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Expansion of *Calamagrostis villosa* in sub-alpine *Nardus stricta* grassland: Cessation of cutting management or high nitrogen deposition?

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ABSTRACT

Calamagrostis villosa has recently expanded in *Nardus stricta*-dominated sub-alpine grassland of the Giant Mountains (Krkonoše/Karkonosze, the Czech Republic). To investigate whether this expansion has been promoted by high nitrogen deposition or by the cessation of agricultural management, grassland plots dominated by *C. villosa* were manipulated with four treatments: control (Con), fertilised (Fer), cut (Cut) and cut–fertilised (Cut–Fer). NH_4NO_3 was used at the rate of 30 kg N ha^{-1} and fertilisation and cutting were performed once a year after data collection in late July between 2000 and 2006.

Plant species composition (analysed by RDA) was significantly influenced by cutting but not by fertilisation. Cutting reduced the cover, biomass, sward height and tiller density of *C. villosa.* Seedlings of *N. stricta* and panicles of *C. villosa* were recorded only in plots with cutting management.

To investigate the effect of treatments on the spread of *C. villosa*, grassland sods dominated by *N. stricta* were transplanted into the experimental plots. Six years later, the density and cover of *C. villosa* spreading into the *N. stricta* sods were highest in Fer treatment.

C. villosa was recognised as a defoliation-sensitive species and this sensitivity cannot be overcome by an increase in N supply. Recent expansion of *C. villosa* in the sub-alpine grassland can by explained by a long-term succession after the cessation of agricultural management and an increase in the N availability in recent decades.

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1. Introduction

In central Europe, mountain areas receive disproportionately larger amounts of atmospheric N deposition than lowland areas. For example, in 2004, the average annual N deposition ranged from 5 to 10 kg ha^{-1} in lowland areas. However, in the Sudetes (a chain of middle mountains in the border land between Poland, Czech Republic and Germany) the range was between 15 and 30 kg ha^{-1} (ČHMÚ, 2005).

There is clear evidence that increased N deposition and the consequent higher availability of N forced changes in N-limited ecosystems toward the dominance of more productive species (Bobbink et al., 1998; Fabiszewski and Wojtuń, 2001; Bohlmann et al., 2005; Hardtle et al., 2006; Honsová et al., 2007). Furthermore, in many areas exposed to high levels of N deposition, the shift in limiting nutrient from N to P and the consequent spread of species well adapted to low P availability occurred (Kirkham, 2001; Tomassen et al., 2004; Wassen et al., 2005; Hejcman et al., 2007a). In mountainous areas of central Europe, recent large-scale expansion of *Calamagrostis villosa* is frequently attributed to both the direct and indirect effects of air pollution. Direct effects consist of changes in soil chemical properties, particularly in regard to the increase in availability of N and soil acidification. The loss of tree needles and the consequent increase in the amount of light reaching the ground are considered the primary indirect effect in spruce forests (Pyšek, 1991, 1993; Malcová et al., 1999; Vacek et al., 1999; Wild et al., 2004; Fiala et al., 2005; Drábek et al., 2007).

C. villosa has recently spread in *Nardus stricta*-dominated sub-alpine grassland in the Giant Mts. (Krkonoše, Karkonosze and Riesengebirge in Czech, Polish and German). Authors of

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observational studies ascribed the expansion exclusively to high N deposition (see Štursová, 1985; Wágnerová, 1991; Kočí, 2001; Hejcman et al., 2005; Chytrý, 2007), although the effect of N enrichment was not investigated experimentally. An alternative explanation was proposed by Hejcman et al. (2006)—the expansion must be attributed to long-term succession after the cessation of agricultural management (cutting) performed in the locality until the end of World War II.

To investigate whether N deposition or the cessation of agricultural management was the leading factor for the *C. villosa* expansion, a manipulative experiment combining N fertilisation and cutting management was established.

