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Disturbance-induced changes in the plant biomass in forests near Plešné and Čertovo Lakes

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ABSTRACT: Two forested catchments in the Bohemian Forest (Šumava Mts.) were investigated according to the species composition of herb layer and aboveground plant biomass. The bark-beetle gradation was observed in the Plešné Lake catchment during this study. The community dynamics depends mainly on the altitudinal zone of the site. Variability in the species composition was more pronounced in the sites of natural broadleaved mixed forests than in the sites of natural Norway spruce forests. Three processes were recorded after the tree layer damage: tree regeneration (very rapid), appearance of some species typical of the clear-cuts (only limited, mainly after windthrows) and disappearance of some species (limited, probably for a short time only). The aboveground biomass was variable. Some relations to the canopy decline were observed for *Vaccinium myrtillus*. The stock changes depend on the population features of this species and can differ (increase or decrease) according to individual localities.

Keywords: aboveground biomass; *Picea abies* forest; stand damage; *Vaccinium myrtillus*

Dynamics of the forest ecosystem and the respective plant community especially is well characterized by understory vegetation (e.g. Matějka, Viewegh 2008). Changes in plant communities in forests can be distinguished based on the time period length. While many processes in the forest can be observed within a framework of several decades, rapid changes are connected with a disturbance of the tree canopy and they are well detectable during several years.

A more or less rapid collapse of forest stands has been observed in Central Europe during the last century in many cases. Massive afforestation, abandonment of agricultural land, pastures, and vineyards, which caused an increase of the forested area, were omitted in this paper. The forest decline was a result of three kinds of processes: (1) air pollution, (2) wind storm, and (3) insect infestation. The air pollution impact occurred mainly in the 1970s and 1980s (Kopáček, Veselý 2005). Rapid tree stand breakdown is often a result of a sudden insect gradation in response to extreme weather (above-average temperatures, droughts, wind disaster) currently. All three effects were observed in Norway spruce forests in the Bohemian Forest (Šumava Mts.), because the bark beetle (*Ips typographus*) showed the last population gradation there (Matějka 2011b) as a consequence of former air pollution combined with extreme weather in 2003 and wind storm in 2007. The disturbance history of Norway spruce forests in the Bohemian Forest was described on the basis of tree ring analysis (Svoboda et al. 2012). Their results point to repeated disturbances which were caused by winds as a probable prevailing factor.

As Dalsgaard (2007) wrote, "In the natural temperate deciduous forest the gap phase is crucial for forest regeneration and succession". While the forest gap dynamics has been studied often (e.g. Pickett, Cadenasso 2005; Bottero et al. 2011; Saniga et al. 2011; Cater et al. 2014; Kramer et al. 2014), papers on the dynamics of Central European mountain climax forests with dominant Norway spruce are less frequent (e.g. Holeksa, Cybulski 2001; Motta et al. 2010; Zach et al. 2010; Zielonka et al. 2010). Gaps are frequent in many forest ecosystems as a result of small-

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scale disturbances, often caused by wind or other factors (SPLECHTNA et al. 2005; KRAMER et al. 2014). Gaps can account for up to 73% of the total forest area under investigation (e.g. BARTEMUCCI et al. 2002). Such conditions are similar to a large-scale disturbance.

A review on the disturbance dynamics of boreal forests in North America was written by BRASSARD and CHEN (2006). The insect population gradations cause damage in the boreal forests similarly like to mountain Norway spruce forests in Central Europe.

Long-term forest dynamics in some mountain regions of the Czech Republic was analysed by MATĚJKA (2011c), who pointed out that changes in the species composition of the herb layer are more variable in the beech-mixed forests (5th [beech with fir; named according to the dominant tree species] to the 7th [spruce with beech] forest altitudinal zone in the sense of Czech forest site typological system; VIEWEGH et al. 2003) compared with ecosystems of Norway spruce (8th [spruce] forest altitudinal zone), particularly in terms of the simple presence of species. Forest dynamics after disturbance in the Bavarian Forest National Park was reported by FISCHER et al. (2002). Long-term dynamics of plant communities in forests of the Bohemian Forest was described earlier (e.g. WILD et al. 2004). The Norway spruce forest dynamics was under interest in other mountain regions of Central Europe (e.g. VÁVROVÁ et al. 2009; CUDLÍN, VÁVROVÁ 2010; JONÁŠOVÁ et al. 2010). From the aspect of tree-layer regeneration, the Norway spruce regeneration after the canopy dieback was studied at both sides of the national borders – in the Bavarian Forest National Park (HEURICH 2009) and in the Šumava National Park (ČÍŽKOVÁ et al. 2011). Both studies report rapid regeneration in a prevailing part of ecosystems affected by bark beetle.

