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BIOMASS FORMATION, NUTRIENT UPTAKE AND RELEASE IN FERN STANDS OF *Athyrium distentifolium* ON DEFORESTED AREAS AFFECTED BY POLLUTION: COMPARISON WITH GRASS STANDS

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Abstract

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Impact of climatic factors and acid deposits resulted at higher altitude in the Beskydy Mts in worse growth parameters of the tall fern *Athyrium distentifolium*. Ferns had here shorter fronds, thinner petioles and lower frond biomass. Similarly, a lower length and biomass of *Calamagrostis arundinacea* shoots was also recorded in similar deforested sites in uppermost mountain zones. In contrast to grass stands of deforested areas, fern stands at a lower aboveground biomass production (194–350 g.m^{-2}) accumulated in it a large amount nitrogen (3.9–7.0 gN.m^{-2}). Thus a higher amount of nitrogen was required in these fern stands for the formation of the same amount of aboveground biomass than in compared grass stands. At the slower decomposition of fern litter (19–25 % dry mass of leaflets and 18–19% stalks per year) than at that of grass litter (35–54% leaves, 17–30% stalks), the release of Ca (54–55%) and Mg (86–87%) was faster and the amount of nitrogen immobilized in one year old fern litter reached up to 46 kgN per ha. A comparison of soil features indicates less favourable soil conditions in fern stands (lower pH values, Ca contents and Ca/Al ratios) than in grass stands. These data thus suggest that fern stand formation on deforested sites has not the same positive ameliorative effect on soil environment as that described for both *Calamagrostis* species.

Key words: growth parameters, litter decomposition, nutrient accumulation, size categories, soil features

Introduction

Subsequent to the death of tree canopy or the logging of damaged tree layer of Norway spruce (*Picea abies* (L.) K a r s t e n), a ground layer of species favourably responding to the altered light, temperature and, eventually, even trophic conditions develops. Grasses such as *Calamagrostis arundinacea* occur in the Beskydy Mts in most clearings while *Avenella flexuosa* and *Calamagrostis villosa* and some tall ferns, such as *Athyrium distentifolium,* become dominant on smaller areas (Zelená, 1996). *A. distentifolium* covers clearings mostly at the elevation above 1100 m, specifically in places of original mountainous Norway spruce forests (Zelená, 1996). In the forest complex of the Kněhyně Nature Reserve, where the tree layer has been damaged, *A. distentifolium* forms large and dense stands in several sites. Similarly as grasses, ferns show the largest positive responses to thinning and canopy openings (Thomas et al., 1999; Vacek et al., 1999; Holeksa, 2003). Grass vegetation of deforested mountain areas was studied intensively by many authors and plenty of data on their development, biomass production, nutrient accumulation and their release during plant matter decomposition have been obtained including their important ameliorative role on forest barrens in mountainous regions affected by pollution (e.g., Pyšek, 1993; Fiala et al., 1998a, 2005). On the other side, there exists a serious gap in understanding the role of fern vegetation of deforested sites in despite of data availability on frond development, fenology, ecological optima and tolerance of *A. distentifolium* along environmental gradients in the western Norway (Odland et al., 1995). In order to specify the role of fern vegetation within deforested areas, the main goals of our studies were as follows:

1. to assess the variation in growth parameters of *A. distentifolium* as well as in production of fern stands growing in various habitats
2. to determine the nutrient uptake and their effective use by plant biomass of ferns
3. to estimate the rates of decomposition processes and nutrient releases from fern litter
4. to describe changes in soil features taking place after deforestation in fern stands
5. to compare the role of fern and grass vegetation on deforested areas.

The purpose of this paper is to summarize our results obtained during three years studies of fern stands growing on areas deforested after damage of forest stands due to acid depositions.

Material and methods

Study sites

The study sites were located on and near the top of the Kněhyně Mt. (49°30´ N, 18°19´ E) in the Moravian-Silesian Beskydy Mts in the Czech Republic. The chain of Moravian-Silesian Beskydy Mts forms a part of the western Carpathians bordering the Czech and Slovak Republics. The Kněhyně Mt. is characterized by annual mean air temperature of about 3.7 °C and average annual precipitation of 1102 mm (Hadaš, 1993). The region was influenced by air pollution from industrial agglomeration in Ostrava (the Czech Republic) and Katowice (Poland). The impact of pollution increased with increasing altitude (Hadaš, 1991). Wet bulk deposits recorded near the top of the Kněhyně Mt. during the growing season 1995 showed 25.3 $kg.ha^{-1}$ $SO4^{-2}$ and 22.8 $kg.ha^{-1}$ of nitrogen input at the rain water pH of 4.02 (Fiala et al., 1998a). The substrate of the studied sites is spodo-dystric cambisol, sandy loam. Rocks are represented by Flysch Godulian sandstone. *Athyrium distentifolium* stands were studied in three different sites: the first site was situated on a top plateau of the Kněhyně Mt. (altitude 1257 m a.s.l.) later referred to as top-site. It was covered by dying thin spruce forest with rich fern stands and with light level reduced to 70% of full sun. This site was exposed to a strong impact of acid depositions (see text above) as demonstrated by a large number of dead spruce. The second site was located at an altitude of about 1170 m with a SW exposure (later referred to as forest-site). Fern stands were located on the floor of a thin spruce forest, hence the light intensity was reduced to 17% of full sun. The third site was located at an altitude of about 1235 m with a south exposure fully exposed to sun (later referred to as clearing-site).