2. Materials and methods

The study site lies above the upper tree line at the altitude of 1370 m a.s.l. in the western part of the Giant Mts. (Harrachov Meadow, 50°45′32″N, 15°32′28″W, Czech Republic). The soil types are podzols, developed on medium grain porphyric granite or granodiorite. The locality lies on a moderate north slope with an inclination of up to 2°. The mean annual temperature is 2 °C and the mean annual precipitation is 1380 mm (Vrbatova Bouda Meteorological Station, period 1960–1990). According to long-term measurements made by Budská et al. (2000), in a neighbouring locality, the range of annual wet N deposition was estimated as being 20–40 kg ha^{-1}. High year-to-year variability in deposition was caused particularly by the variation in precipitation. According to phytosociological nomenclature (Chytrý, 2007), the vegetation of the experimental grassland was classified as a *Nardo strictae–Caricion bigelowii* alliance. The dominant species were *Calamagrostis villosa* (cover 37.2%), *Avenella flexuosa* (21.1%) and *Nardus stricta* (16.1%), followed by *Galium saxatile* (6.5%), *Anthoxanthum alpinum* (4.8%), *Carex bigelowii* (4.6%) and other species. The nomenclature of plant species follows Kubát et al. (2002). The site was used for haymaking and cattle grazing from the 17th century until the World War II and has been without any agricultural management since the end of the War (Lokvenc, 2001).

A randomised complete block experiment with four replicate plots (each 5 m × 5 m) for each treatment was established. To eliminate the edge effect, central 1 m × 1 m plots, using a continuous grid of nine square subplots, were used for data collection. There were two factors with two levels leading to four treatments: unmanaged control (Con), fertilised (Fer), cut (Cut) and cut–fertilised (Cut–Fer). NH_4NO_3 was used at the rate of 30 kg N ha^{-1} per year. Fertilisation and cutting were performed once a year after data collection. Sward was cut on a stable height of 3 cm.

The percentage cover of all vascular species, the number of *C. villosa* tillers, inflorescences and the height of sward before cutting were counted or measured separately in all subplots of each 1 m^2 central plot. Baseline data were collected in 2000 for each plot before the first experimental manipulation. Sward height before cutting was taken as the mean of the highest leaves of ten randomly chosen *C. villosa* tillers. The biomass samples were collected after the vegetation sampling. Samples were sorted into species, oven dried for 48 h at 85 °C and then weighed. To avoid disturbing the permanent 1 m^2 plots in Fer and Con treatments, nearby biomass samples were collected in different places within 5 m × 5 m experimental plots each year. This was done in close vicinity of permanent 1 m^2 plots to minimise bias in the data. All data were collected each year in the last week of July.

To reveal the effect of treatment on the spread of *C. villosa*, a transplantation of sods was performed in 2000. Thirty-two 0.35 m × 0.35 m × 0.2 m sods dominated by *N. stricta* were excavated and placed into experimental 5 m × 5 m plots in holes of the same size. The *N. stricta* sods replaced those dominated by *C. villosa* in the plots. *N. stricta* sods were taken from the surrounding area in the circle of diameter 400 m around experimental plots and placed at least 1 m away from the central 1 m^2 monitoring plot. In each 5 m × 5 m plot, two *N. stricta* sods were used (eight per treatment). The cover and density of *C. villosa* tillers, penetrating into each *N. stricta* sod, were estimated and counted in each experimental season.

2.1. Data analysis

Redundancy analysis (RDA) in the CANOCO program (Ter Braak and Šmilauer, 2002) was used to evaluate the plant species composition data based on cover estimates. A split plot design and the permutation type to cope with repeated measurements was used: whole plots (number of whole plots = number of experimental plots (16)) were freely exchangeable and split plots (number of split plots = number of years with data collection (7)) were permuted as time series or linear transects. 999 permutations were used in all performed analyses and permutations were restricted into blocks defined by covariables. Repeated-measures ANOVA analyses in the Statistica 5.0 program were used to evaluate univariate data: sward height, cover of selected species, biomass production, density of inflorescences and density of tillers. Blocks were treated as a random factor in all ANOVA analyses. To avoid problems with data handling and pseudoreplications, mean values (one value per one experimental plot) were used in all performed analyses instead of rough data from subplots.