Artificial changes in the tree species composition are known in the Šumava Mts. in potential sites of broadleaved mixed forests (up to the 7th forest altitudinal zone). A similar increase of *Picea abies* abundance in forests was recorded also in other parts of Europe (e.g. Romania; FEURDEAN, WILLIS 2008).

The natural early successional habitats following tree layer disturbances have recently been recognised as important for nature conservation because of their high biodiversity as pointed out when different groups of organisms were studied (plants, bryophytes, mushrooms, invertebrates; LEHNERT et al. 2013). In this light, a non-interventional approach to the management of Norway spruce forests within regions of their natural origin in Central Europe can be seen as a remedy in the field of nature conservation (PAILLET et al. 2010).

The dynamics of plant communities should be solved in terms of the fine-scale pattern of the community (e.g. microcoenoses) as had been demonstrated in other regions (e.g. VÁVROVÁ et al. 2009). Another approach can be developed from the population biology (dynamics) of main species in the herb layer. The basic population parameter is represented by species biomass, mainly aboveground (AG) biomass. There is a broad set of data on the biomass of dominant species such as *Calamagrostis villosa* (e.g. PYŠEK 1991). Many studies dealt with the biomass production and other ecosystem functions in grass communities on plots after tree layer damage. Such projects were carried out in the Beskydy Mts. (FIALA 1996). The application of their results for comparison with data from the Bohemian Forest is limited because both environmental conditions and cause of tree-layer damage (air pollution in the Beskydy Mts.) differ.

Catchments of lakes in the Bohemian Forest (Fig. 1) are under long-time investigations (KOPÁČEK, VRBA 2006). The plant biomass was analysed by SVOBODA et al. (2006) for the whole area of the catchments of Čertovo Lake and Plešné Lake. Vegetation dynamics was studied on permanent plots in both catchments. Some plots (mainly near the Plešné Lake) were affected by the bark beetle (*Ips typographus*) gradation during the period of observation. The main aim of this paper is to describe short-time changes in the understory (herb layer) vegetation within the investigated plots in both catchments. Two different approaches were applied. While semi-quantitative relevés describe the coarse structure of a plant community, the AG plant biomass analysis can shed the light on fine changes in the community. The belowground biomass was also sampled, but the interpretation of these results (MATĚJKA 2011a) is very limited because data are highly variable.

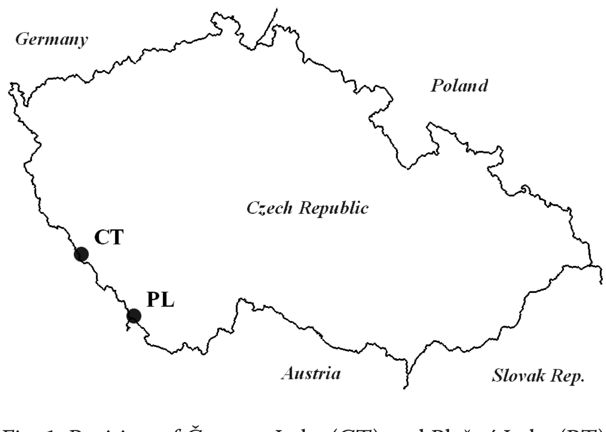

Fig. 1. Position of Čertovo Lake (CT) and Plešné Lake (PT) within the Czech Republic

METHODS

Description of the plots

Catchment of Čertovo Lake. The Čertovo Lake catchment (49°9'55''N, 13°11'50''E; its altitude ranges between 1,027 and 1,343 m a.s.l.; 76 ha of forested area in total) was described in detail by Kopáček et al. (2002b). Average altitude is 1,136 m. Slopes are gentler (Table 1). Geological conditions are not simple. Near the lake, the glacial (Pleistocene) sediments are found. The northeastern part of the catchment is represented by mica schist with garnet and andalusite. It is changed to muscovite-biotite paragneiss with sillimanite in the western to the southwestern part (according to Geological Map of the Czech Republic). Soils in the catchment were analysed by Kopáček et al. (2002b). Cambisol is the most frequent soil type in the catchment (Table 2).