Plant analysis

Athyrium distentifolium plants (genets) are formed by thick rhizomes, branched in the form of fan, at the end of which clumps of fronds (fern leaves, ramets) grow up. We located and studied all *A. distentifolium* plants (genets) in a 5 x 10 m area of the fern stands in each of three sites on July 16, 1997. Diameter of each genet was measured at its base. In addition, the number of clumps of fronds growing from thick rhizomes in each genet were counted. Twenty fully grown, undamaged fronds were collected in order to find and compare their growth parameters. The fronds were collected by cutting at the point of their emergence from rhizomes. Plant samples were transported to the laboratory and the following variables were measured for each frond: total length, length of a petiole (measured from the point of emergence to the base of the frond blade – leafy part of the frond), diameter of frond base, length of longest leaflet. In addition, aboveground parts (fronds) of nine of the 83 plants were also harvested in the top-site to obtain so representatives of all size categories present in the sample area 50 m^2. The number of individual fronds (ramets) in clumps and their biomass for each plant were measured.

The aboveground plant matter of *A. distentifolium* stands was collected from sampling plots (five replicates 1.0 x 0.5 m) in the first half of August in 1994 and 1995 (Fiala, Jakrlová, 1997). The amount of decomposed biomass was assessed by the standard mesh-bag method. Nylon mesh-bags 15x10 cm (1.5 mm of mesh size) in five replications were used. The amounts of decomposed litter per m^2 were calculated from the rates of litter disappearance estimated by the mesh-bag method and from the data regarding annual production of aboveground biomass. All plant samples were dried to a constant weight and weighed. Analyses of N, P, K, Ca and Mg, both in biomass and undecomposed plant litter, were made in the laboratory of the Ústřední kontrolní ústav zemědělský in Brno. Standard international methods applied in agriculture were used. Data on the amount of nitrogen in dry weight of frond biomass at the end of the growing season and in the biomass at the maximum of stand development were used for the calculation of retranslocated and lost nitrogen (phosphorus). On the basis of litter amount estimated at the start and at the end of exposure and of actual content of minerals in both original and exposed litter, the release and/or accumulation of minerals during decomposition were calculated in $g.m^{-2}$.

This paper also includes results of chemical analyses of soil samples taken to the depth of 10 cm (from the rhizosphere of stands) from studied sites (Ježíková, Tůma, 1995a, b). Mixed samples from five soil cores (5 cm in diameter) were used for chemical analyses. A Radelkis (Hungary) pH meter was used for measuring pH–KCl and pH–H_2O. The content of soil organic matter was assessed by incineration at 550 °C. The content of exchangeable cations (Ca^{2+}, Mg^{2+}, H^+, Al^{3-}) was assessed complexometrically (Moravec, 1960).

Results and discussion

Growth parameters

The analyzed plants (genets) of *Athyrium distentifolium* from three different sites fell into five distinct size categories (Table 1). The most plants, i.e. 34.4%, were of the medium size III (31–60 cm). The largest plants we found had the diameter of 101–140 cm. However, there were no great differences in numbers of frond clumps of the same size category between top- and clearing-sites (Table 1). The highest density of individual plants (94 per 5 x 10 m) was recorded in the forest site. However, they formed the smallest number of frond clumps per plant. Thus, the most dens fern stand was developed in the top-site characterized by 83 plants and 1567 frond clumps per 50 m^2, i.e., 31.3 clumps of fronds of *A. distentifolium* per 1 m^2. As seen in Table 2, both the frond and petiole lengths of ferns in the top-site were

T a b l e 1. Number of *Athyrium distentifolium* plants (genets) of different size categories per 5x10 m area and number of clumps of fronds formed at the end of rhizomes for *A. distentifolium* different size categories. Mean values ± 1S.E. (standard error) are given. Recorded by K. Fiala and I. Tůma on July 16, 1997.

Size category/plant diameter (cm)	I (0–10)	II (11–30)	III (31–60)	IV (61–100)	V (101–140)	I–V Total
Number of plants						
Top-site	8	12	37	23	3	83
Clearing-site	9	9	21	17	5	61
Forest-site	13	33	39	9	0	94
Number of clumps of fronds						
Top-site	1.8 ± 0.8	4.8 ± 1.4	8.8 ± 3.3	13.6 ±4.5	24.3 ± 6.2	
Clearing-site	2.2 ± 0.5	7.6 ± 1.4	8.9 ± 1.5	13.6 ± 2.5	25.6 ± 3.8	
Forest-site	1.4 ± 0.5	3.7 ± 1.6	6.1 ± 1.0	9.1 ± 1.5	14.2 ± 3.6	

T a b l e 2. Average length of fronds, longest pinnas, petioles [cm], diameter of frond bases [mm] and biomass of fronds [g dry mass] for *Athyrium distentifolium* from three sites. Mean values and standard deviations (in parenthesis) are given (n = 20). Different letters denote significantly different values at the level P = 0.05. Recorded on July 16, 1997 (Pande, 1998).