3. Results

High year-to-year variability in plant species composition was revealed. The effect of year was significant; it explained 22% of the variability in plant species composition data based on cover estimates in RDA analysis (analysis a1 in Table 1). Interactions of year with both cut and fertilisation factors were significant and explained 27% of the variability in plant species composition data (analysis a2 in Table 1). The introduction of regular cutting management had a decisive effect on plant species composition as the interaction of year with cut was significant and explained 24% of the variability in plant cover data (analysis a3 in Table 1). In contrast to cut, interaction of year with fertilisation explained only an insignificant part of the data variability (analysis a4 in Table 1).

Table 1
Results of RDA analyses of plant species composition data

An.	Expl. var.	Covariables	% ax 1 (all)	F 1 (all)	P 1 (all)
a1	Year	Year × Cut, Year × Fer, ID, Blocks	22.4	30.2	<0.001
a2	Year × Cut, Year × Fer	Year, ID, Blocks	23.8 (27.2)	32.8 (19.6)	<0.001 (<0.001)
a3	Year × Cut	Year, Year × Fer, ID, Blocks	24.1	33.4	<0.001
a4	Year × Fer	Year, Year × Cut, ID, Blocks	5.3	5.8	0.377

An.: number of analyses, Expl. var.: explanatory (environmental in Canoco terminology) variables, % ax 1 (all): species variability explained by canonical axis 1 or by all axes (measure of explanatory power of the environmental variables), F 1 (all): F statistics for the test of the particular analysis, P 1 (all): corresponding probability value obtained by the Monte Carlo permutation test, ID: plot identification.

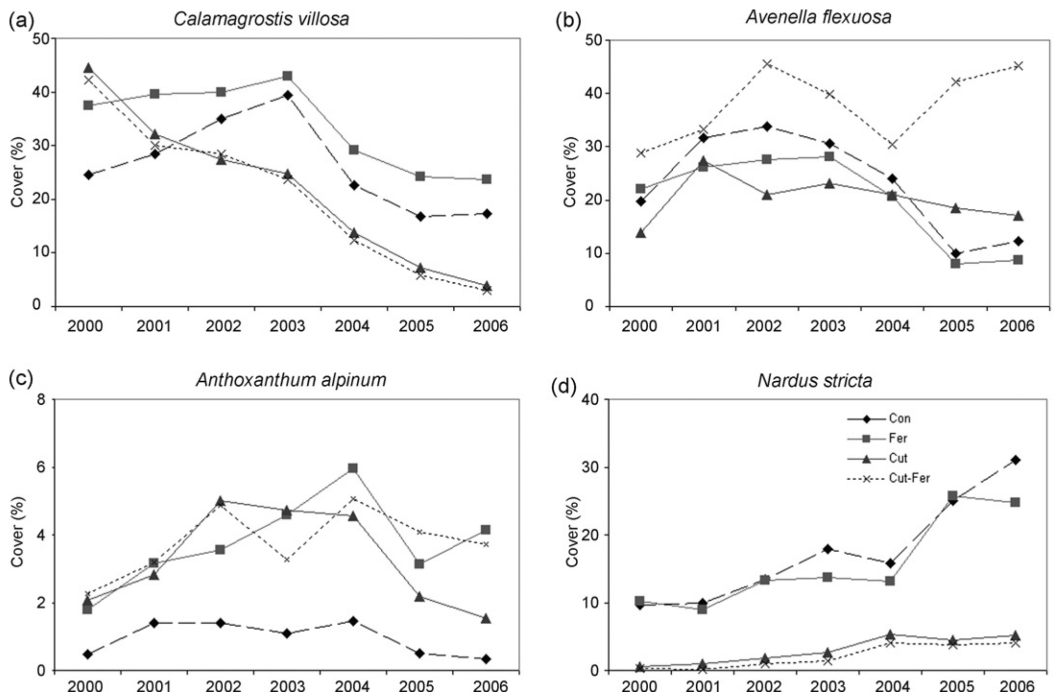

Fig. 1. Effect of treatments on cover of *Calamagrostis villosa* (a), *Avenella flexuosa* (b), *Anthoxanthum alpinum* (c) and *Nardus stricta* (d) in years 2000–2006. Treatment abbreviations: Con, control; Fer, fertilisation; Cut, cutting; Cut–Fer, cutting and fertilisation.