Table 1. Terrain steepness in the catchments – slope

Relative catchment area (%)	Čertovo Lake	Plešné Lake
50	≤ 0.30 (17°)	≤ 0.36 (20°)
75	≤ 0.49 (26°)	≤ 0.57 (30°)
95	≤ 0.82 (39°)	≤ 1.17 (49°)
99	≤ 1.07 (47°)	≤ 2.23 (66°)

Main forest types according to typological map give first insight into vegetation conditions (Matějka 2009). Newly distinguished forest altitudinal zones (Table 3; for the method description see Kindlmann et al. 2012) were delineated using a new model, which employs the digital elevation model and modelling of average temperatures (Matějka 2011b). A different result has been obtained by comparing the actual forest typological map (data prepared by Forest Management Institute, Brandýs nad Labem). A border between the 6th and 7th FAZ corresponds to the 4.5°C modelled isotherm for the period 1961–1990, and a border between the 7th and 8th FAZ coincides with the 3.7°C modelled isotherm. Altitudinal zones with European beech (6th and 7th FAZ) prevail here (Fig. 2).

Table 2. The most frequent soils in the catchments (in percentage of the area)

Group of soil types	Čertovo Lake*	Plešné Lake**
Cambisol	58	27
Podzols	21	29
Undeveloped organic rich soils	17	–
Undeveloped thin soils	–	38

*Kopáček et al. (2002b), **Kopáček et al. (2002a)

Table 3. Forest altitudinal zones (FAZ of the Czech forest site typological system; Viewegh et al. 2003) according to the result of average temperature modelling in the forested area of the Čertovo and Plešné Lake catchments

Catchment	Čertovo Lake		Plešné Lake	
FAZ	area (ha)	%*	area (ha)	%*
6	30.38	39.9 (0.0)	6.06	10.7 (0.0)
7	25.75	33.8 (81.3)	15.71	27.8 (11.9)
8	20.09	26.4 (18.7)	34.72	61.5 (88.1)
Total	76.21	100.0	56.48	100.0

*percent values in brackets are proportions given by the current typological map of the Forest Management Institute, Brandýs nad Labem, 6 – European beech with Norway spruce, 7 – Norway spruce with European beech, 8 – Norway spruce

The association *Calamagrostio villosae-Fagetum* Mikyška 1972 (compare Moravec et al. 1982) is dominant in the potential vegetation (Neuhäuslová et al. 1998). The actual tree layer is composed of prevailing Norway spruce (*Picea abies*) with European beech (*Fagus sylvatica*) and silver fir (*Abies alba*) partly contributing out of the highest part of the catchment.

The research plots (Fig. 2; Table 4) are scattered in the catchment at different altitudes. While plant communities were sampled on all plots, the biomass analysis was carried out on two main plots (CU and CL).

The catchment is located in the Šumava Protected Landscape Area, the main part of the catchment is protected as National Natural Reserve. All select-

