Ekológia (Bratislava) Vol. 30, No. 3, p. 381–395, 2011
doi:10.4149/ekol_2011_03_381

ECOLOGICAL ANALYSIS OF HERBAGE LAYER OF DISTURBED SPRUCE STANDS IN THE NATIONAL NATURE RESERVE KNĚHYNĚ-ČERTŮV MLÝN IN THE BESKYDY MTS

KAREL FIALA[1], IVAN TŮMA[1, 2], PETR HOLUB[1, 3], JAROSLAV ZÁHORA[2]

[1] Department of Vegetation Ecology, Institute of Botany, Academy of Sciences of the Czech Republic, Lidická 25, 602 00 Brno, Czech Republic; e-mail: karel.fiala@ibot.cas.cz, tuma@brno.cas.cz, hugo@brno.cas.cz

[2] Department of Agrochemistry, Soil Science, Microbiology and Plant Nutrition, Faculty of Agronomy, Mendel University in Brno, Zemědělská 1, 613 00 Brno, Czech Republic; e-mail: tuma@mendelu.cz, zahora@mendelu.cz

[3] Global Change Research Centre, Academy of Sciences of the Czech Republic, Bělidla 4a, 603 00 Brno, Czech Republic; e-mail: holub.p@czechglobe.cz

Abstract

Fiala K., Tůma I., Holub P., Záhora J.: Ecological analysis of herbage layer of disturbed spruce stands in the National Nature Reserve Kněhyně-Čertův mlýn in the Beskydy Mts. Ekológia (Bratislava), Vol. 30, No. 3, p. 381–395, 2011.

A comparative floristic and ecological analysis of herbage layers of spruce forests and clear-cut vegetation was performed in the National Nature Reserve Kněhyně-Čertův mlýn in the Moravian-Silesian Beskydy Mts affected by air pollution. Understory vegetation was studied in the following forests: in a spruce stand with partly opened canopy (Site 1), in a less damaged spruce monoculture, with more opened canopy (Site 2), in a thin, dying back forest on the top plateau of the Kněhyně hill (Site 4) and in clear cut area covered by grass vegetation (Site 3). The obtained data demonstrate that favourable light conditions support the spreading of ferns and grasses, particularly. The aboveground dry mass of the whole herbage layer ranged from 580 kg ha^{-1} (Site 2), over 2510 kg ha^{-1} (Site 4), and to 5711 kg ha^{-1} in the Site 3. Both greater concentration and accumulation of nutrients in plant biomass of herb layer were found in the Site 4 and in the Site 1. The highest values of amount of nutrients accumulated in aboveground biomass (e.g., 83.9 kg N ha^{-1}, 6.9 kg P ha^{-1}) were calculated for *Calamagrostis villosa* stands on the clearing (Site 3). The decomposition of *C. villosa* litter was substantially greater than was recorded for *Athyrium distentifolium* litter. In the course of the first year, 35.6% of leaf dry mass and 23.3% of culm dry mass of *C. vilosa* was decomposed. In the same period, 19.1% leaflets and 19.5% stalks dry mass was decomposed in the *A. distentifolium* stand in the Site 4. Average amount of dry mass of aboveground plant parts entering soil of *C. villosa* stand reached 170 g m^{-2}, while in the *A. distentifolium* stand it was substantially lower (37 to 42 g m^{-2} per year). The release of Ca and Mg was slower from fern litter (24.6 and 69.4% respectively) than from *C. villosa* litter (42.5 and 76.8%). In comparison with the soil of spruce forests, the soil pH values and as well as the concentration of Ca^{2+} and Mg^{2+} ions were higher only under the influence of clear-cut grass vegetation.

Key words: nutrient accumulation, nutrient release, plant biomass, plant litter decomposition, soil features

Introduction

Dying of spruce forests caused by pollution, destruction of forest canopy after cyclones and forest clear cutting result in intensive spreading of herbaceous vegetation on deforested areas. Hence improved light conditions, after the destruction of tree canopy, soil acidification and increased N availability were reflected in extensive spreading plants of forest understory, mainly acidophilous perennial grasses *Calamagrostis arundinacea* and *C. villosa* (e.g., Fiala et al., 1989; Pyšek, 1990; Koppisch, 1994; Viewegh, 1994). The expansion of tall fern (*Athyrium distentifolium*) was also observed on some sites. Similarly as grasses, ferns also show a large positive response to thinning of stands and canopy openings. Thus extensive fern stands were found spreading and covering large areas in mountainous regions of Central Europe (Thomas et al., 1999; Vacek et al., 1999; Holeksa, 2003; Tůma et al., 2006). In comparison with perennial grasses (see above), there exists a serious gap in understanding the role of fern vegetation on deforested sites (see Odland et al., 1990, 1995). There is no doubt that the fern understory influences conspicuously the emergence of tree-seedlings; this species may also arrest forest succession (George, Bazzaz, 1999; Hill, Silander, 2001; de la Cretaz, Kelty, 2002). Therefore the role and importance of fern stands after deforestation can not be neglected.

Atmospheric input may substantially affect biogeochemical cycling, especially in areas subjected to high concentrations of air pollutants. One of the major threats to the structure and functioning of ecosystems is high levels of air-borne nitrogen (N) pollution (Kennedy, 1992; Bobbink, Roelofs, 1995; Bobbink et al., 1998). Although some improvements have been made with respect to the reduction of the amount of pollutants in Central Europe (Květ, 1993; Fanta, 1997), acid deposition still occurs and current N loads can exceed the critical loads of plant nutrition in some regions (Hůnová et al., 2004). Acidification by N inputs can be accompanied by unfavourable chemical reactions taking place in the soil, especially after nitrification of ammonium in weakly buffered environment. These processes are associated with subsequent leaching of basic cations (e.g., Nihlgard, 1985; Schulze et al., 1989; Bobbink, 1998). Up to 30–40% of the total leaching of N from forest soils, can originated from clear-cuts (Dahlgren, Driscoll, 1995).

A rapid regeneration of vegetation cover following disturbance tends to minimize losses of nutrients from the ecosystem and to promote a return to steady-state cycling (e.g., Marks, Borman, 1972; Vitousek, Stanford, 1986). In addition, both the concentration of nutrients and soil pH increase in upper soil layers with age of secondary succession (Donaldson, Henderson, 1990).

The aim of this study was to obtain data on the effect of forest disturbance on the expansion, growth and formation of various herbage vegetation in different stages of forest decline and on the clear cutting after felling damaged spruce forest in the National Nature Reserve Kněhyně-Čertův mlýn in the Moravian-Silesian Beskydy Mts. The study was also concerned on estimation of nutrient pool in expanding vegetation, release of nutrients during plant matter decomposition and on the soil chemistry of their habitats.

Problems were studied in cooperation with the Mendel University Brno in the framework of the project “Effect of anthropogenic immissions on forest and forestry of the Beskydy Mts.” and supported by the Ministry of Agriculture of the Czech Republic.