Fertilisation had a negligible effect and cutting a highly significant effect on plant species composition. Mean cover of individual species during the experimental period is visible from Fig. 1. In Con and in Fer treatments, some fluctuations in cover of *C. villosa* and *A. flexuosa* occurred and a gradual increase in cover of *N. stricta* was recorded, especially between years 2004 and 2005. Although the cover of *C. villosa* was lowest in Con treatment before the first experimental manipulation in 2000, cover of *C. villosa* was lowest in both treatments with cut at the end of the experiment in 2006. In 2002, five seedlings of *N. stricta* were recorded in Cut treatment and these seedlings survived until 2006, the last experimental season. Cover of *C. villosa* in Cut and in Cut–Fer treatments was reduced more than four times during the experimental period. Under cutting management, regeneration of *C. villosa* was not increased by N addition in contrast to *A. flexuosa*, which was a species with relatively stable cover under Cut treatment and positively responding to Cut–Fer treatment.

The effect of treatment on biomass production was evaluated separately for each species. The results of repeated-measures ANOVA analyses are present in Table 2 and Fig. 2. Biomass production of *C. villosa* was relatively stable in Con and Fer treatments, but yielded a highly negative response upon regular cutting management. The negative effect of Cut and Cut–Fer treatments on biomass production was consistent with results based upon cover estimates. The biomass production of *A. flexuosa* was affected by year-to-year variability. In Con and Fer treatments, a moderate decrease of biomass production was recorded within the study period. In Cut–Fer treatment, biomass

Table 2
Results of ANOVA analyses

Tested variable		Cut	Fer	Cut × Fer	Year	Year × Cut	Year × Fer	Year × Cut × Fer
Height of *Calamagrostis*[a]	F	104.4	13.1	5.3	214.2	90.2	3.3	4.4
	P	**<0.001**	**<0.001**	**0.023**	**<0.001**	**<0.001**	**0.003**	**<0.001**
Number of tillers[a]	F	10.7	1.3	10	201.2	37.4	3.5	4.3
	P	**0.001**	0.261	0.002	**<0.001**	**<0.001**	**0.002**	**<0.001**
Total biomass[b]	F	26.3	4.1	0.21	14.6	5.1	0.22	0.59
	P	**<0.001**	0.067	0.653	**<0.001**	**0.001**	0.954	0.707
Biomass of *Calamagrostis*[b]	F	7.1	2.7	2.4	15.9	14.9	0.5	0.6
	P	**0.021**	0.127	0.152	**<0.001**	**<0.001**	0.793	0.719
Biomass of *Avenella*[b]	F	2.7	1.5	4.8	4.2	1.8	0.5	0.4
	P	0.129	0.239	**0.049**	**0.002**	0.129	0.758	0.862
Biomass of *Anthoxanthum*[b]	F	0.01	2.7	0.02	2.5	0.5	1.2	0.1
	P	0.937	0.126	0.897	0.044	0.746	0.330	0.982
Number of *C. villosa* tillers	F	9.77	10.71	3.06	58.73	6.68	3.19	1.31
Penetrating into *Nardus* sods[a]	P	**0.004**	**0.003**	**0.091**	**<0.001**	**<0.001**	**0.005**	0.256
Cover of *C. villosa*	F	9.51	7.98	0.79	34.66	2.7	2.43	0.25
Penetrating into *Nardus* sods[a]	P	**0.005**	**0.009**	0.382	**<0.001**	**0.016**	**0.028**	0.957

Degrees of freedom were 1 for Cut and Fer and Cut × Fer interaction, 6 (or 5 in the case of biomass production) for Year, Year × Cut, Year × Fer and Year × Cut × Fer effects. *F*: *F* value, *P*: obtained probability value, significant results are faced in bold.

[a] Data available for all years.

[b] Data available for all years except of the year 2000.

