given, in original data sources. Habitat type in which the biomass was sampled is indicated: * original spruce forest, ! bare spot. Total aboveground plant mass is understood as a sum of living aboveground plant mass and standing dead. Total plant mass includes litter as well. Root/shoot ratio is the ratio between total underground/total aboveground plant mass. Sources: 1 - Fiedler et Höhne 1987:112; 2 - Lokvenc 1971:128; 3 - Pyšek 1991:11 (a - spruce forest, b - forest clearing, c - deforested sites); 4 - Fiala, Jakrlová et Zelená 1989:209, Jakrlová 1989a:61 (a - flat site, b - steep slope), 5 - Morávková-Lipnická 1991:71 (a - spruce forest, b - deforested sites).

Source	1	2	3	3	3	4	4	5	5
Site			a	b	c	a	b	a	b
Habitat type	*	!	*	*/!	!	!	!	*	!
Number of samples	30	?	6	6	6	10	10	6	6
Plant mass:									
Total aboveground	195	523	108	323	350	726	321	116	598
Litter	–	652	137	865	870	260	216	87	474
Total underground	197[1]	3461	1295	2149	2595	2854	3300	291	2250
Total plant mass	392	4636	1540	3337	3815	3840	3837	494	3322
Root/shoot ratio		6.6	11.9	2.8	2.1	3.9	10.3	2.5	3.8

[1]) only rhizomes

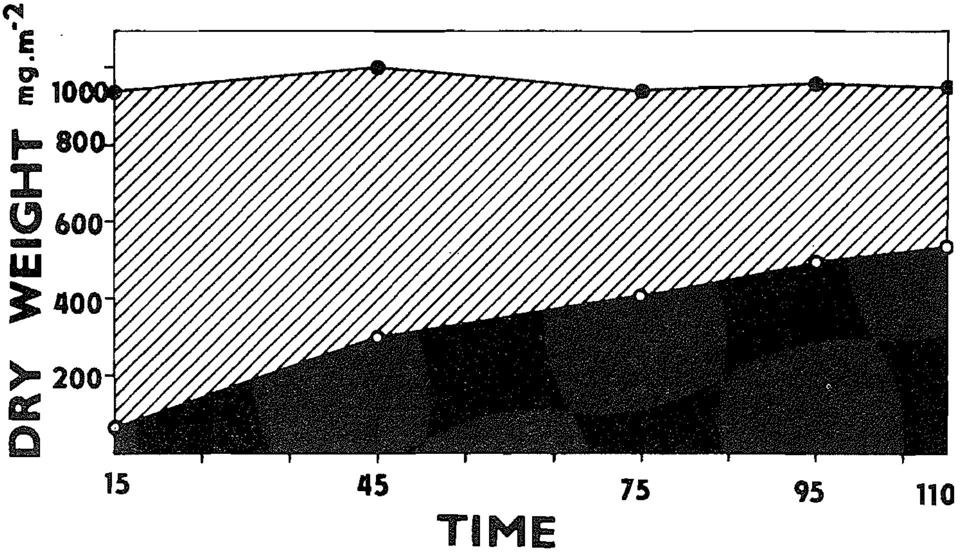

Fig. 2. Dynamics of the above-ground plant mass accumulation and litter decomposition (in mg/m^2) in *Calamagrostis villosa* during the growing period. Time axis is expressed as the number of days from April 1. The litter decomposition (hatched area) is more or less compensated by increasing production of above-ground plant mass (solid area). Recalculated on the basis of data from Morávková-Lipnická (1991: Tab. 15, mean values for all sites are shown).

Fiala 1989). High concentration of underground organs in the soil may be demonstrated by (a) 24.6% of soil volume being occupied by roots and rhizomes in the upper 5 cm layer (Fiala 1989, Fiala, Jakrlová et Zelená 1989) and, (b) 500-700 m of rhizomes/m^2 (Fiala 1989, but see Lokvenc 1971). Generally, 70-80% of total underground plant mass is formed by living rhizomes and roots (Fiala, Zelená et Jakrlová 1993). A form of rhizome growth was reported from deforested sites (Morávková-Lipnická 1991) differing from that occurring in forest in being shorter which leads to the forming of locally packed clusters of tillers.

Litter decomposition

Decomposition rate decreases during the growing period; in deforested areas of the Jizerské hory Mts. (Morávková-Lipnická 1991) it started in spring with 12.8 g/m^2, was lower in summer presumably due to a decrease in soil moisture (Moorhead et Reynolds 1989) and approximately 50% of the litter accumulated were decomposed by the onset of winter. After then, decomposition drops down during winter and increases dramatically in spring again. Laminae decompose more readily than culms. There was a considerable variation in litter decomposition between studied sites which might be explained by different microclimatic characteristics (Morávková-Lipnická 1991). Fig. 2 demonstrates that the sum of total above-ground plant mass and litter is being determined by two more or less balanced processes, i.e. (1) litter decomposition, and (2) accumulation of current-year plant mass. However, a more precise experiment using polythene bags (Moore et Chapman 1986) revealed that the half-life of litter decomposition was 1.1-1.5 years on the forest floor and 1.4-1.8 years in deforested sites (Morávková-Lipnická 1991); these results may be considered as an explanation for litter accumulation on the soil surface in deforested sites. In forest, on the contrary, the amount of plant mass produced and consequently becoming a part of litter, is much lower (Table 4) and the conditions are more favourable for its decomposition.