Material and methods

The study sites were located in spruce forests in the National Nature Reserve (NNR) Kněhyně-Čertův mlýn in the Moravian-Silesian Beskydy Mts in the Czech Republic. The annual mean air temperature of the Kněhyně hill (49°29´44´´ N, 18°18´46´´ E, altitude 1257 m) is 3.7 °C while annual precipitation averages 1102 mm (see Fiala et al.,1998). Wet bulk deposits recorded near the top of the Kněhyně hill during the growing season 1995 showed 25.3 kg SO_4^{2-} ha^{-1} and 22.8 kg ha^{-1} of nitrogen input at the rain water pH of 4.02. The substrate of the studied sites is Spodo-Dystric Cambisol, sandy loam. Rocks are represented by Flysh Godulian sandstone. In the studied areas mostly Norway spruce (*Picea abies*) forests dominated and two grasses, *Calamagrostis villosa* and *C. arundinacea* often occurred in the understory. Fern stands of *Athyrium distentifolium* were found in patches through the spruce forests. A comparative floristic and ecological analysis was curried out in four sites in different stages of forest damage (later referred to as Site 1 to Site 4, Fig. 1). In the Site 1, a spruce stand was developed with partly opened canopy and with fern stands on the bottom (altitude about 1175 m, SE exposure). The second site (Site 2) was located at an altitude of about 1170 m with a SW exposure. Fern stands occurred on the floor of a less damaged spruce forest with more opened canopy, hence the light intensity was reduced to 17% of full sun. The third site (Site 3) was clearing, at least five years old, fully expose to sun. Stands of *Calamagrostis villosa* were located at an altitude of about 1240 m with SW exposure. The fourth site was a plateau on the top of Kněhyně hill (altitude1250 m) (Site 4). The light level was reduced to 70% of full sun. The plateau was covered by dying damaged spruce forest mostly with patches of young sparse *C. villosa* stands (Site 4 A), with stands dominated by *Athyrium distentifolium* fern (Site 4 B) and partly without cover of herb layer on forest floor (Site 4C). This site was exposed to a stronger impact of acid deposition as demonstrated by a large number of dead spruce.

The main part of studies was conducted on August 12, 1993. Plant litter decomposition was recorded in winter period (November 3, 1993–May 12, 1994) and in 1-year period (November 3, 1993–October 12, 1994). Presence of individual plant species and their percentage cover were recorded in selected large plots (200 m^2 – Site 1, 2, or 300 m^2 – Site 4 in forests and 25 m^2 on the clearing). Aboveground biomass of prevailing plant species was taken randomly from five areas 0.2x0.5 m, biomass of tall fern *A. distentifolium* from five areas 0.5x1.0 m. Twenty soil cores (5 cm in diameter, 10 and 20 cm in length – according to soil depth) were used to assessed belowground plant biomass of *Calamagrostis villosa* and *Athyrium distentifolium* stands. The roots were washed free of soil over a 0.5 mm mesh sieves. Plant samples were dried and weighed. The litter-bag method was also used in order to assess decomposability and nutrient release from plant litter. Nylon mesh-bags 15x10 cm in size (1.5 mm of mesh size) were used. After the exposure of 10 samples, the decrease in dry mass of original plant litter was determined and decomposition rates calculated. The chemical analyses of plant biomass and soils were made at the chemical laboratory of the AGROLAB company in Troubsko, CZ. Standard international analytical methods applied in agriculture were used. Accumulation of nutrients was calculated by multiplying the dry mass of biomass by nutrient concentrations. Obtained data were evaluated using the statistical package STATISTICA 6.0.

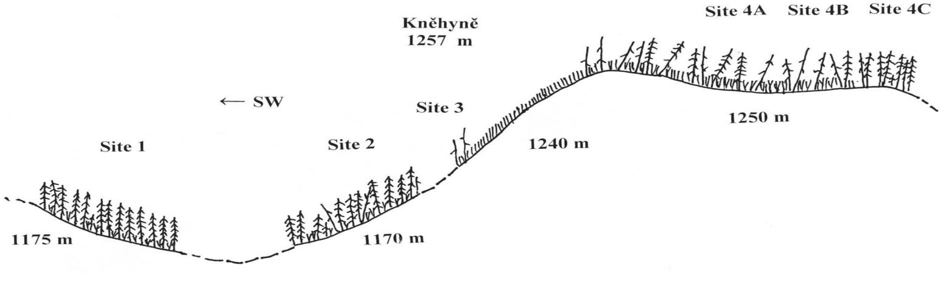

Fig. 1. Schema showing the location of studied sites in the NNR Kněhyně-Čertův mlýn.

Results and discussion

In the NNR Kněhyně-Čertův mlýn, opening the canopy of spruce forests resulted in an increase of dominance of ferns in understory vegetation, above all stands of *Athyrium distentifolium* and *Calamagrostis villosa* on clear cut sites near the top of the Kněhyně hill (Fig. 2). The percentage cover of ferns reached 67 to 83%, in areas of Sites 1 and 2, respectively. Percentage cover of *Vaccinium myrtilus* attained up to 40% on the surface of the top plato (Site 4). Favourable light conditions in damaged spruce stands can resulted in significantly

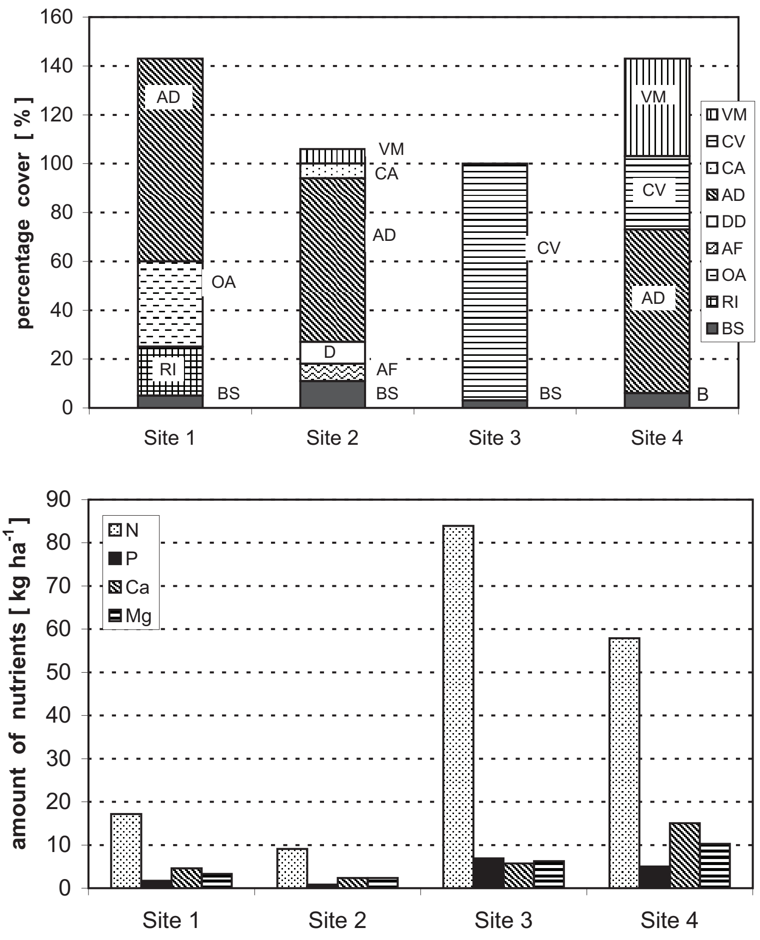

Fig. 2. Percentage cover of *Vaccinium myrtilus* (VM), *Calamagrostis villosa* (CV), *Calamagrostis arundinacea* (CA), *Athyrium distentifolium* (AD), *Driopteris dilatata* (DD), *Avenella flexuosa* (AF), *Oxalis acetosella* (OA), *Rubus idaeus* (RI) and bare forest soil (BS) in studied different spruce stands and on clearing in the NNR Kněhyně-Čertův mlýn. Amounts of accumulated nutrients in herbage layers of different spruce stands and on clearing in the NNR Kněhyně-Čertův mlýn are also given.