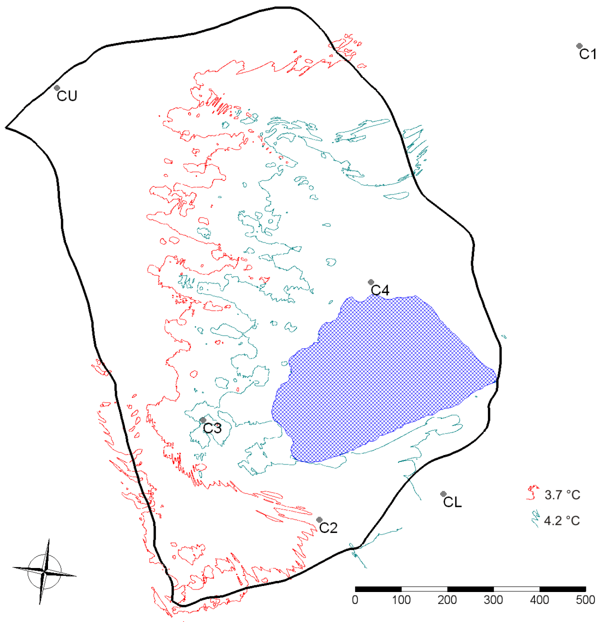

Fig. 2. Localization of the plots within the Čertovo Lake catchment. Isolines are drawn according to the PlotOA thermal model with 0.2 m in pixel size (Matějka 2013)

Table 4. A list of the investigated plots and comparison of their notation in different studies

Study plot	Another notation	Tree layer damage since	Comment
Čertovo Lake			
C1		–	
C2	CT1 is at 70 m distance (Kopáček et al. 2002b)	–	
C3	CT3 is at 140 m distance (Kopáček et al. 2002b)	–	
C4	CT9 (Kopáček et al. 2002b)	–	
CL	CT-L (Kopáček, Cudlín et al. 2010; Kopáček, Hruška 2010; Kopáček et al. 2009, 2011) TF-1 (Kopáček et al. 2000)	–	intensively studied plot
CU	CT-H (Kopáček et al. 2010; Kopáček, Hruška 2010; Kopáček et al. 2009, 2011) TF-2 (Kopáček et al. 2000) CT12 is at 130 m distance (Kopáček et al. 2002b) CN9 is at 130 m distance (Kopáček et al. 2002b)	near the windthrow area (2007) and cut plots (2008); the plot tree layer was influenced	intensively studied plot
Plešné Lake			
PJ1		2005–06	
PJ2		2004 (?)	
PJ3	PL-HN (Kopáček et al. 2010); PL-H (Kopáček, Hruška 2010; Kopáček et al. 2009, 2011) PL-IX (Kopáček et al. 2002a)	2005	intensively studied plot
PJ4	PL-L (Kopáček et al. 2010; Kopáček, Hruška 2010; Kopáček et al. 2009, 2011) PL-I (Kopáček et al. 2002a)	2007–08	intensively studied plot
P19	PL-HS (Kopáček et al. 2010) PL-II is at 130 m distance (Kopáček et al. 2002a)	2009	plot belongs to the altitudinal gradient (Matějka 2011b)
P20	PL-III is at 150 m distance (Kopáček et al. 2002a)	2010	plot belongs to the altitudinal gradient (Matějka 2011b)

ed plots under study have been without any active forest management for a long time.

Catchment of Plešné Lake. The research was carried out in/near the catchment of Plešné Lake (48°46'35"N, 13°52'0"E; altitude ranges between 1,090 and 1,375 m a.s.l.; total forested area is 56 ha) in the Bohemian Forest. Basic information describing the lake, its catchment, and the forest stands was provided by Kopáček et al. (2002a). Environmental conditions are represented mainly by higher altitudes (average altitude is 1,187 m a.s.l.). Slopes are steepest (Table 1). The geological bedrock is composed of porphyric muscovite-biotite granite (Eisgarn type) – according to Geological Map of the Czech Republic (1:50,000). The soil conditions were reported in Kopáček et al. (2002a); compare Table 2.

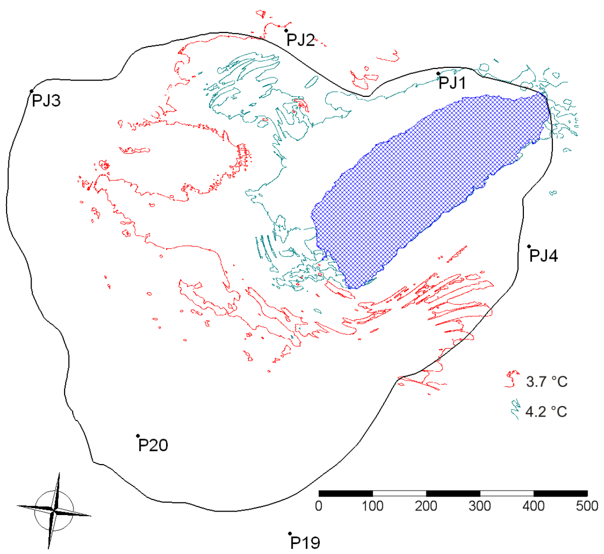

Fig. 3. Localization of the plots within the Plešné Lake catchment. Isolines are drawn according to the PlotOA thermal model with 0.2 m in pixel size (Matějka 2013)