Parameters	Top-site	Forest-site	Clearing-site
Length of fronds	140.9 ± 8.2a	152.3 ± 6.0b	151.6 ± 7.4b
Length of longest pinna	18.4 ± 1.2a	20.3 ± 2.2b	17.4 ± 1.7a
Length of petiole	32.3 ± 4.6a	36.9 ± 4.7b	35.8 ± 6.5b
Diameter of frond base	10.4 ± 1.5a	10.8 ± 1.8ab	11.7 ± 1.2c
Frond biomass	8.0 ± 1.1a	8.4 ± 1.5a	9.3 ± 1.2b

significantly lower (140.9 cm frond length) than those in the other two sites (152.3 cm in forest-site and 151.6 cm clearing-site). Although the average length of fronds as well as the average petiole lengths of ferns growing in shaded area (forest-site) was longer than that of fronds growing in open area (clearing-site), the differences were not significant. Significantly smaller diameter of frond base (10.4 mm) was measured in the top-site than in the clearing-site (11.7 mm). However, the difference between the top-site and the forest-site (10.8) (Table 2) was not significant. Lower level of radiation in the forest-site resulted in the increase in length of the longest pinna. The average length of the longest pinna in the forest-site was found to be 20.3 cm which was significantly different from the average lengths of the longest pinnas in the other two sites (18.4 cm and 17.4 cm for top-site and clearing-site, respectively). The most significant effects of radiation were observed in the frond biomass of ferns. Clearing-site, which had the highest level of radiation, also had the highest frond biomass (9.3 g) in comparison with top-site (8.0 g) and forest-site (8.4 g) and the respective differences were statistically significant (Table 2).

T a b l e 3. Length [cm] and biomass of shoots [g dry mass] for grasses growing in sites situated at lower and higher altitudes (Holub, 2003). Data are mean values (vegetative shoots n = 50, flowering shoots n = 20) and their ranges (in parenthesis) recorded at four localities in two years (1994, 1995). Recorded by Holub (2003).

Parameters	*Calamagrostis arundinacea*		*Calamagrostis villosa*	
Altitude	lower	higher	lower	Higher
Shoot length				
Vegetative shoot	61 (54–71)	55 (48–59)	50 (46–55)	52 (44–58)
Flowering shoot	131 (108–148)	103 (100–109)	–	–
Shoot biomass				
Vegetative shoot	0.51 (0.40–0.56)	0.53 (0.28–0.47)	0.18 (0.15–0.23)	0.17 (0.15–0.24)
Flowering shoot	1.42 (1.12–1.88)	1.07 (0.88–1.49)	–	–

The growth of aboveground shoots of *Calamagrostis arundinacea* was also substantially reduced under the influence of climatic factors and the acidification of environment at the higher altitude (Tables 3, 4). Similar conclusions followed from transplanting young *C. arundinacea* tufts to several sites under different climatic and pollution impacts (Tůma, 2003). No significant effect of similarly altered environmental conditions was found on the growth of aboveground shoots of *C. villosa* (Holub, 2003, Table 3). A hydroponic cultivation experiment has shown that the relative growth rate of *C. villosa* plants was higher even at pH 3.5 (Gloser et al., 1996). However, there were significantly lower values of the ratio of root to whole plant dry mass. Nevertheless, results obtained after transferring the soil blocks with *C. villosa* into the locality fully exposed to acid deposits in the Beskydy Mts indicate reduction of the length and dry weight of shoots. The effect of this environment resulted in significant reduction of both root and rhizome growth as well as of root/shoot ratios of *C. villosa* (Fiala, 1998, 2000). The plants have some capacity to adapt to environment pollution so that the impact on photosynthesis is accommodated by increasing the leaf area. This is at the expense of non-photosynthetic plant parts, especially roots (Mansfield, 1988). Nevertheless, the overall effect of pollution and worse soil features (acidity and excess of Al ions) may have resulted in the poor growth of plants (see also Anderson, Brunet, 1993). Plants growing at a lower radiation tended to decrease the investment in dry matter and increase their size (e.g. Corre, 1983). Den Dubbelden, Knops (1993) found that some species of ferns such as *Dicranopteris linearis*, *Dryopteris championii* etc., had significantly longer petioles when grown in dense stands than ferns growing in open stands with little competition for light. Our results are in accord with observations of above mentioned authors since both petiole and frond lengths reached the highest values in the forest-site. In addition, the effect of stress conditions (acidification, climatic impact) in the top-site may have resulted in an impaired growth of ferns. Higher density of frond clumps recorded in the top-site seems to be also associated with habitat conditions. In sites at higher altitudes, higher inputs of nitrogen in wet depositions can be reflected in the production of more offspring, since increased nitrogen or nutrient availability reduces the degree of apical dominance and releases dormant buds from inhibition (Carlsson, Callaghan, 1990; McItyre, 1972). Similarly, the

T a b l e 4. Comparison of the aboveground dry mass [g.m^{-2}] of *Athyrium distentifolium*, *Calamagrostis arundinacea* and *C. villosa* stands on deforested areas in the Beskydy Mts. Data are mean values (n = 5) and their ranges (in parenthesis) recorded in grass stands at four localities in 1994 and 1995 (Jakrlová[1], 1996a, b; Fiala, Jakrlová[2], 1997; Holub[3], 2003).