higher mean length and weight of bilberry twinges (on the average by 33%) (Kukla, Kuklová, 2008). Extensive stands of *Athyrium distentifolium* were found in other mountainous regions of Central Europe (Thomas et al., 1999; Vacek et al., 1999; Holeksa, 2003). *A. distentifolium* covers clearings mostly at an elevation above 1100 m, specially in cleared mountainous Norway spruce forests. This fern may be dominant in edaphically rich areas (Odland, 1991). Generally, species richness and plant biomass herbaceous forest species increased with light availability (e.g., Elemans, 2004; Hofmeister et al., 2009). The advance growth of *Sorbus aucuparia* L. originated spontaneously under disintegrating Norway spruce stands was recorded in the Beskydy Mts (Tesař et al., 1994). Thank to further thin out of spruce stands, mountain ash also responded very sensitively to external grow conditions in our studied sites during last fifteens years. In sites 2 and 3 and in their surroundings, percentage cover of young ash trees ranged between 5 to 10% in spruce stands and their heights reach mostly 2 to 4 m. During last two decades, the top plateau of the Kněhyně hill was completely covered by compact and dense stands of *Calamagrostis villosa*. According to Tesař et al. (1994) mountain ash stands originated spontaneously by natural regeneration should be supported as stands with a climate-protection role. They can be used to mitigate the effect of air pollution synergetically enhanced by mountain to climate.

Average values of dry mass of aboveground biomass of stands of main, prevailing plant species in understory of spruce forests and in the clearing in NNR Kněhyně-Čertův mlýn are summarized in Table 1. *Athyrium distentifolium* formed only 79 g m^{-2} in slightly opened canopy (Site 1). However, in the area in the less damaged spruce stand (Site 2), the aboveground biomass formed by *A. distentifolium* attained 194 g m^{-2}. The average value of its total (living + dead) belowground dry mass was 2412 g m^{-2}. The *Vaccinium myrtilus* and grasses represented only relatively lower amount of aboveground dry mass. In the dying and felling spruce stand in the upper part of the Kněhyně hill (Site 4), 194 g m^{-2} of dry mass of aboveground parts of fern was recorded. Nevertheless, a higher aboveground biomass of *Athyrium distentifolium* was also recorded in the same region (355 g m^{-2}, Fiala, Jakrlová, 1997). In the Site 4, the above-

T a b l e 1. Average values (± standard error) of dry mass (in g m^{-2}) of stands of prevailing plant species in herbage layer of spruce forests and in the clearing in the NNR Kněhyně-Čertův mlýn.

	Site 1	**Site 2**	**Site 3**	**Site 4**
Aboveground biomass				
Athyrium distentifolium	79±16.5	194±21.8	-	194±43.9
Vaccinium myrtilus	-	39±6.3	-	210±22.3
Calamagrostis villosa	-	-	572±91.0	122±17.8
Calamagrostis arundinacea	-	36±19.7	-	-
Avenella flexuosa	-	14±5.7	-	-
Oxalis acetosella	7.0±2.4	-	-	-
Total	86	283	572	526
Belowground biomass				
Athyrium distentifolium	-	2412±326	-	-
Calamagrostis villosa	-	-	2900±361	-

ground biomass of *Vaccinium myrtilus* reached higher values (210 g m^{-2}) than was recorded in other studied sites. Dry mass of aboveground parts of young *Calamagrostis villosa* stands was only 122 g m^{-2}. However, the old *C. villosa* stand attained 572 g m^{-2} of aboveground biomass and 2900 g m^{-2} of the total belowground dry mass (Site 3). In the Beskydy Mts, aboveground biomass recorded in various stands of *C. villosa* attained 471 g m^{-2} on the average (Fiala et al., 1998). Thus the aboveground biomass of these grass species reached values which were often twice as high as the biomass of fern stands in the Beskydy Mts and as well as in other similar regions of the Central Europe (e.g., Pyšek, 1993; Koppisch, 1998; Fiala et al., 1994).

Assessed values of aboveground biomass of the most of presented plant populations (see text above) and their participation in percentage cover of studied plots (200 and 300 m^2) of different forests enable us to roughly estimate species participation and the amount of total aboveground biomass of herbage layer in individual of studied sites. In the spruce stands, the dry mass of total aboveground biomass, involving biomass of all present plant populations occurring in analyzed plots, ranged from 580 kg ha^{-1} in Site 2 (the less damaged spruce stand), over 2510 kg ha^{-1} in the damaged spruce stand on the top of the hill, up to 5711 kg ha^{-1} in the *C. villosa* stand on old clearing. There were mostly ferns which participated greatly on total aboveground biomass of herbage layer in studied spruce stands. In the Site 2 and on the top plateau of the Kněhyně hill, ferns comprised about 50% of aboveground biomass of whole herbage layer and in the thinning stand (Site 1) they even attained up to 90% of whole biomass (17 kg ha^{-1}). Lower values of aboveground biomass of herbage layer (240 to 600 kg ha^{-1}) were reported by Kubíček et al. (1989) mostly in spruce forest communities in the Beskydy Mts (Kysuce region) and estimated using the methods of indirect sampling. Similarly only 0.51 to 231 kg ha^{-1} of aboveground biomass of herbage layer was assessed in broad-leaves forests and variations in aboveground biomass values depended on floristic structure of studied communities (Kollár et al., 2010).

Higher concentrations of mineral nutrients (above all N, P, Ca and K) were assessed in herbage biomass of both damaged spruce stand on the top plateau (Site 4) and in the

T a b l e 2. Percentage concentration of nutrients bounded in aboveground biomass of stands of prevailing plant species in spruce forests and in the clearing in NNR Kněhyně-Čertův mlýn).