Variation in individual size, density and other population characteristics

Mean size of individual tillers showed a great variation both within and between contrasting habitat types, i.e. forest understorey, clearing and deforested sites (Pyšek 1991). Both variation in the tiller size and the skewness of tiller weight distribution increased with density, i.e. were higher in the deforested sites (coefficient of variation 41.5 % for forest and 70.7 % for deforested sites).

Total tiller density in deforested sites generally exceeds 2500/m^2 (Fiala, Jakrlová et Zelená 1989, Pyšek 1991, Morávková-Lipnická 1991) with maxima of about 3800-3900/m^2. In spruce forests, the density rarely exceeds 900/m^2 (Morávková-Lipnická 1991, Pyšek 1991).

Both studies in which leaf area was estimated (Morávková- Lipnická 1991, Pyšek 1991) confirmed that (a) Leaf Area Index was higher in deforested sites (3.3 and 4.5, respectively) than in forest understoreys (2.71, and 2.05); (b) Specific Leaf Area (e.g. Rychnovská 1987) was lower in the populations of deforested sites which suggests that the understorey population formed thinner leaves, and (c) higher Leaf Weight Ratio in forests (0.57 and 0.58, respectively) than in deforested sites (0.37, and 0.35) indicates that a higher proportion of resources is being invested into leaves under shaded conditions. This corresponds to the more intense competition for light that may be expected in deforested sites (Pyšek 1991), the fact being a possible reason for higher investment in culms in order to promote growth in height.

Reproductive ecology

The number of caryopses produced per m^2 was estimated to range between 5,400 and 21,300 (Morávková-Lipnická 1991; calculated as the mean number of caryopses per panicle x mean number of flowering shoots per m^2) and shown to remain stable (81,870-91,910 - Pyšek 1992a, estimated on the same basis) over 15 years on humus-rich fertile soils where *C. villosa* retained its dominance. However, in humus-poor soils the values were much lower (10,190-13,060) and eventually decreased to 3,700 as *C. villosa* was replaced in succession. The reproductive allocation decreased over 15 years of succession (Pyšek 1992a).

The proportion of developed caryopses (i.e. of those containing developed endosperm) varied between 4.0-9.3 % for particular years and sites (Morávková-Lipnická 1991). Germination rates of developed caryopses ranged from 20% to more than 70%. When both developed and undeveloped caryopses were taken into account (i.e. the total caryopses production), the germination rate did not exceeed 10% (Morávková-Lipnická 1991, 1993). The percentage of developed caryopses was lower in forest understorey than in deforested sites which may be related to the vegetative strategy, i.e. that one might expect to prevail in the latter type of environment. As no significance tests are given in Morávková-Lipnická (1991) and there was a low number of replicates, these otherwise interesting results remain only at an exploratory level. Germination rate showed a great variance between years. No dormancy mechanisms were involved and no decrease in germination was found up to 3 years after release (Morávková-Lipnická 1991).

Spatial distribution of flowering shoots follows a typical pattern of "year-to-year shifting patches" (P. Pyšek, unpublished data). Intensity of flowering (expressed as a percentage of flowering tillers) seems to be lower in dense stands (i.e. in deforested sites) (Šmarda 1963 sec. Lokvenc 1971, Pyšek 1991, Morávková-Lipnická 1991).

Response to perturbations

Mowing (Morávková-Lipnická 1991) reduced both total above-ground plant mass and root mass in the year of treatment (this result, however, strongly depends on at which time of the growing period the perturbation is made). No clear trends were revealed concerning the litter response to mowing (Morávková- Lipnická 1991). Increase in the overall tiller density and decrease in the density of flowering tillers were among the main responses to mowing in other experiments (Jakrlová 1989a). In the study of Fiala, Jakrlová et Zelená (1989) the response to mowing was site-dependent: once-a-year cutting in the flat site decreased root biomass by the end of the 2nd year, whereas no such response was detected on the steep slope.

As shown by Morávková-Lipnická (1991), liming encouraged *C. villosa* by an increase in living above-ground plant mass in two years following its application; among underground organs, the increase in root mass was balanced by a decrease in rhizome mass.

Herbicide applications (Morávková-Lipnická 1991, Fiala, Zelená et Jakrlová 1993) reduced above-ground or both above- and underground production. Moreover, the treatment affected the spatial structure of *C. villosa* population and resulted in dense clustering of tillers which was reflecting reduced penetration of rhizomes into the surrounding toxic environment (Morávková-Lipnická 1991). In general, the restrictive effect of herbicides and its duration was proportionate to the dose applied (Wagner 1987, Wagner et York 1987).