Type of stand/Locality	*Athyrium distentifolium*[2]		Grasses[1, 3]	
	forest-site	top-site	*C. arundinacea*	*C. villosa*
Aboveground biomass	194	291 (197–350)	635 (455–884)	471 (128–1039)
Plant litter	–	355	354 (220–560)	373 (238–569)
Total aboveground	–	705	950 (730–1100)	796 (375–1159)

density of *Calamagrostis arundinacea* shoots was twice as high in stands at the higher than at the lower altitude in the Beskydy Mts (Jakrlová, 1996a). Increasing neighbour density can also reduce the frond lengths (cf. Rünk et al., 2004).

Plant biomass and nutrient uptake

Aboveground biomass of herbage layer, formed by *Athyrium distentifolium* in damaged spruce stands of the Kněhyně Mt., ranged from 194 g.m^{-2} (forest-site, in 1994) to 350 g.m^{-2} (top-site, in 1995) (Table 4). The amount of old fern litter assessed in top-site reached 355 g.m^{-2}. Aboveground fern biomass was also estimated form data on the number of plants in different size categories and their dry mass in top-site. We found 83 plants of *A. distentifolium* in a 5 x 10 m area of the stand. By multiplying the average dry mass per clump by the number of clumps of each category, the above ground biomass would be 327 g.m^{-2} (Table 5). In the Beskydy Mts, the average values of aboveground biomass of grasses attained 635 g.m^{-2} (*Calamagrostis arundinacea*) and 471 g.m^{-2} (*C. villosa*) (Table 5). Thus the aboveground biomass of both *Calamagrostis* species reached values which were often twice as high as

T a b l e 5. Estimation of aboveground dry mass of *Athyrium distentifolium* five size categories in relation to number of clumps and number of fronds in clumps in top-site. Mean values ± 1 S.E. are given (n refers to the number of analyzed plants). Recorded on July 16, 1997 (Fiala et al., 1998b).

Size category	I	II	III	IV	V
Plant diameter (cm)	2.6 ± 2.1 (n = 8)	21.0 ± 3.7 (n = 8)	41.2 ± 7.4 (n = 32)	68.6 ± 8.5 (n = 27)	104.9 ± 14.7 (n = 8)
Number of clumps (no/plant)	1.8 ± 0.8 (n = 8)	4.8 ± 1.4 (n = 8)	8.8 ± 3.3 (n = 32)	13.6 ± 4.5 (n = 27)	24.3 ± 6.2 (n = 8)
Number of fronds (no/plant)	5 (n = 1)	17 (n = 1)	41 ± 4.6 (n = 3)	69 ± 8.7 (n = 3)	100 (n = 1)
Aboveground biomass (g/plant)	8.5 (n = 1)	43.5 (n = 1)	170 ± 23.3 (n = 3)	284 ± 27.7 (n = 3)	353 (n = 1)

T a b l e 6. Comparison of the concentration of nutrients [%] in aboveground parts of *Athyrium distentifolium, Calamagrostis arundinacea* and *C. villosa* stands on deforested areas in the Beskydy Mts. Data are mean values (n = 5) and their ranges (in parenthesis) recorded in grass stands at four localities in 1994 (Fiala, Jakrlová, 1996, 1997).

Type of stand/ Locality	*Athyrium distentifolium*		Grasses	
	forest-site	top-site	*C. arundinacea*	*C. villosa*
N				
Aboveground parts				
Living	2.01	3.03	0.96 (0.70–1.29)	1.3 (1.08–1.68)
Dead	1.97	3.23	–	–
Plant litter	–	2.09	0.39 (0.29–0.49)	1.45 (1.08–1.96)
P				
Aboveground parts				
Living	0.17	0.25	0.08 (0.07–0.10)	0.14 (0.12–0.17)
Dead	0.16	0.27	–	–
Plant litter	–	0.21	0.05 (0.04–0.06)	0.11 (0.08–0.13)
K				
Aboveground parts				
Living	1.56	2.31	0.13 (0.10–0.14)	1.22 (0.64–1.62)
Dead	0.23	2.58	–	–
Plant litter	–	3.09	0.08 (0.07–0.11)	0.28 (0.18–0.50)
Ca				
Aboveground parts				
Living	0.36	0.78	0.27 (0.21–0.35)	0.16 (0.11–0.28)
Dead	0.53	0.76	–	–
Plant litter	–	0.63	0.11 (0.07–0.16)	0.16 (0.12–0.21)
Mg				
Aboveground parts				
Living	0.66	0.63	0.09 (0.07–0.10)	0.12 (0.10–0.20)
Dead	0.34	0.55	–	–
Plant litter	–	0.40	0.04 (0.03–0.04)	0.05 (0.04–0.07)

the biomass of fern stands in the Beskydy Mts and as well as in other similar regions of the Central Europe (e.g., Pyšek, 1991; Koppisch, 1994).