Aboveground biomass	N	P	Ca	Mg	K	Na
Site 1						
Athyrium distentifolium	2.25	0.22	0.59	0.41	2.94	0.005
Oxalis acetosella	3.38	0.42	1.06	0.88	2.68	0.007
Site 2						
Athyrium distentifolium	2.1	0.17	0.36	0.66	1.56	0.005
Vaccinium myrtilus	1.25	0.14	0.50	0.17	0.48	0.006
Site 3						
Calamagrostis villosa	1.47	0.12	0.10	0.11	1.62	0.006
Site 4						
Athyrium distentifolium	3.03	0.25	0.78	0.63	2.31	0.008
Vaccinium myrtilus	1.43	0.14	0.54	0.20	0.63	0.005
Calamagrostis villosa	1.75	0.15	0.10	0.11	1.86	0.005

Site 1, characterized by thinning forest canopy (Table 2). On the contrary, lower content of nutrients was found in fern of the less damaged spruce stand (Site 2). The highest concentrations of nitrogen and phosphorus were mostly recorded in live aboveground parts of *Athyrium distentifolium* (3.03–2.1% N, 0.17-0.25% P) and *Calamagrostis villosa* (1.47–1.75% N, 0.12–0.15% P). Both these plant species were also characterized by higher concentration of potassium (1.56–2.94% *Athyrium distentifolium*, 1.62–1.86% – *Calamagrostis villosa*). Similarly, Wardle et al. (2002) assessed the highest initial concentrations of N (1.36%) and P (0.13%) in fresh fern litter in comparison with monocots. Kuklová and Kukla (2008) found that nitrogen content in herbs varied in spruce stands between 1.41–3.01% (control stand) and 1.22–3.15% (damaged stand) - maximum values were also assessed in fern – *Dryopteris dilatata*.

In spite of a lower amount of frond biomass, relatively high amount of nitrogen was accumulated in it (5.86 g m^{-2} – Site 4, Table 3). However, the largest amount of nitrogen was accumulated in aboveground biomass of *Calamagrostis villosa* (8.41 g m^{-2} – Site 3). Holub (1999, 2003) reported that the aboveground biomass of *C. villosa* stands accumulated on the average 7.6 g N m^{-2}, whereas that of *C. arundinacea* only 2.6 g N m^{-2} on deforested areas of the Beskydy Mts. He found a negative correlation between altitude and nitrogen use efficiency in *C. villosa* stands. *Athyrium distentifolium* accumulated more Ca and Mg in aboveground biomass (e.g., Ca – 0.36–0.78% and 0.47–1.51 g m^{-2}) than was found in *Calamagrostis villosa* (Ca – 0.10%, 0.12–0.57 g m^{-2}).

In spruce ecosystems, Kuklová and Kukla (2008) found that the most abundant nutrients in all herb species were nitrogen and potassium. Nitrogen content varied between 1.41–3.01% (control stand) and 1.22–3.15%, (damaged stand) - maximum was assessed in the *Dryopteris dilatata* fern and *Rubus idaeus*) Mean contents of nutrients in dry matter (in %) in herbs sampled in spruce stands decreased as follows: N (1.97–2.19) > K (1,3–1,6) > Ca (0.34– 0.41) > Mg (0.27–0.28) > P (0.10–0.12).

Table 3. Amount of nutrients accumulated in aboveground biomass (g m^{-2}) of stands of prevailing plant species in spruce forests and in the clearing in the NNR Kněhyně-Čertův mlýn).

Aboveground biomass	N	P	Ca	Mg	K	Na
Site 1						
Athyrium distentifolium	1.78	0.17	0.47	0.32	2.32	0.004
Oxalis acetosella	2.37	0.29	0.74	0.62	1.88	0.005
Site 2						
Athyrium distentifolium	4.07	0.33	0.70	1.28	3.03	0.01
Vaccinium myrtilus	0.49	0.05	0.20	0.07	0.19	0.002
Site 3						
Calamagrostis villosa	8.41	0.69	0.57	0.63	9.27	0.03
Site 4						
Athyrium distentifolium	5.86	0.49	1.51	1.22	4.48	0.02
Vaccinium myrtilus	3.00	0.29	1.13	0.42	1.32	0.01
Calamagrostis villosa	2.14	0.18	0.12	0.13	2.27	0.006

Data on aboveground biomass of different plant stands and nutrient accumulation in it and their percentage stand cover in studied plots, was used to calculate an approximate amount of nutrients accumulated in whole aboveground plant biomass of herb layers. Naturally, an accumulation of nutrients in herbage layers increased concurrently with increasing thinning, damage, dying and felling of spruce stands. A substantial amount of nutrients (in kg per ha) was accumulated in the aboveground biomass of the herbage layer in the damaged forest on the top plateau of the Kněhyně hill (Site 4), due to the vigorous development of herbage layer (Fig. 2). 57.9 kg N, 5.0 kg P and 15.1 kg Ca per ha was estimated for this site. The amount of nutrients accumulated here in aboveground biomass represented values mostly four to seven times higher than values recorded in the less damaged spruce forest, where accumulation of nutrients were the lowest (Site 2). Nevertheless**,** the highest values of amount of nutrients accumulated in aboveground biomass (i.e., 83.9 kg N ha^{-1}, 6.9 kg P ha^{-1}) were calculated for *Calamagrostis villosa* stands on the clearing (Site 3).

Main herbaceous species dominating in the understory of studied forests (*Athyrium distentifolium* and *Calamagrostis villosa*), were also examined to know their feedback effect on habitats. Therefore decomposition rates of their litter and release of nutrients during decomposition, and variability of soil features were also examined.

Recorded relative losses of dry mass of decomposing plant litter are summarized in Table 4. 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. The decomposition of *C. villosa* litter was substantially greater than was recorded for *Athyrium distentifolium* litter in

T a b l e 4. Mean values of relative decreases in dry mass (%) and in decomposition rate (g $g^{-1}day^{-1}$) of plant litter recorded in winter period and in 1-year period in *Athyrium distentifolium* and *Calamagrostis villosa* stands in spruce forests and in the clearing in the NNR Kněhyně-Čertův mlýn. Estimated total amounts of decomposed plant matter (gm^{-2} $year^{-1}$) are also given.

	Site 2		**Site 3**		**Site 4**	
Athyrium distentifolium	leaflets	stalks	leaves	stalks	leaflets	stalks
Decomposed dry mass						
Winter period	11.0	6.8	-	-	11.2	8.1
1-year period	24.6	18.2	-	-	19.1	19.5
Decomposition rate						
Winter period	0.61	0.37	-	-	0.62	0.45
1-year period	0.82	0.59	-	-	0.62	0.63
Calamagrostis villosa						
Winter period	-	-	17.9	12.3	-	-
1-year period	-	-	35.6	23.3	-	-
Decomposition rate						
Winter period	-	-	1.04	1.28	-	-
1-year period	-	-	1.28	0.77	-	-
Amount of decomposed plant matter	42		170		37	