Role in the community

Response to environmental factors

Light was shown to act as the main factor promoting the expansion of *C. villosa* (Samek 1988, Pyšek 1991, 1993a). This process starts in the very early phase of spruce damage, i.e. in the period the changes are still not visually apparent but the density of needles decreases and light penetration to the understorey is enhanced (Samek 1988). The levels of light penetrating to the vegetation surface which were obtained from a single synchronized measurement showed 18-22% of full light getting to the understorey of spruce forest with canopy closed, 34-40% to the partly opened spruce forest, and 82-87% to the bare spot vegetation surface (Morávková-Lipnická 1991). The next phase of expansion proceeds under gaps in spruce canopy. Other factors favouring *C. villosa* expansion are (a) its resistance to atmospheric pollution, (b) adaptability to changed soil conditions, and (c) resistance to pathogens and herbivores (Samek 1988).

Vegetation pattern in areas deforested due to air pollution was shown to be ruled by a relatively low number of environmental factors (Pyšek 1993a). Concerning the soil characteristics, acidity was found to be the main soil factor responsible for structuring community composition whereas the role of nutrients, especially nitrogen, was of minor importance (Pyšek 1993a). The vigour of *C. villosa* population was obviously highest in acid sites and decreased with increasing moisture (Fig. 3). Although the species is capable

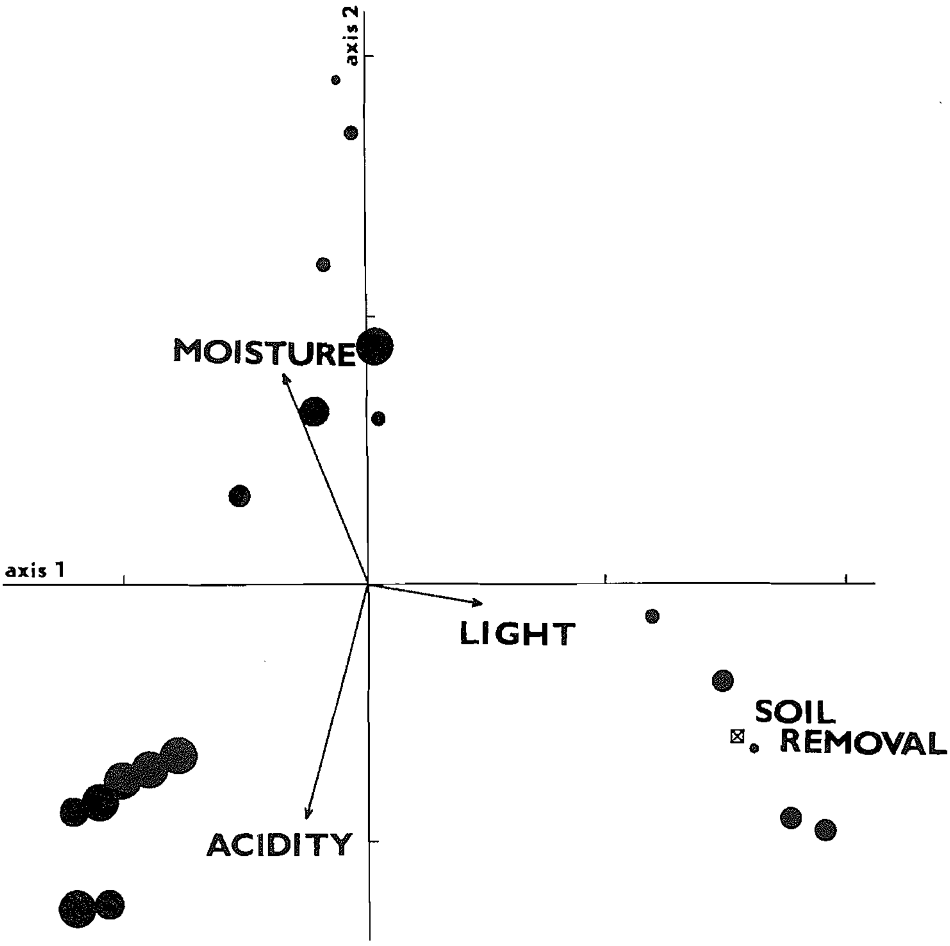

Fig. 3. Ordination plot (CANOCO) showing the vigour of *Calamagrostis villosa* stands with respect to the main environmental factors acting in bare spot vegetation. Details on ordination procedure used may be found in Pyšek 1993a. Values of *C. villosa* in Braun-Blanquet scale are shown for particular relevés by different symbols: ● 5 ● 4 • 3 • 2 · 1.
Note that the position in the ordination space reflects the presence of other species so that the lesser abundance in moist sites does not necessarily mean that *C. villosa* is not able to reach high cover there but rather that it is limited by competition from other species.

of growing in wet or waterlogged conditions, the competition from other species adapted to high water table (*Juncus effusus, Deschampsia caespitosa*) increases along the moisture gradient and the performance of *C. villosa* is restricted. Fig. 4 relates selected characteristics of *C. villosa* population to the moisture gradient: both tiller height and thickness of the litter layer decreased with soil moisture. Species diversity H' (expressed as Shannon index) was not related to the moisture level but it was shown to be correlated positively with available light and negatively with soil acidity; these two predictors explained 60.9% of variance in the data set where H' was concerned and 76.3% where the number of species was taken into account (Pyšek 1993a).