A comparison of the concentration and accumulation of nutrients in fern and various grass stands growing on deforested areas have shown several differences between them. The highest concentrations of nitrogen and phosphorus were recorded in live aboveground parts of *C. villosa* and *Athyrium distentifolium* (Table 6). Similarly, Wardle et al. (2002) found the highest initial concentrations of N (1.36%) and P (0.13%) in fresh fern litter in comparison with monocots. These both plant species were also characterized by higher concentration of potassium. In spite of a lower amount of frond biomass, relatively high amount of nitrogen was accumulated in it (39–70 $kg.ha^{-1}$, top-site) and in fern litter as well (74 $kg.ha^{-1}$) (Table 7). However, of the three compared plant species, the largest amount of nitrogen was accumulated in aboveground biomass and plant litter of *Calamagrostis vil-*

T a b l e 7. Comparison of the accumulation of nutrients [kg.ha^{-1}] in aboveground parts of *Athyrium distentifolium, Calamagrostis arundinacea* and *C. villosa* stands on deforested areas in the Beskydy Mts. Data are mean values (n = 5) and their ranges (in parenthesis) recorded in grass stands at four localities in 1994 (Fiala, Jakrlová, 1996, 1997).

Type of stand/Locality	*Athyrium distentifolium*		Grasses	
	forest-site	top-site	*C. arundinacea*	*C. villosa*
N				
Aboveground biomass	5.8	39.4–70.3	48.3 (37.3–68.1)	52.8 (14.8–99.9)
Plant litter	–	74.2	13.2 (6.3–17.6)	56.6 (33.3–86.6)
Total aboveground	–	129.0	61.5 (49.6–85.7)	109.4 (48.1–186.5)
P				
Aboveground biomass	0.49	3.2–5.9	4.25 (3.4–5.3)	5.72 (1.6–8.8)
Plant litter	–	7.4	1.65 (1.1–2.1)	4.38 (2.7–5.3)
Total aboveground	–	11.9	5.9 (5.3–7.1)	10.1 (8.2–12.0)
K				
Aboveground biomass	4.25	30.0–54.6	6.37 (4.8–7.4)	48.9 (17.0–109.4)
Plant litter	–	109.7	2.80 (1.5–4.0)	11.9 (4.4–22.1)
Total aboveground	–	152.0	9.17 (7. 2–11.4)	60.8 (21.4–131.5)
Ca				
Aboveground biomass	1.4	10.1–12.6	13.5 (10.1–18.4)	6.3 (1.8–10.2)
Plant litter	–	22.4	3.9 (1.5–5.9)	5.9 (0.2–8.4)
Total aboveground	–	33.7	17.4 (13.1–24.3)	12.2 (5.5–18.5)
Mg				
Aboveground biomass	1.91	8.2–23.1	4.37 (3.7–5.3)	4.82 (1.4–7.4)
Plant litter	–	14.2	1.30 (0.7–1.6)	2.18 (1.0–3.4)
Total aboveground	–	29.8	5.67 (5.3–6.8)	7.0 (2.4–10.7)

losa. Athyrium distentifolium, similarly as *Calamagrostis arundinacea*, accumulates more Ca in aboveground biomass. In comparison with both grass stands, *Athyrium distentifolium* stands are characterized, particularly, by substantially greater accumulation of K, Ca and Mg in fern litter.

Calculation of the effective use of nitrogen and phosphorus indicates that greater losses of both nutrients (amount of nutrients remaining in dead plant matter at the end of growing season – fresh litter) in the forest site corresponded to 72.1% N and 64.7% P of the contents in maximum aboveground biomass (Table 8). Nitrogen use efficiency (NUE) in the *Calamagrostis arundinacea* stands increased with increasing altitude, while no relationship between altitude and NUE was found in the *C. villosa* stands (Holub, 2003). Low nutrient losses at the end of the growing season are favourable in nutrient-poor conditions (Berendse, 1985). The amounts of nitrogen retranslocated from aboveground to belowground parts were assessed in the *C. arundinacea* stands as 23.5% and in the *C. villosa* as 40.0% of nitrogen contents at the maximal development of stands (Holub, 2003, Table 8). At the top-site, N retranslocation in the fern stand represented even 53%. More intensive retranslocation of nutrients in *C. villosa* and *Athyrium distentifolium* stands is due to a large net of rhizomes formed by these plants. In contrast to grass stands of deforested areas, the

T a b l e 8. Comparison of retranslocation and losses of N and P [%] in *Athyrium distentifolium* and grass stands on deforested areas in the Beskydy Mts. Data calculated from mean values (n = 5) and their ranges (in parenthesis) recorded in grass stands at four localities in 1994 (Holub[1], 2003; unpubl.[2]).