habitats of studied forest sites. After one year, 35.6% of dry mass of leaves of *Calamagrostis villosa* was decomposed. These data corresponded to decomposition rates of 1.28 mg g^{-1} d^{-1}. Obtained data also demonstrated faster decomposition rates of litter of both plant species during growing season (Table 4). The most slower decomposition of *Athyrium distentifolium* leaflets was recorded on the top plateau (Site 4), where 19.1% of original dry mass was decomposed. Obtained data and data on the net annual production of aboveground biomass (Jakrlová et al., 1994) enable to estimate approximate amount of yearly decomposed dry mass. Estimated values indicate that the amount of decomposed biomass production were four times greater in the *Calamagrostis villosa* stand on the clearing (Site 3, 170 g m^{-2} y^{-1}) than in studied *Athyrium distentifolium* stands (37 and 42 g m^{-2} y^{-1}, Site 4, 2). Thus the *Calamagrostis villosa* stand contributed much higher amounts of organic matter to the detritus food chain. Since values of decomposition rate of plant litter can be underestimated in comparison with reality due to the apply methods (Tesařová, 1976), differences in amount of decomposed litter in studied stands may be probably even greater. Data on decomposition rate of *C. villosa* leaves corresponded with results obtained at other localities in the Beskydy Mts (decomposed 36% leaves and 25% of stalks, Tůma, 2002). The rates of litter decomposition found for ferns were also lower than those determined for most of other plant species (Wardle et al., 2002). The comparison of several groups of plants has shown that ferns contain greater amounts of lignin and phenols than monocots, whereas monocots had more cellulose (Wardle et al., 2002). In the Beskydy Mts, altitude correlated negatively and mean annual air temperature positively with the disappearance of leaf matter of *C. arundinacea* (Tůma, 2002). These facts seam to be also associated with slower decomposition of dead matter of fern leaflets recorded at studied locality situated at a higher altitude.

Data obtained in fern and *C. villosa* stands shown on a similar mobility series of Mg>K>Ca>P>N. At the end of the first year, 24.6–33.9% of Ca and 69.4–70.0% of Mg con-

T a b l e 5. Release and accumulation of nutrients in decomposing plant litter of *Athyrium distentifolium* and *Calamagrostis villosa* in spruce forests and in the clearing in the NNR Kněhyně-Čertův mlýn. Quantity of accumulated (+) or released (-) nutrients from their original amount in litter. Percentage nutrient release (in %) and the amount of released nutrients (in v kg ha^{-1} yr^{-1}) are given.

	Nutrients				
Site 2	N	P	K	Ca	Mg
Athyrium distentifolium					
Percentage values	+0.09	-1.7	-56.6	-33.9	-70.0
Amount of nutrients	+0.03	-0.45	-5.99	-5.11	-4.92
Site 3					
Calamagrostis villosa					
Percentage values	-2.8	-42.1	-55.1	-42.5	-76.8
Amount of nutrients	-0.09	-0.16	-1.13	-0.40	-0.53
Site 4					
Athyrium distentifolium	N	P	K	Ca	Mg
Percentage values	+11.9	-9.5	-17.8	-24.6	-69.4
Amount of nutrients	+3.48	-0.16	-0.99	-3.11	-5.03

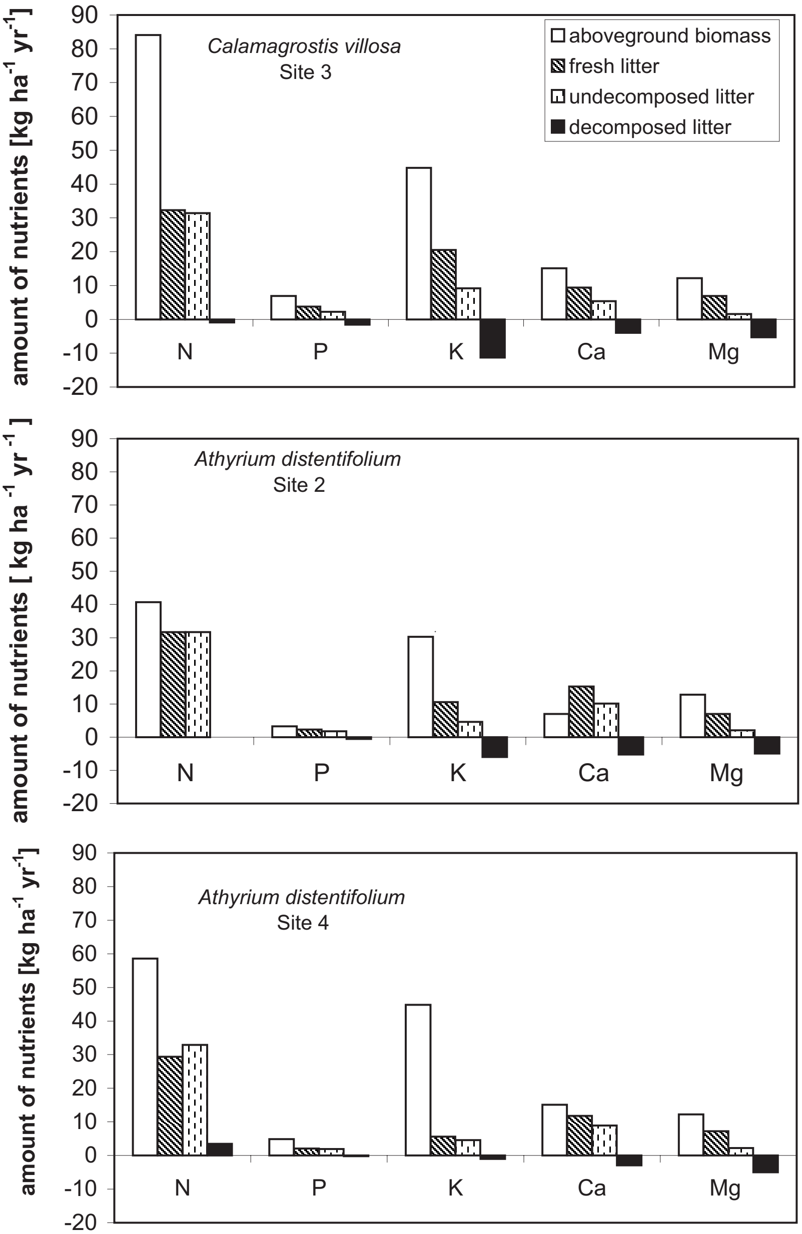

Fig. 3. Amount of nutrients (in kg ha^{-1}) in aboveground biomass, in fresh litter, undecomposed 1-year old litter and calculated release and accumulation of nutrients in decomposing plant litter in the NNR Kněhyně-Čertův mlýn.

tained in plant matter at the beginning of exposition were released from fern litter (Table 5, Fig. 3). The release of Ca and Mg was slower from fern litter than from *C. villosa* litter. Nevertheless, their released absolute amounts are comparable (Fig. 3). Thus studied fern stands can also return rapidly basic cations to the upper soil layer of the plant-soil system, retaining them within the ecosystem. Therefore we assumed that this fact can be reflected in soil features of the habitat of deforested areas. Greater accumulation of N in fern litter, exceeding the initial value, was recorded in the top-site. P and K were released faster from *C. villosa* stand. Emmer (1999) concluded that greater amounts of acidifying compounds may cause a higher release of Ca and Mg from plant litter. His data indicated the release 40−50% of Ca from *C. villosa* litter. Comparison of the decomposition of litter of different clearcut grasses in the Beskydy Mts suggest, that 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).