Competitive relationships, effect on species diversity

When studied at the small-scale hierarchical level, the diversity pattern within a *C. villosa*-dominated deforested sites was shown to be principally affected by the performance of this dominant species (Pyšek 1990). Both the number and total biomass of other species were reduced by the presence of *C. villosa*; the negative effect of litter on the other species was stronger than that of living above-ground biomass. The majority of other creeping and prostrate herbs were negatively correlated with the dry mass of *C. villosa* and this held also for grasses and grass-like species (*Juncus effusus, Holcus mollis*). The highest level of significance was found in the latter group which perhaps indicates that the similar growth form may lead to more intense competition as the space for niche differentiation is reduced (Begon et al. 1986, Keddy 1990).

Success of other species in *C. villosa* stands therefore appears to be conditioned by (a) plant height and growth rate – potentially tall, tough forbs more readily penetrate the litter layer and then escape from its influence by rapid growth in height, (b) capability to spread vegetatively and produce their own litter, and (c) local site conditions (Pyšek 1990). However, the retreat of some species is suggested to have occurred not only due to the competitive pressure imposed from *C. villosa* but also as a consequence of a more complex issue, e.g. decrease in soil mycorrhizas is believed to have contributed to a decrease in abundance of *Vaccinium myrtillus*. Regarding the relationships of main species of deforested sites to soil conditions, it appears that rhizomatous grasses producing a large amount of litter which is, in addition, difficult to decompose are successful on acid soils. High ability to cope with disturbances (e.g. those associated with reclamation procedures) was more typical of forbs (Pyšek 1993a).

In terms of Grime's strategy scheme (Grime 1979), *C. villosa* is considered to be a C-strategist (Frank et Klotz 1990) in its natural undisturbed habitats. In secondary habitats, the CSR-strategy would describe better the real species behaviour (Pyšek 1993a).

Efforts to study the competitive relationships of *C. villosa* with other species have mostly been determined by practical needs, i.e. the necessity to assess its effect on spruce or krummholz saplings being replanted. Spatial differentiation of root distribution through the soil profile was proved to occur when *Picea abies* and *C. villosa* grow together. In spruce, compared to pure stands, the proportion of roots located in the upper 5 cm of soil (which is occupied by *C. villosa*) decreased from 40-50% to 20-30% and majority of roots "shifted" to 5-10 cm (40-60% compared to 30% in pure stands). In contrast, *C. villosa* even increased the proportion of roots in the uppermost soil layer (80% compared to 65% in pure stands). Hence the spruce clearly diminished the root competition by shifting its main absorption area deeper into the soil profile (Huml 1970).