Newly delineated borders between forest altitudinal zones using the same model as in the Čertovo Lake catchment (Table 3, Fig. 3) represent a partly distinct insight into environmental conditions comparing data of the official forest typological map. The 6th FAZ is presented here, the area of the 8th FAZ is lower. The association *Calamagrostio villosae-Piceetum* Hartmann in Hartmann et Jahn 1967 is the main unit of potential vegetation in the catchment.

There are altogether six plots in the catchment (Fig. 3; Table 4). Plant communities were sampled on all plots. Plots P19 and P20 belong to the transect representing an altitudinal gradient on the eastern slope of Plechý Mt. (Matějka 2008). Its vegetation dynamics was described by Matějka, Viewegh (2008). The biomass analysis was carried out on three plots (PJ3, PJ4 and P19).

This catchment is situated in the Šumava National Park, within the area with special management – no forestry intervention was carried out there (only local felling was allowed in special cases: near paths and near the state border; cut stems must be left in the site).

Comparing both catchments (Tables 1–3), the climate in the Plešné catchment is more severe. Almost all trees in the catchment are represented by Norway spruce (*Picea abies*), although European beech and silver fir have natural representation in the potential vegetation of this locality. The catchment is surrounded by a wide belt of forests without any strong human impact. The spruce was also planted at lower altitudes around the catchment.

More detailed information on the plots (including the stand structure and environmental conditions) was given by Matějka (2008).

Plant community dynamics. Phytosociological relevés (standard area was 400 m^2 in size) were recorded (in August of each year) on the plot three to four times in order that short-time variability in the species composition could be evaluated. The Braun-Blanquet scale was used. Similarity in the species composition of plant communities on the selected plots was evaluated by numerical classification (Ward's method with the square of Euclidean distance; McCune, Grace 2002). Data on species in the herb layer was employed. Each grade of the abundance-dominance scale was replaced by average coverage in percent. Data of each relevé was standardized on the sum over all species to obtain the total cover of the herb layer. Average value over all relevés from the plot was used as species representation value (= data on the herb layer average composition).

Diversity indices (α-diversity) were calculated for the herb layer as species richness (S) – the number of present species, and total diversity – Shannon-Wiener index (H'):

$$H' = -\sum_{i=1}^{c} p_i \times \log_2 p_i \qquad (1)$$

where: p_i – representation of the i-th species (Magurran 2004)

Variability in the species composition was evaluated as β-diversity along the temporal gradient on the basis of Shannon-Wiener indices:

$$dH = H_{\text{tot}} - \text{avg}(H_r) \qquad (2)$$

where:

H_{tot} – Shannon-Wiener index of diversity for "total relevé". The total (or average) relevé was calculated in the same manner as data on the herb layer average composition above,

H_r – Shannon-Wiener index of diversity for a single relevé in the r-th year and avg is arithmetic mean.

Similar index dS for species richness can be calculated as the difference between the total number of species in all relevés on the plot and the average number of species in a relevé (S_r)

$$dS = S_{\text{tot}} - \text{avg}(S_r) \qquad (3)$$

Biomass sampling, analyses and data processing. A 0.5 × 0.5 m frame was used to sample the aboveground (AG) biomass of the herb layer (understory vegetation). The frames were randomly placed within each plot to cover variability in the set of plant microcoenoses according to dominant species (*sensu* Matějka 1992a). The number of biomass samples for each plot depended on the vegetation variability, and generally it did not decrease below 5 samples per year and plot.

For each sample site, the plant material of aboveground biomass was cut near the soil (litter) surface using scissors, put into a plastic bag and labelled. The samplings were carried out in August 2007–2010. The AG biomass samples were brought to the laboratory where individual plant species were separated. The AG biomass of *V. myrtillus* was separated into green part (leaves and annual shoots) and woody stems. The samples were dried at 80°C until constant weight.