In the studied sites of the NNR Kněhyně-Čertův mlýn, average soil pH (H_2O) values fluctuated in range of 3.53 to 3.97 in the 0−10 cm soil layer soil, which classified these soils as very acid (see Ježíková, Tůma, 1995). The highest values of pH were measured in old *C. villosa* stand on clearing (Site 3) (Fig. 4). Increased acidity of forest soils, typical for regions affected by pollution loads, was also approved in the Beskydy Mts (Klimo, Vavříček, 1991). A lower soil acidity recorded in the Site 3 was associated with the highest concentrations of Ca^{2+} and Mg^{2+} and lowest amount of Al^{3+} ions. Differences between soil features in the grass stand on clearing and forest habitats are obvious. The spruce litter can slowdown decomposition and increase C-substances in the H-horizont and also decrease C-substances in the organic mineral horizons (Vavříček et al., 2008). Content of soil organic matter recorded in the 0-10 cm soil layer ranged from 37.8 to 57.7% in the spruce forest (Site 4C) and in the fern stand growing on the top plateau of the Kněhyně hill (Site 4B), respectively. Ježíková (1996) summarized data recoded in several forest and clearings in the Beskydy Mts and reported that soil pH values in the forest stands were probably controlled by acidity of organic compounds evolving from soil organic matter (OM), since negative correlation was found between OM and pH. The contents of OM were generally lower on clearings than in forest stands. The increase in pH and in Ca^{2+} and Mg^{2+} concentrations was very conspicuous in clearings in comparison to control forest sites. Ježíková (1996) also recorded, that proportion of basic cations substantially increased together with a decrease of Al^{3+} and H^+ contents. Thus this features can be exhibited importantly in restriction of the effect of acid rain, because these soils react sensitively on the proton imputes.

The stands of grasses were demonstrated to mitigate the acidification of soil solution and leaching of calcium and magnesium from soil (Takamatsu et al., 1997; Fiala et al., 2005). Both species of *Calamagrostis (C. arundinacea* and *C. villosa)* act as a sink of N as they take up and immobilize these elements in plant biomass and undecomposed litter (Fiala et al., 2005). Thus grass stand formation has a positive effect on the soil environment. Similarly, the first obtained data indicate that *Athyrium distentifolium* ferns growing in lysimeters may bound a great part of added N in their biomass and partly eliminate soil acidification and leaching of N and basic cations, similar to that in percolates collected from lysimeters with growing grasses (Tůma et al., 2008). A rapid regeneration of vegetation cover following dis-

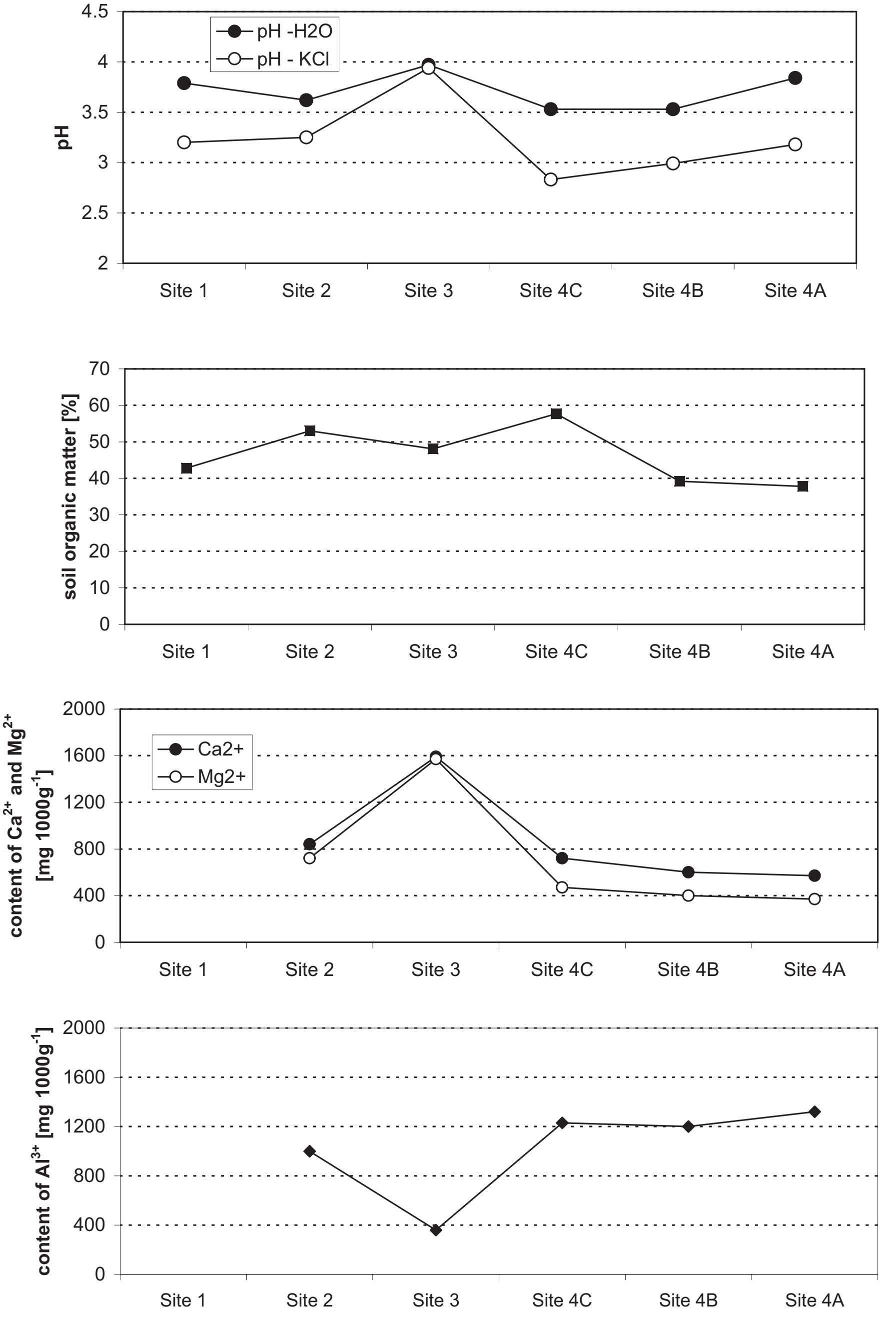

Fig. 4. Soil features (0–10 cm) recorded in studied sites in the NNR Kněhyně-Čertův mlýn.

turbance tends to minimize losses of nutrients from the ecosystem and to promote a return to steady-state cycling (e.g., Marks, Borman, 1972; Vitousek, Stanford, 1986). A removal of grass cover on clearings in the Beskydy Mts was followed by a decrease in the contents of Ca^{2+}, Mg^{2+} and pH values in soil (Sedláková et al., 1999). The soil under *Calamagrostis villosa* grass cover exhibited also higher pH values in the Jizera Mts affected by strong acid deposition and the content of basic cations was also slightly higher here (Drábek et al., 2007). Higher pH values, content of calcium and magnesium in soil were also found in grass stands developed in thinned areas compared to closed spruce stands (Peřina, Květ, 1975). This implies that plant stand formation, and grass stands particularly, can have a positive effect on the soil environment of deforested areas.