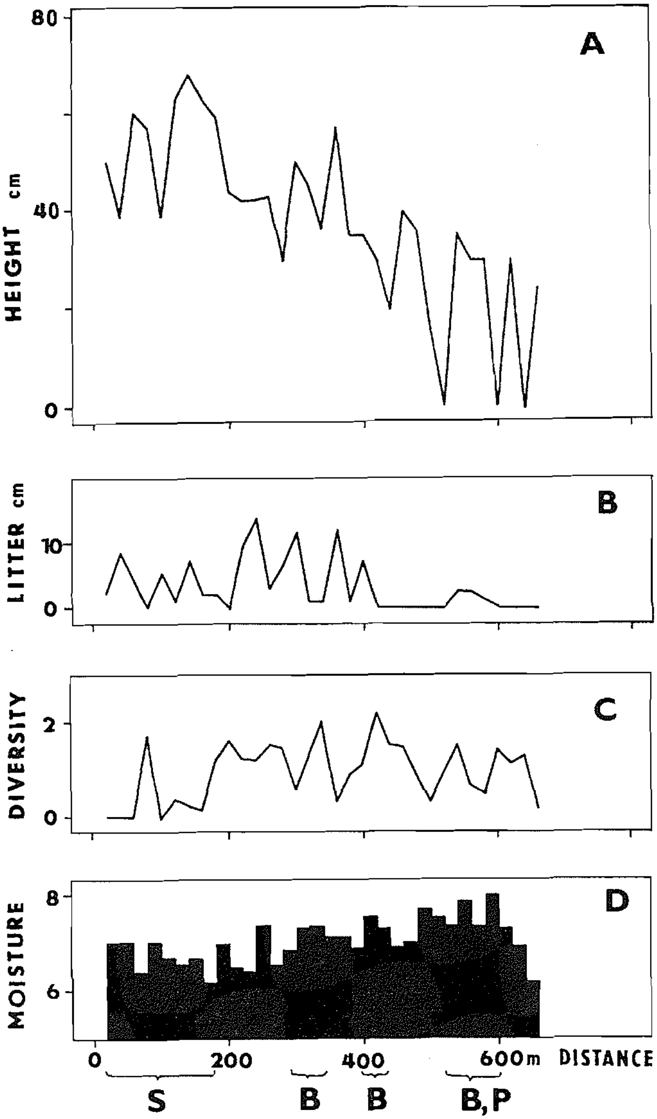

Fig. 4. Changes of selected *Calamagrostis villosa* population and community characteristics on a transect running from spruce forest across the deforested sites to the brook valley (see the bottom located symbols showing the type of vegetation at particular parts of the transect: S - spruce forest, B - brook, P - peat, not indicated - deforested sites), surrounding of the Fláje reservoir, the Krušné hory Mts., Czech Republic (see e.g. Pyšek 1990 for site characteristic). Plots 5 x 5 m in size were sampled at 20 m intervals. Moisture, expressed as mean Ellenberg indicator value (Ellenberg et al. 1991) calculated after transformation of Braun-Blanquet scale to 1-7 scale and considering species quantities, was found to be a factor whose change on the transect was significant (M-indicator value was positively correlated with distance from the beginning of the transect, Spearman rank correlation coefficient $r_S = 0.45$, $P<0.01$). Note that the vigour of *C. villosa* population expressed as its height (A) and thickness of the litter layer (B) decreased with moisture; the relationship was significant for the height ($r_S=-0.51$, $P<0.001$) and at the border of significance for litter ($r_S=-0.30$, $P=0.08$). Species diversity H' was lowest in the forest part of the transect but obviously did not follow any clear trend with respect to the moisture ($r_S=0.15$, $P=0.39$).

Spreading ability, succession

Surprisingly, few detailed data concerning the spreading ability of *C. villosa* are available. Fiala, Zelená et Jakrlová (1993) estimated the annual rate of spread at 0.25-0.5 m. A series of micromaps showing changes in cover of present species in three successive years (Morávková-Lipnická 1991) showed that *C. villosa* increased its original cover (assessed as 100%) up to 170-1000%. The values were, however, very variable, depending on starting site conditions and the associated species. During this short term observations, *Vaccinium myrtillus* was mostly suppressed by expanding *C. villosa* whereas *Deschampsia flexuosa* was able to compete successfully, especially in drier places with shallow soil layer (Morávková-Lipnická 1991).

These results correspond to the conclusions from a 15 years of succession (the course of succession was inferred from comparing differently aged sites, Pyšek 1992a) in reclaimed plots from which the uppermost soil layer with *C. villosa* rhizomes was removed to make the spruce replanting easier. In these sites, *C. villosa*, which was the best early colonizer because of its low caryopsis weight and large pool of diaspores available in the surroundings, was gradually replaced by *Deschampsia flexuosa*. In mounds formed of the material removed from reclaimed plots, *C. villosa* regenerated vegetatively from rhizomes and retained its dominance over 15 years of succession (Pyšek 1992a). It was suggested (Pyšek 1993b) that *C. villosa*, being a species preferring deep humus-rich soils, was outcompeted from plots because of lack of organic matter content. This hypothesis is further supported by the fact that, under different soil and climatic conditions, successional trends may be the opposite, i.e. *C. villosa* replacing *D. flexuosa* (Lepš, Michálek et Pyšek, unpublished data).

Šrůtek et Samek (1987) assessed trends in spruce forest development over 50 years in the Jizerské hory Mts. by repeating phytosociological relevés in sites studied by Müller (1936) and concluded that *C. villosa* increased its cover considerably during this period.

Positive and negative consequences of the *Calamagrostis villosa* expansion

Expansion of *C. villosa* in mountain regions of the Czech Republic causes considerable difficulties to the forest management. The negative effects may be divided in several groups.

1. Replanting efforts

Competition from grasses may be a cause of reduction in tree or shrub saplings' cover. Lokvenc (1971) estimated that the 50% cover of replanted *Pinus mugo* stands above the timberline was reduced to 8.7% by the presence of *C. villosa* stands. Consequently, 50% of costs spent on replantation were lost. Furthermore, dense *C. villosa* stands provide suitable habitats for small mammals, namely field vole (*Microtus agrestis*) and common shrew (*Sorex araneus*) which can damage tree saplings considerably by browsing. The same effect is generated by the uniform diet provided to large grazers; this consists predominantly of one unpalatable species and the grazers thus tend to prefer browsing the trees (Samek 1988).

2. Decrease in species diversity

Although the number of plant species present in deforested sites does not substantially differ from the species richness of original forests (see Table 3), species diversity is reduced due to the dominance of *C. villosa*. Natural revegetation of woody species is prevented and succession to forest communities is extremely slow or even impossible (Pyšek 1993a).

3. Hydrological consequences

After timber extraction, the deforested sites become wet or locally waterlogged. On the other hand, during the spring snow melting, most of the water flows on the settled-down surface of *C. villosa*; consequently, infiltration into soil is lowered and a large proportion of precipitation is lost from the site. Due to the uniformity of vast areas, the period of melting is getting shorter which may increase the danger of flooding (Samek 1988).