Type of stand	Nitrogen		Phosphorus	
	retranslocation	losses	retranslocation	losses
A. distentifolium[2]				
Top-site	53.2	46.8	60.0	40.0
Forest-site	27.9	72.1	35.3	64.7
Grasses[1]				
C. arundinacea	36.9 (11.8–68.4)	63.1 (31.6–88.2)	–	–
C. villosa	39.8 (6.9–68.0)	60.2 (32.0–93.1)	–	–

studied fern stands require higher availability of nitrogen at a lower aboveground biomass production. Average nitrogen productivity (productivity of aboveground biomass dry mass per unit of nitrogen in the plant) recorded in grass stands was about 115 (*Calamagrostis arundinacea*) and 82 $g.gN^{-1}.year^{-1}$ (*C. villosa*) (Holub, 2003), whereas N productivity was only about 50 $g.gN^{-1}.year^{-1}$ in well developed fern stands in the top-site. Thus a higher amount of nitrogen was required by these fern stands for the formation of the same amount of aboveground biomass than by compared grass stands. Therefore an intensive spreading and formation of large *Athyrium distentifolium* stands may be supported by higher nitrogen input in wet depositions.

Decomposition processes

19.1 to 24.6% of dry mass of leaflets (small fern leaves) and 18.2 to 19.5% of frond stalks (spindles) were decomposed after one year in fern stands (Table 9). The decomposition rates of dead aboveground fern parts represented 0.58 to 0.82 $g.g^{-1}.day^{-1}$. Thus only about 39 $g.m^{-2}$ of dry mass was decomposed from 194 $g.m^{-2}$ of yearly production of aboveground biomass recorded in studied fern stands in 1994. Both *Calamagrostis* stands contributed much higher amounts of organic matter to the detritus food chain (up to 199 $g.m^{-2}$ after one year). All these data indicate substantially slower decomposition and turnover of plant matter in fern stands than those in *Calamagrostis* stands (Table 9). After one year of fresh litter decomposition, the amount of undecomposed dead plant matter contributing to the pool of older litter was about 155 $g.m^{-2}$ in fern stands and even up to 402 $g.m^{-2}$ in *Calamagrostis* stands (Tůma, 2002).

The rates of litter decomposition found for ferns were lower than those determined for most of other plant species (Wardle et al., 2002). The slower rates of decomposition of old dead material are mostly correlated with the higher initial C/N or lignin/nitrogen ratios of plants, reflecting differences in structural and secondary compounds (e.g. cellulose, lignin, phenols) (see Tůma, 2002). The comparison of several groups of plants has shown the ferns to contain greater amounts of lignin and phenols than monocots, whereas monocots had more cellulose (Wardle et al., 2002). Microbiological activities closely correspond with habitat characteristics (soil temperature, soil moisture, soil nitrogen). In the Beskydy Mts, negative correlations were recorded for both soil moisture and precipitation increasing with altitude and the activity of cellulolytic microorganisms on habitats with *C. arundinacea* (Tůma, 1998). Altitude correlated negatively and mean annual air temperature positively with the disappearance of leaf matter of *C. arundinacea* (Tůma, 2002). Activity of soil microbes was reduced and organic matter decomposition decreased with increasing pollution level and the influence of acid deposits (e.g. Zwoliński, 1994; Letl, Hýsek, 1994). All mentioned facts seem to be associated with slower decomposition of dead matter of fern recorded at localities situated at higher altitudes linked with lower temperatures, higher soil moisture and acidification of habitats.

In spite of slower decomposition of dead fronds, a fast release of calcium and magnesium was recorded from fern litter in studied sites (Table 10). At the end of the second year, 54–55% of Ca and 86–87% of Mg contained in plant matter at the beginning of exposition of fern litter were released. Emmer (1999) concluded that greater amounts of acidifying compounds may cause a higher release of Ca and Mg from plant litter. His data (released 40–55% of Ca from *C. villosa* litter) are close to our data recorded in fern stands. The contents of K and P decreased rapidly from fern matter in the forest-site. Release of nitrogen showed a different trend. However, the accumulation of N in fern litter, exceeding the initial value, was recorded only in the top-site. Immobilisation of considerable amounts of N in fern litter (accumulated to 46 kgN.ha^{-1} in

T a b l e 9. Comparison of relative decrease in dry mass [%] and decomposition rate [g.g^{-1}.day^{-1}] of dead plant matter of fern and grasses in deforested sites in the Beskydy Mts in winter period (November 3, 1993 – May 12, 1994) and in 1-year period (November 3, 1993 – October 12, 1994). Data on decomposition of ferns and grasses are mean values (n = 5) and their ranges (in parenthesis) recorded in grass stands at four localities (Tůma[1], 2002; unpubl.[2]).

Type of stand/Locality	*Athyrium distentifolium*[2]				Grasses[1]			
	forest-site		top-site		*C. arundinacea*		*C. villosa*	
Plant parts	leaflets	stalks	leaflets	stalks	leaves	stalks	leaves	stalks
Decomposed dry mass								
Winter period	11.0	6.8	11.2	8.1	25.5 (20.3–31.3)	9.05 (7.6–10.5)	16.6 (14.4–17.9)	9.3 (7.7–12.3)
1-year period	24.6	18.2	19.1	19.5	45.4 (38.9–53.8)	23.8 (17.5–28.9)	38.0 (34.9–41.2)	26.2 (23.3–29.7)
Decomposition rate								
Winter period	0.61	0.37	0.62	0.45	1.55 (1.19–1.97)	0.49 (0.42–0.58)	0.95 (0.81–1.04)	0.55 (0.42–0.69)
1-year period	0.82	0.59	0.62	0.63	1.78 (1.44–2.25)	0.79 (0.56–0.99)	1.39 (1.25–1.55)	0.89 (0.77–1.03)

T a b l e 10. Comparison of amounts of released (-) and/or accumulated (+) nutrients (in kg ha^{-1}) in decomposing litter of *Athyrium distentifolium* fern and in grass stands in deforested areas in the Beskydy Mts during two years (November 3, 1993 – October 8, 1995). Percentage of original amounts of nutrients released or accumulated in plant litter [%]. Data on nutrient release from litter of ferns and grasses are mean values (n = 5) and their ranges (in parenthesis) recorded in grass stands at four localities (Tůma[1], 2002; unpubl.[2]).