Conclusion

Obtained data shown on the conspicuous role of forest herb layers, represented particularly by *Athyrium distentifolium* and *Calamagrostis villosa* stands. Naturally, the role of herb layers increased markedly with increasing forest disturbance (opening the spruce canopy, dying and felling of trees), due to the increasing production of plant biomass, accumulation and turnover of nutrients. A rapid cycling of nutrients leads to retaining them within the ecosystem. Both grass and fern stands can effect positively of soil environment (reduction of losses of nitrogen and basic cations from soil, Fiala et al., 2005; Tůma et al., 2008), nevertheless soil data obtained in fern stands did not indicate such pronounced effect as it was found in the soil of *C. villosa* stands.

Translated by the authors
English corrected by R. Marshall

References

Bobbink, R., Roelofs, J.G.M., 1995: Nitrogen critical loads for natural and semi-natural ecosystems: the empirical approach. Water Air Soil Pollut., 85: 2413–2418. http://dx.doi.org/10.1007/BF01186195

Bobbink, R., 1998: Impacts of tropospheric ozone and airborne nitrogenous pollutants on natural and seminatural ecosystems: a commentary. New Phytol., 139: 161–168. http://dx.doi.org/10.1046/j.1469-8137.1998.00175.x

Bobbink, R., Hornung, M., Roelofs, J.G.M., 1998: The effect of air-born nitrogen pollutants on species diversity in natural and semi-natural European vegetation. J. Ecol., 86: 717–738. http://dx.doi.org/10.1046/j.1365-2745.1998.8650717.x

de la Cretaz, A.L., Kelty, M. J., 2002: Development of tree regeneration in fern-dominated forest understories after reduction of deer browsing. Restor. Ecol., 10: 416–426. http://dx.doi.org/10.1046/j.1526-100X.2002.02037.x

Dahlgren, R.A., Driscoll, C.T.,1995, The effects of whole-tree clear-cutting on soil processes at the Hubbard Brook experimental-forest, New Hampshire, USA. Plant Soil, 158: 239–262. http://dx.doi.org/10.1007/BF00009499

Donaldson, J.M., Henderson G.S., 1990: Nitrification potential of secondary-succession upland oak forests: I. Mineralization and nitrification during laboratory incubations. Soil Sci. Soc. Am. J., 54: 892–897. http://dx.doi.org/10.2136/sssaj1990.03615995005400030047x

Drábek, O., Borůvka, L., Pavlů, L.,, Nikodem A., Pírková, I., Vacek, O., 2007: Grass cover on forest clear-cut areas ameliorates some soil chemical properties. J. Inorg. Biochem., 101: 1224–1233. http://dx.doi.org/10.1016/j.jinorgbio.2007.06.011

Elemans, M., 2004: Light, nutrients and the growth of herbaceous forest species. Acta Oecol. Inter. J. Ecol., 26: 197–202. http://dx.doi.org/10.1016/j.actao.2004.05.003
Emmer, I.M., 1999: Litter decomposition and soil nitrogen dynamics (1995, 1996) in the Krkonoše National Park. J. For. Sci., 45: 316–327
Fanta, J., 1997: Rehabilitating degraded forests in Central Europe into self-sustaining forest ecosystems. Ecol. Eng., 8: 289–297. http://dx.doi.org/10.1016/S0925-8574(97)00024-4
Fiala, K., Jakrlová, J., Zelená, V., 1989: Biomass partitioning in two *Calamagrostis villosa* stands on deforested sites. Folia Geobot. Phytotax., 24: 207–210.
Fiala, K., Jakrlová, J., 1997: Biomasss and amount of nutrients bound in herbaceous vegetation of deforested sites (Kněhyně – The Beskydy Mts) (in Czech). The Beskids Bulletin, 9: 109–112.
Fiala, K., Tůma, I., Jakrlová, J., Ježíková, M., 1998: The role of grass ecosystems of deforested areas in the region affected by air pollution (the Beskydy Mts, the Czech Republic). Ekológia (Bratislava), 17, Suppl. 1: 241–255.
Fiala, K., Tůma, I., Holub, P., 2005: The role of *Calamagrostis* communities in preventing soil acidification and base cation losses in deforested mountain area affected by acid deposition. Plant Soil, 268: 35–49. http://dx.doi.org/10.1007/s11104-004-0185-8
George, L.O., Bazzaz, F.A., 1999: The fern understory as an ecological filter: emergence and establishment of canopy-tree seedlings. Ecology, 80: 833–845. http://dx.doi.org/10.1890/0012-9658(1999)080[0833:TFUAAE]2.0.CO;2
Hill, J.D., Silander, A., 2001: Distribution and dynamics of two ferns: *Dennstaedtia punctilobula* (*Dennstaedtiacea*) and *Thelypteris noveboracensis* (*Thelypteridaceae*) in a Northeast mixed hardwoods-hemlock forest. Amer. J. Bot., 88: 894–902. http://dx.doi.org/10.2307/2657041
Hofmeister, J., Hošek, J., Modrý, M., Roleček, J., 2009: The influence of light and nutrient availability on herb layer species richness in oak-dominated forests in central Bohemia. Plant. Ecol., 205: 57–75. http://dx.doi.org/10.1007/s11258-009-9598-z
Holeksa, J., 2003: Relationship between field-layer vegetation and canopy openings in a Carpathian subalpine spruce forest. Plant Ecol.,168: 57–67. http://dx.doi.org/10.1023/A:1024457303815
Holub, P., 1999: Evaluation of nitrogen uptake and its retranslocation by grasses in deforested areas. J. For. Sc., 45: 358-364.
Holub, P., 2003: The effect of increased altitude on the growth and nitrogen use efficiency of *Calamagrostis arundinacea* and *C. villosa*. Biologia (Bratisl.), 58: 1–11.
Hůnová, I., Šantroch, J., Ostatnická, J., 2004: Ambient air quality and deposition trends at rural stations in the Czech Republic during 1993–2001. Atmos. Environ., 38: 887–898.
Jakrlová, J., Zelená, V., Fiala, K., Tůma, I., Holub, P., 1994: Herbage vegetation of deforested areas and soil nutrient content of their habitats (Beskydy - Kněhyně) (in Czech). In Tesař, V., Kula, E. (eds), Vliv imisí na lesy a lesní hospodářství Beskyd. Zpravodaj Beskydy, 6: 149–154.
Ježíková, M., Tůma, I., 1995: Influence of grass stands on chemical features of soils in the Kněhyně nature reserve (in Czech). In Tesař, V., Kula, E. (eds), Vliv imisí na lesy a lesní hospodářství Beskyd. Zpravodaj Beskydy, 7: 139–144.
Ježíková, M., 1996: Some chemical properties of soil on the clearings in the region Beskydy Mts. In Fiala, K. (ed.), Grass ecosystems of deforested areas in the Beskydy Mts. Preliminary results of ecological studies. Institute of Landscape Ecology, Brno, p. 173–185.
Kennedy, I.R., 1992: Acid soil and acid rain. John Wiley & Sons, New York, 241pp.
Klimo, E., Vavříček. D., 1991: Acidification and liming of forest soils in the Beskydy Mts. Forestry, 17: 61–72.
Kollár, J., Kubíček, F., Šimonovič, V., Kanka, R., Balkovič, J., 2010: Production-ecological analysis of the broad-leaved forest ecosystems herb layer biomsss in the Žalostínská vrchovina upland and Zámčisko (Western Slovakia). Ekológia (Bratislava), 29: 113–122.
Koppisch, D., 1994: Nährstoffhaushalt und Populationsdynamik von *Calamagrostis villosa* (C h a i x.) J.F. G m e l., einer Rhizompflanze des Unterwuchses von Fichtenwäldern. Bayreuther Forum Ökologie, Bayreuth.
Kubíček, F., Šimonovič, V., Szabo, J., 1989: Biomass of the herb and moss layer in several forest ecosystems influenced by air pollution. The Beskydy Mountains (part Kysuce). Ekológia (ČSFR), 8: 23–34.
Kukla, J., Kuklová, M., 2008: Growth of *Vaccinium myrtillus* L. (*Ericaceae*) in spruce forests damaged by air pollution. Pol. J. Ecol., 56: 149–155.
Kuklová, M., Kukla, J., 2008: Accumulation of macronutrients in soils and come herb species of spruce ecosystems. Cereal Res. Commun., 36: 1319–1322.