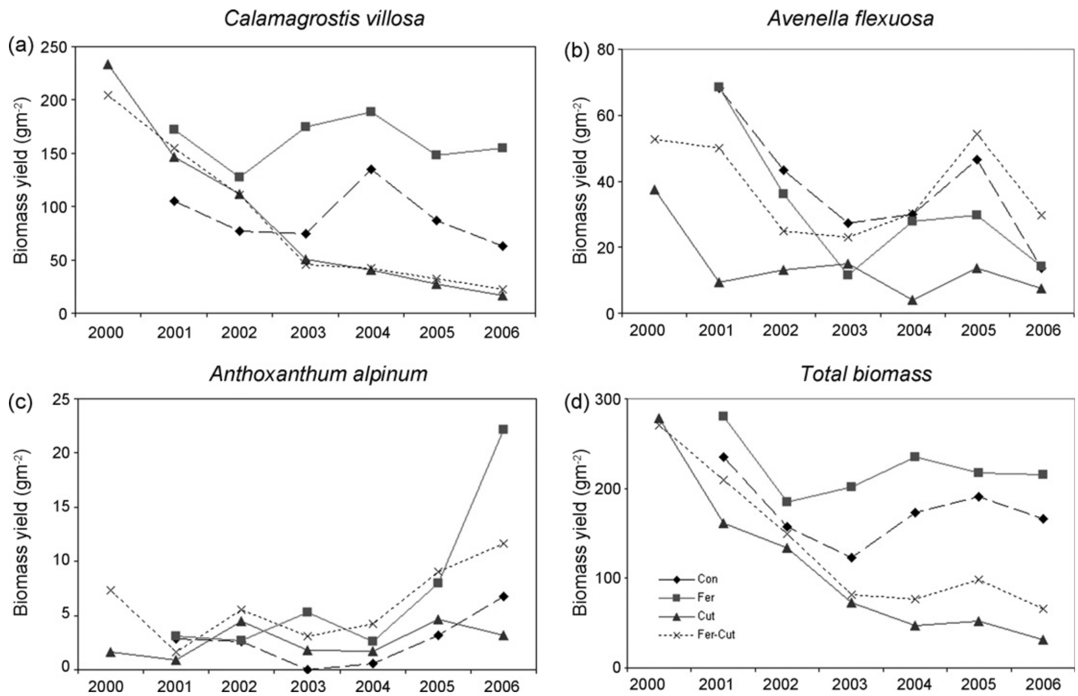

Fig. 2. Effect of treatments on dry matter biomass production of *Calamagrostis villosa* (a), *Avenella flexuosa* (b), *Anthoxanthum alpinum* (c) and all recorded species together (d) in years 2000–2006. Treatment abbreviations: Con, control; Fer, fertilisation; Cut, cutting; Cut–Fer, cutting and fertilisation. Baseline biomass production collected in 2000 was not available for control and fertilisation treatments.

production was highest of all treatments in 2005 and 2006 and this was consistent with results of cover estimates. Although there was a moderate increase in biomass production of *A. alpinum* caused by fertilisation in 2005 and 2006, biomass production was only significantly affected by the effect of year. Total biomass reflected in all treatments biomass production of the dominant species. In Cut and Cut–Fer treatments, total biomass production was parallel with biomass production of *C. villosa* and decreased by 4.1 and 8.6 times after 6 years of the experiment.

The height of *C. villosa* leaves was significantly affected by all tested effects (Table 2). The lowest heights were recorded in all treatments in 2004. Plants of *C. villosa* were highest in Fer and Con treatments and lowest in Cut–Fer and Cut treatments in all years after the start of the experiment. Cutting management reduced sward height considerably, whereas the positive effect of fertilisation on sward height was only negligible (Fig. 3b).

Tiller density of *C. villosa* was significantly affected by all tested effects, with the exception of the effect of fertilisation (Table 2). The gradual decrease of tiller density was revealed in all treatments within the study period. Although there was a relatively high variability in the data, the lowest tiller density was recorded in Cut–Fer and Cut treatments and the highest in Fer treatment in 2006 (Fig. 3a).

Cutting management immediately increased density of *C. villosa* inflorescences from 0 in 2000 to more than 80 inflorescences per m^2 recorded in Cut and Cut–Fer treatments after the first year of the experiment in 2001. This number was in sharp contrast to the 5 and 0 inflorescences recorded in Fer and Con treatments. During the next experimental years, a gradual decrease of inflorescence density was recorded in both cut treatments (Fig. 3c).

The density of *C. villosa* tillers penetrating into transplanted *Nardus* sods was significantly affected by both cutting and fertilisation tested effects (Table 2, Fig. 4). In 2006, the highest tiller density was recorded in Fer treatment followed by Con, Cut–Fer and Cut treatment. The most significant result was the positive effect of N addition without cutting management in Fer treatment. Cover of *C. villosa* responded in the same way as the tiller density.