Athyrium distentifolium [2]					
Forest-site					
Period	N	P	K	Ca	Mg
1-year	-0.03	-0.45	-5.99	-5.11	-4.92
%	-0.1	-19.7	-56.6	-33.5	-70.3
2-years	-0.13	-0.69	-6.34	-8.39	-6.03
%	-0.4	-30.2	-60.0	-55.0	-86.1
Top-site					
Period	N	P	K	Ca	Mg
1-year	+3.48	-0.16	-0.99	-3.11	-5.03
%	+11.9	-7.9	-17.6	-26.4	-69.5
2-years	+2.92	-0.42	-1.04	-6.41	-6.32
%	+9.9	-20.4	-18.6	-54.3	-87.2
Grasses [1]					
Calamagrostis arundinacea					
Period					
1-year	-3.6 (-0.9–5.6)	-1.4 (-0.7–2.2)	-3.08 (-2.61–3.64)	-1.0 (-0.01–-0.19)	-2.3 (-0.13–-0.32)
%	-15.6 (-5.7–-22.8)	-39.8 (-27.6–-52.4)	-90.5 (-89.7–-90.1)	-16.7 (-1.9–-26.8)	-56.5 (-47.9–-63.2)
2-years	-0.14 (-0.22–+0.24)	-0.17 (-0.09–-0.26)	-2.50 (-2.03–-3.07)	-0.11 (-0.09–-0.22)	-0.25 (-0.14–-0.36)
%	+5.1 (-4.1–+15.1)	-51.8 (-29.4–-62.0)	-73.2 (-70.4–-76.1)	-21.6 (-16.1–-34.5)	-63.2 (-48.9–-71.6)
Calamagrostis villosa					
Period					
1-year	+0.02 (-0.03–+0.19)	-0.04 (-0.14–+0.03)	-0.88 (-0.54–-1.03)	-0.34 (-0.21–-0.55)	-0.28 (-0.12–-0.48)
%	+1.60 (-1.8–+10.2)	-13.6 (-42.1–+26.1)	-73.0 (-55.1–-88.2)	-46.7 (-42.3–-54.7)	-72.9 (-63.1–-77.0)
2-years	+0.11 (-0.08–+0.26)	-0.05 (-0.8–+0.02)	-0.68 (-0.27–-0.95)	-0.43 (-0.25–-0.68)	-0.29 (-0.13–-0.48)
%	+5.1 (-4.9–+14.5	-17.2 (-34.4–+17.7)	-46.4 (-51.6–-68.7)	-59.5 (-52.2–-68.7)	-76.2 (-64.3–-83.6)

1-year old litter) may be associated, beside microorganisms entering the litter, with enrichment from external sources (Zimka et al., 1990; Emmer, 1999), e.g. from inputs of N in wet depositions representing about 23 kgN.ha^{-1} at Kněhyně Mt. during growing season. Data obtained in fern stands suggest a mobility series of Mg > K > Ca > P > N. During the decomposition of grass litter, Ca and Mg were released faster in *C. villosa* stands, while a more rapid turnover of N, P and K was in *C. arundinacea* stands (Tůma, 2002) (Table 10). In spite of lower amount of decomposed dead fern matter, values of nutrients entering into soil during decomposition of dead fern fronds given in Table 10 are mostly close to the data recorded in grass stands on deforested areas.

Soil features

Soil analyses have shown higher contents of soil organic matter and lower pH values in fern stands than those in an adjacent spruce forest without herbage layer (Table 11) (Ježíková, Tůma, 1995a, b). There were no great differences in contents of Ca, Mg and Al between soils of fern stands and the forest. Table 11 gives only results of chemical analyses of soil samples taken on October 12, 1994. Nevertheless, data obtained in the same sites earlier, i.e., in autumn 1993 and in spring 1994 were very close to presented values (Ježíkova, Tůma, 1995b). In the Beskydy Mts, data on soil features assessed in stands of both *Calamagrostis* species represent mostly more favourable soil conditions than those found in both fern and forest stands (Ježíkova, Tůma, 1995a, b; Fiala et al., 1998a). Soil pH measured in fern stands did not even reach the lowest pH values determined in soil of old grass stands (Table 11). Comparison of Ca/Al ratios in soils of fern stands (0.58–0.84) and grass stands (1.92 and

T a b l e 11. Comparison of the soil features of 0–10 cm soil layer in *Athyrium distentifolium*, and in grass stands on deforested areas in the Beskydy Mts. Data are results of individual analysis of mixed soil samples from 5 soil cores (5 cm in diameter) and their ranges (in parenthesis) recorded in grass stands at four localities on October 20, 1994 (Ježíková, Tůma, 1995a,b). Data assessed in adjacent spruce forest are also given.