4. Recreational aspects

Obviously, vast uniform areas of deforested sites are less attractive for leisure activities; their value decreases due to aesthetic reasons, mechanical barriers restricting access and making walking difficult (logs, fallen trunks, depressions), and the sites are more exposed to bad weather.

Positive effects of the presence of *C. villosa* stands are (a) prevention from soil erosion, and (b) closed nutrient cycling maintaining the soil chemicals in the site.

Outlook on future research directions

Undoubtedly, the deforested sites in which *C. villosa* has expanded became an attractive research topic, especially at the turn of the eighties and nineties (Table 1). Most studies have focused upon estimating the plant mass production at the level of the whole population; considering the level of an individual tiller has been rather exceptional so far. Moreover, demographical studies using non-destructive methods are still missing; this is associated with the difficulties the researcher must face when attempting to mark individual tillers in order to identify them at subsequent sampling. The tillers are too delicate to be marked with plastic rings (Pyšek 1993c). Moreover, considerable tiller density in bare spots makes it difficult to handle individual tillers without damage. Also the important processes running under the soil surface that are crucial for the plant's population dynamics are very difficult to follow in the field due to extremely high density of both rhizomes and roots; in addition, the soils in which the underground organs are located are mostly not easy to sample.

It is probable that the low proportion of viable caryopses, low germination rate and difficulties with transplanting clones have prevented the species being used up to now for controlled laboratory experiments.

Surprisingly, practical implications and recommendations to the forest management are still restricted to statements about the negative effect of *C. villosa* on replanting success. The results of perturbation experiments (Morávková-Lipnická 1991) are, to a certain extent, inconclusive and were not sufficiently used to provide practical outputs. At present, I would recommend making more use of spontaneous or directed succession in deforested areas (Pyšek 1992a); provided that the air pollution is not substantially reduced, the problems associated with replanting would probably persist.

Bearing in mind that the research in this field is probably to be continued, there are some topics which deserve our attention as they appear to be interesting from the viewpoint of species ecology and we still do not know much, if anything, about them (Pyšek 1993c):

- Genetical structure of the populations (occurrence of particular genotypes and their relative success either in vegetative strategy, which may be assumed to prevail during the expansion in deforested sites, or in the reproductive one, influencing far distance spread into newly created sites).

- Relationships between *C. villosa* and other trophical levels: (1) role of grazing at the early phenostages when this species is, due to its early emergence, the main component of grazers' diet, (2) plant-herbivore interactions that may emerge in newly created habitats (Pyšek 1992b), (3) the role of mycorrhizas.
- Still, little is known about the role of litter and its effect on the long-term population dynamics.
- The pattern of flowering also requires further study (what is the role of environmental factors, population characteristics, and species' physiology in triggering the reproductive phase?).

Calamagrostis villosa may be considered, despite some methodical difficulties emerging in the field, a very suitable species for ecological studies. If no else, in this species we are provided with vast monotonous areas covered by nearly monospecific stands and this situation is being repeated over a relatively wide geographical range.

Acknowledgments

My thanks are due to František Krahulec, Průhonice, and Roger L. Hall, Oxford, for their comments on the manuscript and to the latter for improving my English. Jana Pyšková and Eva Švejdová kindly drew the figures.

Souhrn

V důsledku znečištění ovzduší, zejména SO_2 imisí, vznikl ve středoevropských horách nový ekologický fenomén: rozlehlé plochy byly po odumření smrkových lesů kolonizovány expanzívní trávou *Calamagrostis villosa*. Je pochopitelné, že se tento druh stal předmětem četných ekologických studií, jejichž počet vzrostl zejména na přelomu osmdesátých a devadesátých let. Tato práce se pokouší shrnout současný stav výzkumu a zhodnotit dosažené výsledky z hlediska (1) fytocenologie společenstev, v nichž *C. villosa* dominuje, (2) populačních charakteristik (produkce biomasy, reprodukční ekologie, reakce na zásahy do porostu), (3) reakce na faktory prostředí, (4) kompetičních vztahů s ostatními druhy holin, (5) sukcese a (6) praktických dopadů využitelných pro lesní hospodářství. V závěru jsou diskutovány některé problémy, s nimiž se výzkum tohoto druhu střetává, a nastíněny okruhy, na něž by podle autora tohoto příspěvku bylo vhodné zaměřit další výzkum.

References

Andresová J. (1979): Lesní a paseková společenstva lesa Království I u Dvora Králové. - Thesis [depon. in Dept. Bot. Charles Univ. Prague].

Begon M., Harper J. L. et Townsend C. R. (1986): Ecology. Individuals, populations, communities. - Blackwell, Oxford.

Berciková M. (1976): Rostlinná společenstva s účastí *Molinia coerulea* v alpínském stupni Krkonoš. I. část: Svazy *Montion, Juncion trifidi, Nardion, Calamagrostion villosae*. - Opera Corcontica, Vrchlabí, 13:95-129.