RESULTS AND DISCUSSION

Species composition of the communities

All detailed data (individual relevés and composition of single biomass data) are available via the Internet (Matějka 2011a). Vegetation dynamics in the Plešné catchment was also analysed in Kindlmann et al. (2012).

The average composition of plant communities (Table 5) follows variability in environmental conditions (mainly altitude). *Picea abies* was a dominant tree species on all plots. The other species (*Fagus sylvatica* and *Abies alba*) are more abundant on the plots near the Čertovo Lake except for the highest plot (CU) in the Norway spruce altitudinal zone (8th FAZ). All communities are poor in the number of species. There are three distinct classification groups of plant communities (Fig. 4):

– Relatively species rich spruce and beech-spruce communities without any marked dominant species in the herb layer (plots C1, C3, PJ1, PJ2 and PJ3); they represent typical variants of the associations

Table 5. Average composition of the plant communities on the investigated plots. Species representation is given as mean cover value in percent. See Matějka (2011a) for individual relevés

	Plot (n)									
	C1(4)	C2(3)	C3(3)	C4(3)	CL(4)	CU(4)	PJ1(4)	PJ2(4)	PJ3(4)	PJ4(4)
E_3										
Picea abies	30	18	28	49	28	24			0.5	3.3
Fagus sylvatica	14	11	30	1	1.6					
Abies alba	3.1	3.2			1.6					
Sorbus aucuparia					0.31					
E_2										
Sorbus aucuparia	0.04	5.1	0.3	5	0.03	0.05	32	16	0.8	0.46
Picea abies	0.04	20	0.07	0.03			28	34	0.98	0.54
Fagus sylvatica	0.07	0.93	7				5.8			
Abies alba		0.93					0.95			
Betula pendula								1		
E_1										
Vaccinium myrtillus	7.1	25	2.9	25	47	0.03	11	14	11	24
Avenella flexuosa	16	7.4	0.1	0.51	3.6	52	0.77		22	1.9
Calamagrostis villosa	5	7.9	11	18		25	3.5	5.9	16	
Picea abies	0.41	2.6	0.35	3.3	0.37	0.05	15	12	2.9	3.2
Dryopteris dilatata	4.1	1.2	1.8	1.8	1.5	6	4.9	9.9	7.9	0.63
Sorbus aucuparia	1.7	0.16	0.35	4.1	0.77	0.1	11	1.7	7	0.24
Rubus idaeus	0.13		0.11		0.04	0.03	6	9	0.3	0.08
Lycopodium annotinum	6.2	2.6		1.1	0.08	0.48				
Abies alba	4.1	1.6	0.02	0.35	0.37					
Fagus sylvatica	0.33	0.16	0.27		0.1		1.1			0.02
Blechnum spicant	0.04	0.21	0.35	0.03						
Homogyne alpina	0.02		0.25						2.4	
Maianthemum bifolium	0.02	0.02	0.64				0.3			
Luzula sylvatica		0.26	0.25	0.23		0.53			7.3	
Dryopteris carthusiana		0.06	0.02							
Prenanthes purpurea		0.04	0.8	0.31			0.3	0.06		
Oxalis acetosella		0.03	0.75	0.51		0.03	13	0.83	0.32	
Gymnocarpium dryopteris			0.02							
Hieracium lachenalii			0.02							
Lastrea limbosperma			0.02							
Rubus fruticosus agg.			0.02							
Melampyrum pratense				0.04						
Epilobium angustifolium					0.02			11	0.32	1.5
Vaccinium vitis-idaea					0.02					1
Mycelis muralis							0.1			
Solidago virgaurea							0.04			
Trientalis europaea									2	
Betula pubescens									0.04	0.1
Senecio ovatus										0.01

n – number of relevés

Calamagrostio villosae-Piceetum and *Calamagrostio villosae-Fagetum* with *Picea abies* in the tree canopy. The species diversity is higher compared to the next two groups (H_{avg} was between 2.3 and 2.8).