Type of stand/ Locality	Spruce forest	*Athyrium distentifolium*		Grasses	
	top-site	forest-site	top-site	*C. arundinacea*	*C. villosa*
pH-H_2O	3.84	3.62	3.53	3.89 (3.77–4.06)	3.84 (3.49–4.19)
pH-KCl	3.31	2.97	2.84	3.43 (3.24–3.55)	3.32 (2.99–3.02)
Organic matter [%]	37.8	53.0	57.7	30.8 (17.4–45.0)	39.2 (34.7–46.1)
Ca^{2+} [mg.1kg^{-1}]	570	840	720	781 (425–420)	801 (170–1710)
Mg^{2+} [mg.1kg^{-1}]	370	720	470	670 (278–1216)	833 (413–1486)
Al^{3+} [mg.1kg^{-1}]	1320	1000	1230	663 (338–1638)	554 (325–981)

1.37 – calculated from average values recorded at four localities in *C. arundinacea* and *C. villosa* stands, respectively) indicates a greater soil acidification and more unfavourable soil conditions in fern stands. Grass cover may improve (and its removal may deteriorate) the soil environment, e.g. it may decrease the soil acidity, increase the base cation contents etc. (Zelená et al., 1996; Peřina, Květ, 1975; Sedláková et al., 1999; Takamatsu et al., 1997). Both grasses bound and accumulate large amount of nitrogen in their aboveground and, particularly, in belowground parts (Fiala et al., 2005). *C. villosa* prefers taking up nitrates instead of ammonium salts (Gloser et al., 1996) and therefore is likely to make the soil solution more alkaline (Kenedy, 1992). The ability of these grass stands to reduce excess of soil nitrogen is associated with the elimination of soil acidification and the reduction of nutrient losses (Fiala et al., 2005). In fern stands, high nitrogen uptake by aboveground parts and immobilization of nitrogen in undecomposed litter was also recorded. Unfortunately, data on belowground parts of *Athyrium distentifolium* are not available. Grass stands could affect chemical properties of soil more effectively due to a greater amounts of mineral nutrients entering into the soil from decomposed plant litter and to the grass stand ability to mobilize efficiently mineral nutrients in the shorter time period necessary for biomass turnover. The amount of decomposed belowground grass parts represented, for example, about 760 $g.m^{-2}.year^{-1}$ (Fiala, 1998). Ferns can probably develop a herbage layer in dying forests relatively early by creating special microclimatic conditions. This can be a reason for a higher soil organic matter content in fern stands than in grass stands. Generally, deforestation leads to high organic matter decomposition, since considerable changes in microclimate cause more favourable conditions for the development and activity of soil microorganisms (e.g., Cudlín et al., 1997; Tůma, 1998; Emmer, 1999). We can suggest that fern stand formation on deforested sites has not the same positive effect on soil environment as was described for both species of *Calamagrostis*. Nevertheless, the feed back effects of tall fern vegetation on soil environment of sites affected by acid depositions still require further studies.

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Tůma I., Fiala K., Holub P., Pande K.: **Tvorba biomasy, odběr živin a jejich uvolňování v porostech kapradiny** *Athyrium distentifolium* **na odlesněných plochách ovlivněných polutanty: srovnání s porosty trav.**

Nepříznivý vliv klimatických faktorů a kyselých depozic vyskytující se ve vyšších nadmořských výškách Moravskoslezských Beskyd se projevil v horších růstových parametrech kapradiny *Athyrium distentifolium*. Listy kapradiny byly zde kratší, řapík tenčí a biomasa listů menší než kapradin rostoucích v nižších polohách. Podobně byla také na odlesněných plochách ve vyšších polohách Beskyd zaznamenána kratší délka a menší biomasa prýtů *Calamagrostis arundinacea*. Na rozdíl od travinných porostů odlesněných ploch, porosty kapradin při nižších hodnotách produkce nadzemní biomasy (194–350 g.m^{-2}) hromadily v ní velká množství dusíku (3,9–7,0 gN.m^{-2}). Proto zřejmě v porostech kapradin bylo třeba větší množství dusíku k vytvoření téhož množství nadzemní biomasy než tomu bylo ve srovnávaných travinných porostech. Při pomalejších rozkladech opadu kapradiny (za rok 19–25% hmotnosti sušiny lístků a 18–19% vřetene listu) než bylo u opadu trav (35–54% listů, 17–30% stonků), uvolňování Ca (54–55%) a Mg (86–87%) bylo rychlejší a množství dusíku imobilizovaného v rok starém opadu dosáhlo až 46 kg N na hektar. Srovnání půdních vlastností ukazuje na méně příznivé půdní podmínky (nižší hodnoty pH, obsahu Ca a poměrů Ca/Al) než bylo v travinných porostech. Tato data ukazují, že vytvoření porostů kapradin na odlesněných plochách nemusí znamenat tentýž pozitivní vliv na půdní prostředí, jak byl popsán pro oba dva druhy *Calamagrostis*.