Burešová Z. (1976): Alpínská vegetace Krkonoš: Struktura a ekologie porostů na Luční (1547 m) a Studničné hoře (1555 m). - Opera Corcontica, Vrchlabí, 13:67-94.

Chrtek J. jun. (1991): Bibliografie prací s mapami rozšíření cévnatých rostlin v Československu. 2. Práce publikované v letech 1975-1989. - Severočes. Přír., Litoměřice, 25:1-91.

Conert H. J. (1989): *Calamagrostis villosa*. - In: Hegi G.: Illustrierte Flora von Mitteleuropa. 3. ed. Band I., Teil 3, Lieferung 5, Bg. 21-25, p. 365-367, Paul Parey, Hamburg.

Ellenberg, H. et al. 1991. Zeigerwerte von Pflanzen in Mitteleuropa.-Scr. Geobot., Göttingen, 18:1-248.

Fiala K. (1989): Underground biomass of three typical grass stands growing on areas deforested by air-pollution. - Ekológia (ČSSR), Bratislava, 8:105-115.

Fiala K., Jakrlová J. et Zelená V. (1989): Biomass partitioning in two *Calamagrostis villosa* stands on deforested sites. - Folia Geobot. Phytotax., Praha, 24:207-210.

Fiala K., Zelená V. et Jakrlová J. (1993): Struktura a produkce porostů s dominantními druhy rodu *Calamagrostis* na imisních holinách. - Zpr. Čs. Bot. Společ., Praha, 28/Mater. 13 [in print].

Fiedler H. J. et Höhne H. (1987): Stoffproduktion und Nährelementgehalt von *Calamagrostis villosa* (Chaix) J. F. Gmelin im Fichtenforst. - Flora, Jena, 179:109-123.

Frank D. et Klotz S. (1990): Biologisch-ökologische Daten zur Flora der DDR. - Martin-Luther-Univ., Halle.

Fuhrer E. (1990): Forest decline in Central Europe. Additional aspects of its cause. - For. Ecol. Manag., Amsterdam, 37:249-260.

Grime J.P. (1979): Plant strategies and vegetation processes. - J. Wiley, Chichester.

Grulich V. (1986): Klíč k určování československých druhů rodu *Calamagrostis*. - Muzeum a Současnost, Roztoky, ser. natur., 1986/1:31-40.

Hartmann F.-K. et Jahn G. (1967): Waldgesellschaften des mitteleuropäischen Gebirgsraumes nördlich der Alpen. - G. Fischer Verl., Stuttgart.

Heine R. et Leuschner D. (1972): Beitrag für die Verwendung der Blütenmerkmale bei der Aufstellung von Subtaxa bei *Calamagrostis villosa* (Chaix) J. F. Gmelin. - Wiss. Z. Friedrich-Schiller Univ. Jena, ser. math.-nat., 21:1023-1028.

Huml V. (1970): Příspěvek k otázkám kořenové konkurence. - Thesis [depon. in Dept. Bot. Charles Univ. Prague.]

Jakrlová J. (1989a): Úloha travinných porostů s *Calamagrostis* sp. v imisní oblasti Beskyd. - In: Ekológia travného porostu, p. 192-201, Bratislava.

Jakrlová J. (1989b): Travinné systémy jako dočasná náhradní společenstva lesů v oblastech postižených imisemi. - Zprávy ÚSEB, Brno, 1989:58-62.

Jeník J. (1984): Occurrence of *Calamagrostis villosa* in the Bieszczady Mts., the Eastern Carpathians. - Preslia, Praha, 56:153-158.

Jeník J., Bureš L. et Burešová Z. (1980): Syntaxonomic study of vegetation in Velká kotlina cirque, the Sudeten Mountains. - Folia Geobot. Phytotax., Praha, 15:1-28.

Keddy P. A. (1990): Competition. - Chapman & Hall, London et New York.

Krause G. H. M. (1989): Forest decline in Central Europe: The unravelling of multiple causes. - In: Grubb P. J. et Whittaker J. B. [red.]: Toward a more exact ecology, p. 377-399, Blackwell, Oxford.

Lokvenc T. (1971): Vliv rostlinných společenstev na růst kosodřeviny. - Opera Corcontica, Vrchlabí, 7-8:125-140.

Májovský J., Murín A. et al. (1987): Karyotaxonomicky prehĺad flóry Slovenska. - Veda, Bratislava.

Meusel H. et Buhl A. (1962): Verbreitungskarten mitteldeutscher Leitpflanzen, 10. Reihe. - Wiss. Z. Martin-Luther-Univ. Halle-Wittenberg, ser. math.-nat., 11:1245-1318.

Mikyška R. (1968): Geobotanická mapa ČSSR. České země. - In: Vegetace ČSSR 2:1-204, Academia, Praha.

Mikyška R. (1972): Wälder der Böhmischen Mittleren Sudeten und ihrer Vorberge. - Rozpr. Čs. Akad. Věd., ser. math.-nat., Praha, 1982/3:1-162.