– The communities with dominant *Vaccinium myrtillus* (plots C2, C4, CL and PJ4) represent a subassociation (*Calamagrostio villosae-Piceetum vaccinietosum myrtilli* Jirásek 1996; Husová et al. 2002) or variant of both associations. The herb layer can be poor to moderately low (H_{avg} from 0.8 to 2.1).

– The community with dominant grass *Avenella flexuosa* was recorded only on plot CU. It can be syntaxonomically described as *Calamagrostio villosae-Piceetum typicum* var. *avenellosum* Jirásek

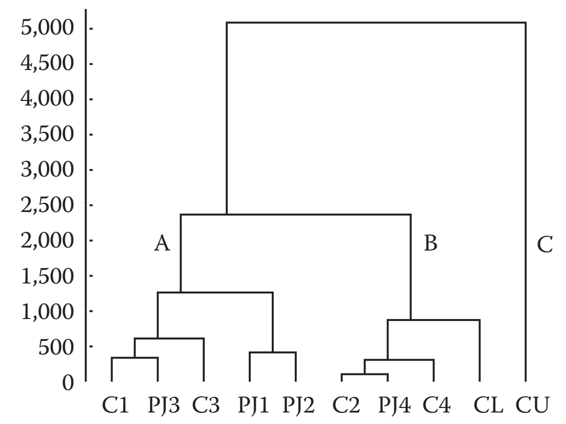

Fig. 4. Classification (Ward's method) of the plant communities of selected plots using data on the average composition of herb layer (Table 2)

1996. Regarding the high grass dominance, diversity is lower (H_{avg} = 1.3).

Changes in the species composition of the plant communities were mainly linked to changes in the total tree layer coverage, which followed bark beetle outbreak (mainly near the Plešné Lake) and wind disturbances. The main changes were:

– Start of tree regeneration and growth of young trees (they may be present in the ecosystem before the point of the tree layer dieback). Two main regenerating tree species (Norway spruce and rowan) are of different growth dynamics as follows from their different autecology: rowan can dominate in the shrub layer for several years, mainly at lower altitudes (6th and 7th FAZ). Total cover of the shrub layer can be very high on some plots at lower altitudes, while the herb layer would be limited there due to the lack of light in the ground layer.
– An apperance of some species typical of the clear--cuts (*Epilobium angustifolium*, *Rubus idaeus*, *Senecio ovatus*, *S. hercynicus*) is more noticeable in the 6th and 7th FAZ, where these species would reach higher cover. A new occurrence of the species growing in wet soils (e.g. *Carex canescens*) would be related to the windthrows, which modify water availability in some microsites.
– Disappearance of some species was observed – e.g. *Luzula sylvatica* (plot PJ3), *Avenella flexuosa* (PJ1, PJ2 and PJ4), and *Oxalis acetosella*.

The most stable communities with minimal changes in the species composition were found near the Plešné Lake (PJ2 and PJ3). However, the tree canopy was damaged on all plots in the Plešné catchment, the plant communities are relatively more stable on these plots. The highest species turnover was recorded on plot C3 under the spruce-beech mixed canopy (Table 6). Changes which were evaluated using the β-diversity (*dH* index) were minimal and comparable in both catchments, because the species dominance had not been touched during the period of observation. All plots with the highest changes according to both indices dS and dH (C2, C3, PJ1 and PJ4) are at localities at the lowest altitudes, in the 6th or 7th forest altitudinal zone.

Table 6. The basic diversity parameters in the investigated plots during 2007–2010

Plot		FAZ	n	S_{tot}	H_{tot}	S_{avg}	H_{avg}	e_{avg}	dS	dH
C1		6	4	13	2.66	10.5	2.61	0.77	2.5	0.05
C2		7	3	15	2.23	12.3	2.09	0.58	2.7	0.14
C3		6/7	3	20	2.40	13.7	2.32	0.61	6.3	0.08
C4		6	3	13	2.10	11.3	2.05	0.58	1.7	0.05
CL		6	4	11	0.81	8.0	0.77	0.26	3.0	0.04
CU		8	4	10	1.34	7.3	1.31	0.47	2.8	0.03
PJ1		6/7	4	13	2.87	10.5	2.76	0.82	2.5	0.11
PJ2		7/8	4	9	2.72	8.3	2.69	0.88	0.8	0.04
PJ3		8	4	13	2.89	12.3	2.82	0.78	0.8	0.07
PJ4		7	4	11	1.47	8.3	1.29	0.43	2.8	0.19
Average	Čertovo Lake			13.7	1.92	10.5	1.86	0.55	3.2	0.07
	Plešné Lake			11.5	2.49	9.8	2.39	0.73	1.7	0.10
Average		6–7							3.1	0.09
		8							1.5	0.05