4. Discussion

A steep decrease in cover and biomass production of tall grass *C. villosa* under cutting management indicates its high sensitivity on regular defoliation in a sub-alpine vegetation zone of the Giant Mts. This sensitivity cannot be overcome by N enrichment. This greatly contrasts with the low response of *A. flexuosa*, a short grass with the majority of its photosynthetic active biomass under cutting height. Cutting management must therefore be considered as a highly selective process, negatively affecting predominantly tall growing species and not affecting or supporting short growing species. This is consistent with the results of many other authors (see Diaz et al., 2001; Pavlů et al., 2003; De Bello et al., 2005), showing that plant height is in many cases the best predictor of response of a particular species on defoliation.

A high sensitivity of *C. villosa* on defoliation is visible from the tiller density data as well. In treatments with cutting management, a continuous decrease of tiller density occurred and the density was the lowest of all treatments in 2005 and 2006. The decrease in tiller density was combined with a decrease in tiller size (tiller weight—calculated by biomass production divided by the number of tillers per plot). This was not consistent with the tiller size/density compensation principle. According to this principle, a decrease in tiller size under intensive defoliation is compensated by a substantial increase in tiller density in grass species which tolerate defoliation (see Matthew et al., 1995; Pavlů et al., 2006; Roscher et al., 2007). The tiller size/density principle did not apply to *C. villosa* as the decrease in tiller density together with tiller size was recorded using Cut and Cut–Fer treatments. Cutting

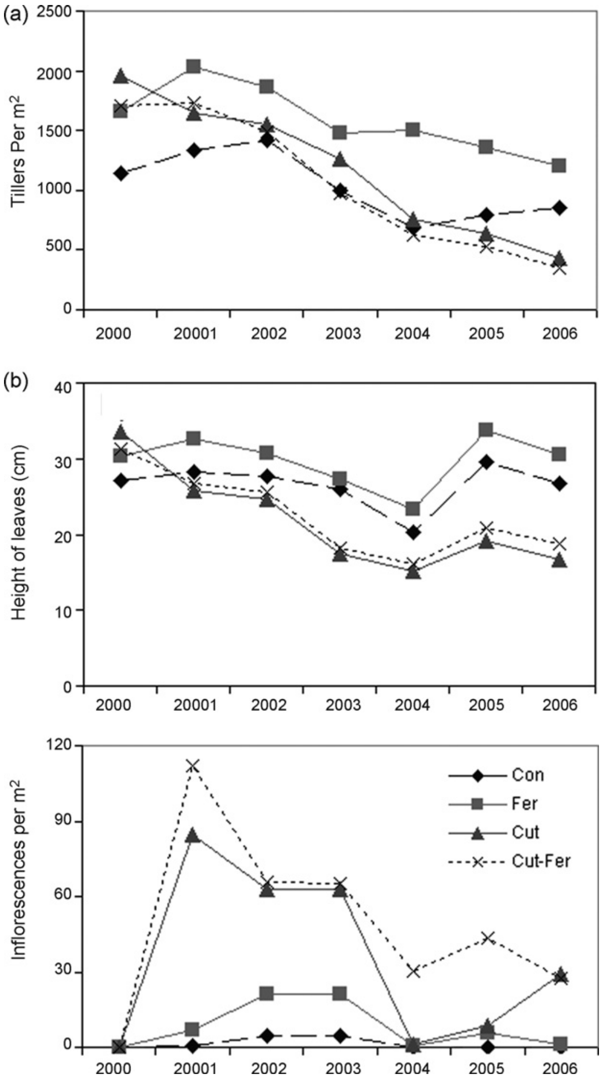

Fig. 3. Tiller density (a), height of highest leave (b) and inflorescences density (c) of *C. villosa* under investigated treatments in years 2000–2006. Treatment abbreviations: Con, control; Fer, fertilisation; Cut, cutting; Cut–Fer, cutting and fertilisation.

management was able to restrict the dominance of *C. villosa* to the benefit of short sward components, particularly *A. flexuosa* and *N. stricta.* Furthermore, Cut treatment resulted in the opening of the canopy, thus allowing germination of caryopses and the emergence of *N. stricta* seedlings. This supports the conclusions by Hejcman et al. (2005) that *N. stricta* is able to regenerate by means of germinable caryopses and can spread under agricultural management in sub-alpine grasslands of the Giant Mts. Taking into account the high defoliation sensitivity of *C. villosa*, its recent increase must be attributed, at least partly, to its long-term natural succession after the cessation of agricultural management.