Květ, J., 1993: Ecological crisis in post-communist Central Europe. J. Aquat. Plant. Manag., 31: 13–17.
Marks, P.L., Borman, F.H., 1972: Revegetation following forest cutting: mechanisms for return to steady state nutrient cycling. Science, 176: 914–915. http://dx.doi.org/10.1126/science.176.4037.914
Nihlgard, B., 1985: The ammonium hypothesis - an additional explanation to the forest dieback in Europe. Ambio, 14: 2–8.
Odland, A., Birks, H.J.B., Line, J.M., 1990: Quantitative vegetation-environment relationships in west Norwegian tall-fern vegetation. Nordic J. Bot., 10: 511–533.
Odland, A., 1991: A synecological investigation of *Athyrium distentifolium*-dominated stands in western Norway. Nordic J. Bot., 11: 651–673. http://dx.doi.org/10.1111/j.1756-1051.1991.tb01278.x
Odland, A., Birks, H.J.B., Line, J.M., 1995: Ecological optima and tolerances of *Thelypteris limbosperma*, *Athyrium distentifolium*, and *Matteuccia struthiopteris* along environmental gradients in western Norway. Vegetatio, 120:115–129. http://dx.doi.org/10.1007/BF00034342
Peřina, V., Květ, J., 1975: The effect of montane spruce thinning on the biomass production of the ground vegetation. Lesnictví, 21: 659–686.
Pyšek, P., 1990: The influence of *Calamagrostis villosa* on the species diversity of deforested sites in the Krušné hory Mts. Preslia, 62: 323–335.
Pyšek, P., 1993: What do we know about *Calamagrostis villosa*? A review of the species behaviour in secondary habitats. Preslia, 65: 1–20.
Schulze, E.D., Oren, R., Lange, O., 1989: Processes leading to forest decline: a synthesis. Ecol. Stud., 77: 459–468. http://dx.doi.org/10.1007/978-3-642-61332-6_22
Sedláková, I., Fiala, K., Tůma, I., 1999: Effect of application of herbicide on soil features of immission barrens with grass cover in the Beskydy Mts. J. For. Sci., 45: 328–336.
Takamatsu, T., Kohno, T., Ishida, K., 1997: Role of the dwarf bamboo (*Sasa*) community in retaining basic cations in soil and preventing soil acidification in mountainous areas of Japan. Plant Soil, 192: 167–179.
Tesař, V., Kypet, V., Procházka, J., 1994: Growth of mountain ash in high elevations of the Moravian-Silesian Beskids (in Czech). In Tesař, V., Kula, E. (eds), Vliv imisí na lesy a lesní hospodářství Beskyd. Zpravodaj Beskydy, 6: 199–204.
Tesařová, M., 1976: Litter production and disappearance in some alluvial meadows (Preliminary results). Folia Geobot. Phytotax., 11: 63–74.
Thomas, S.C., Halpern, C.B., Falk, D.A., 1999: Plant diversity in managed forests: Understory responses to thinning and fertilization. Ecol. Applic. 9: 864–879. http://dx.doi.org/10.1890/1051-0761(1999)009[0864:PDIMFU]2.0.CO;2
Titus, B.D., Malcolm, D.C., 1992: Nutrient leaching from the litter layer after clearfelling of Sitka spruce stands on peaty gley soils. Forestry, 65: 389–416. http://dx.doi.org/10.1093/forestry/65.4.389
Tůma, I., 2002: Release of nutrients from decomposing litter on deforested areas affected by air pollution in the Beskydy Mts. Ekológia (Bratislava), 21: 201–220.
Tůma, I., Fiala, K., Holub, P., 2006: Biomass formation, nutrient uptake and release in fern stands of *Athyrium distentifolium* on deforested areas affected by pollution: comparison with grass stands. Ekológia (Bratislava), 25: 264–279.
Tůma, I., Holub, P., Fiala, K., 2008: New data on stands of fern *Athyrium distentifolium* /Opiz/ in the Beskyd Mts. Beskydy, 1: 89–94.
Vavříček, D., Pecháček, J., Staněk, L., Pancová-Šimková, P., 2008: Soil taxonomical units and influence of species composition on selected qualitative humus parameters in the flysch belt of the National Nature Reserve Čertův mlýn (6th and 7th forest vegetation belt). Beskydy, 1: 199–208.
Vacek, S., Bastl, M., Lepš, J., 1999: Vegetation changes in forests of the Krkonoše Mts over a period of air pollution stress (1980–1995). Plant Ecol., 143: 1–11. http://dx.doi.org/10.1023/A:1009833313509
Viewegh, J., 1994: Forest herb layer changes in Moravskoslezské Beskydy Mts (with a view to reservation). In Tesař, V., Kula, E. (eds), Vliv imisí na lesy a lesní hospodářství Beskyd. Zpravodaj Beskydy, 6: 125–132.
Vitousek, P.M., Stanford, R.L., 1986: Nutrient cycling in moist tropical forest. Ann. Rev. Ecol. Syst., 17: 137–169.
Wardle, D.A., Bonner, K.I., Barker, G.M., 2002: Linkages between plant litter decomposition, litter quality, and vegetation responses to herbivores. Funct. Ecol., 19: 585–595. http://dx.doi.org/10.1046/j.1365-2435.2002.00659.x