Mladý F. (1978): *Calamagrostis villosa* (Chaix) J. F. Gmel. (a další druhy jako příklady chorologické indikace v území). - In: Kubát K. [red.]: Floristické materiály ke květeně Kadaňska, Severočes. Přír., Litoměřice, 8-9(2):85-86.

Moore P. D. et Chapman S. B. (1986): Methods in plant ecology. - Blackwell, Oxford.

Moorhead D. L. et Reynolds J. F. (1989): Mechanisms of surface litter mass loss in the northern Chihuahuan desert: a reinterpretation. - J. Arid Env. 16:157-163.

Moravec J. et al. (1983): Rostlinná společenstva České socialistické republiky a přehled jejich ohrožení. - Severočes. Přír., Litoměřice, Příl. 1983/1:1-110.

Morávková-Lipnická K. (1991): Ekologie třtiny chloupkaté (*Calamagrostis villosa* (Chaix) J. F. Gmelin) v imisní postižené oblasti Jizerských hor. - Thesis [depon. in Dept. Bot. Charles Univ. Prague.]

Morávková-Lipnická K. (1993): Generativní rozmnožování třtiny chloupkaté (*Calamagrostis villosa*) v Jizerských horách. - Zpr. Čs. Bot. Společ., Praha, 28/Mater. 13 [in print].

Müller J. (1936): Lesní typy Jizerských hor. - Lesnická práce, Praha, 15:1-47.

Neuhäuslová Z. et Kolbek J. (1982): Seznam vyšších rostlin, mechorostů a lišejníků střední Evropy užitých v bance geobotanických dat BÚ ČSAV. - Bot. Inst. Czechoslov. Acad. Sci., Průhonice.

Pyšek P. (1990): The influence of *Calamagrostis villosa* on the species diversity of deforested sites in the Krušné hory Mts. - Preslia, Praha, 62:323-335.

Pyšek P. (1991): Biomass production and size structure of *Calamagrostis villosa* populations in different habitats. - Preslia, Praha, 63:9-20.

Pyšek P. (1992a): Dominant species exchange during succession in reclaimed habitats: a case study from areas deforested by air pollution. - For. Ecol. Manag., Amsterdam, 54:27-44.

Pyšek P. (1992b): Seasonal changes in response of *Senecio ovatus* to grazing by the chrysomelid beetle *Chrysomela speciosissima*. - Oecologia, Berlin, 91:596-602.

Pyšek P. (1993a): Pattern of species dominance and factors affecting community composition in areas deforested due to air pollution. - Vegetatio, Dordrecht [in print]

Pyšek P. (1993b): Effect of soil characteristics on succession in sites reclaimed after acid rain deforestation. - Ecol. Engin. [in print].

Pyšek P. (1993c): Studium autekologie *Calamagrostis villosa* na imisních holinách v Krušných horách a srovnání výsledků s jinými oblastmi České republiky. - Zpr. Čs. Bot. Společ., Praha, 28/Mater. 13 [in print].

Rothmaler W. (1986): Exkursionsflora für die Gebiete der DDR und der BRD. - Volkseig. Verl., Berlin.

Rychnovská M. (1985): Ekologie lučních porostů. - Academia, Praha.

Rychnovská M. et al. (1987): Metody studia travních ekosystémů. - Academia, Praha.

Samek V. (1988): Expanze třtiny chloupkaté v imisních oblastech hor. - Živa, Praha, 36:45-46.

Sofron J. (1981): Přirozené smrčiny západních a jihozápadních Čech. - Studie ČSAV, Praha, 1981/7:1-127.

Sofron J. (1985): Vrcholový fenomén hory Můstek na Šumavě. - Zpr. Muz. Západočes. Kraje-Přír., Plzeň, 30-31:19-31.

Söyrinki N. (1954-1956): Vermehrungsökologische Studien in der Pflanzenwelt der bayerischen Alpen. - Annal. Bot. Soc. Zool. Bot. Vanamo, Helsinki, 27/1:1-232.

Sýkora T. (1983): *Junco effusi-Calamagrostietum villosae*, významné společenstvo po smrkových lesích v Západních Sudetech. - Preslia, Praha, 55:165-172.

Šrůtek M. et Samek V. (1987): Světlostní stádia smrkových porostů poškozených imisemi v Jizerských horách. - Sborn. Severočes. Muz.-Přír. Vědy, Liberec, 16:159-166.

Wagner W. (1987): Entwicklung der Phytomasse (Vegetationsentwicklung) nach Herbizideinsatz auf Kahlschlagen im Mittelgebirge und Hügelland. - Hercynia, Dresden, ser. n., 24:266-270.

Wagner W. et York P. (1990): Vegetationsentwicklung nach Herbizidapplikation auf Schlagflächen im Mittelgebirge und Hügelland. - In: Ökologie von Schlagflächen und ihre Wiederauffortsetzung im Immissionschadgebieten des Erzgebirges, p. 54-62, Dresden.

Received 16 November 1992
Accepted 25 February 1993