Cutting management substantially supported the flowering of *C. villosa*. Flowering of this species was rare above the upper tree limit; so frequent panicles in treatments with cutting management sharply contrasted with neighbouring panicles-free grasslands. Flowering was probably induced by a change in ratio of aboveground to belowground biomass. Increased flowering induced by defoliation stress is known in several forage grasses (Loeppky and Coulman, 2001; Havstad et al., 2004), but it has never been described for *C. villosa*. The increase in flowering of *C. villosa* under defoliation seems to be an evolutionary strategy to increase the probability of survival under disturbance. In the last years of the experiment, reserves depletion probably resulted in the decrease in flowering intensity in both treatments with cutting management.

A. alpinum positively responded to increased N availability, although the enhancement in cover, and more so in biomass production, was only moderate. Cover data better reflected the positive effect of N fertiliser application because *A. alpinum* is a short-growing species and the majority of its biomass was recorded below cutting height. The positive effect of fertilisation on *A. alpinum* corresponded with results of other fertiliser experiments performed in the sub-alpine zone of the Giant Mts. (Hejcman et al., 2007b; Semelová et al., 2008). Filipová and Krahulec (2006) considered *A. alpinum* as a S strategist (sensu Grime et al., 1988) but its flexible response to fertilisation is a trait rather than a characteristic of other strategies.

The positive effect of N addition on the spread of *C. villosa* was clearly demonstrated by the transplantation experiment. The highest number of tillers and cover of *C. villosa* was recorded in *Nardus* sods transplanted into Fer treatment. The long-term increase in cover and tiller density substantially differed from other treatments. This supports conclusions drawn by other authors (Kočí, 2001; Hejcman et al., 2005; Chytrý, 2007) that the spread of *C. villosa* is promoted by the increase in N availability in sub-alpine grasslands. The increase in cover of *C. villosa* due to N deposition has also been reported from forest ecosystems where this grass is a common species of understory vegetation (Vacek et al., 1999; Fabiszewski and Wojtuń, 2001; Hédl, 2004; Wild et al., 2004). This study's primary result is that the positive effect of N deposition on the spread of *C. villosa* can be observed only under undefoliated sward.

C. villosa was recognised as a defoliation-sensitive species. This sensitivity cannot be overcome by an increase in N supply. Recent expansion of *C. villosa* in the sub-alpine grassland must be attributed to both the long-term succession after cessation of agricultural management and to the increase in N availability in recent decades.

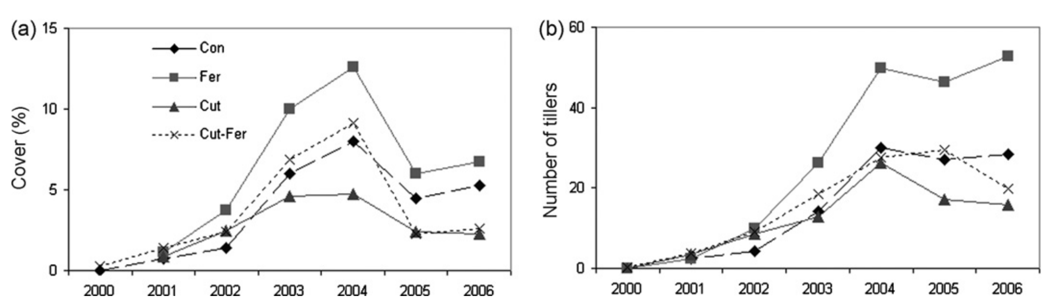

Fig. 4. Cover (a) and number of tillers (b) of *C. villosa* penetrating into transplanted *Nardus* sods in years 2000–2006. Treatment abbreviations: Con, control; Fer, fertilisation; Cut, cutting; Cut–Fer, cutting and fertilisation.

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