FAZ – forest altitudinal zone; n – number of relevés; S_{tot} – total number of species; H_{tot} – Shannon-Wiener index of diversity for "total relevé"; S_{avg} – average number of species in relevé; H_{avg} – average Shannon-Wiener index of diversity; e_{avg} – average species equitability; dS and dH are measures of the β-diversity calculated according to Equations (3) and (2)

Table 7. Dry aboveground biomass on plots CL and CU near the Čertovo Lake (all mass values in g·m^{-2}, for original data see Matějka 2011a)

Plot (MFC type)	CL(V)				CU(A)				CU(C-A)			
	2007	2008	2009	2010	2007	2008	2009	2010	2007	2008	2009	2010
No. of samples	5				4	3	3	3	5	3	3	3
Standing dead mass									9.20		5.10	4.40
Avenella flexuosa	0.04				62.4	69.6	118.	103.	9.90	34.6	53.2	21.9
Calamagrostis villosa						0.00			95.6	60.8	97.6	92.4
Dryopteris dilatata		0.12										
Fagus sylvatica			0.08									
Lycopodium annotinum	0.16	0.24							0.00			
Picea abies			1.64	1.48								
Vaccinium myrtillus	692.	242.	266.	408.								
V. myrtillus – green	452.	148.	182.	255.					0.00			
V. myrtillus – wood	242.	94.0	84.0	153.					0.00			
V. myrtillus green:total	*0.65*	*0.61*	*0.69*	*0.63*								
Total	692.	242.	267.	408.	62.0	69.6	118.	103.	114.	95.6	156.	119.
Total without wood	452.	149.	184.	256.								

microphytocoenosis (MFC) type according to dominant species: V – *Vaccinium myrtillus*, A – *Avenella flexuosa*, C – *Calamagrostis villosa*, in italics – ratios

Plant biomass

The highest stock of aboveground plant biomass was found on the plots with *Vaccinium myrtillus* microcoenosis (CL, P19, PJ3 and PJ4). The mean stock of AG biomass was 403 g·m^{-2} (CL, *Vaccinium myrtillus* microcoenosis), 88 and 121 g·m^{-2} (CU, *Avenella flexuosa* and *Calamagrostis villosa-Avenella flexuosa* microcoenosis, respectively) in the Čertovo Lake catchment. The *Vaccinium myrtillus* microcoenoses were recorded on plots P19, PJ3 and PJ4 in the Plešné Lake catchment with the average AG biomass stock of 659, 822 and 465 g·m^{-2}, respectively. The *Avenella flexuosa* microcoenoses were sampled on plots PJ3 and PJ4 with values of 201 and 119 g·m^{-2}, respectively. Similar microcoenosis *Calamagrostis villosa-Avenella flexuosa* had slightly higher AG biomass (297 g·m^{-2}). The *Luzula sylvatica* microcenosis grows at relatively wet microsites on PJ3 plot. The high AG biomass stock (591 g·m^{-2}) corresponds to the more favourable microsite environmental conditions (Tables 7 and 8).

Average maximal AG biomass ("carrying capacity") according to the previous whole-catchment study (Svoboda et al. 2006) was comparable near the Čertovo Lake (88 g·m^{-2} in *Avenella flexuosa*, 154 g·m^{-2} in *Calamagrostis villosa* and 561 g·m^{-2} in *Vaccinium myrtillus* microcoenosis) and near the Plešné Lake (160 g·m^{-2} in *Avenella flexuosa*, 198 g·m^{-2} in *Calamagrostis villosa*, 226 g·m^{-2} in *Luzula sylvatica* and 713 g·m^{-2} in *Vaccinium myrtillus* microcoenosis). The herb layer AG biomass was studied in the Norway spruce ecosystems in the Boubín massif (Matějka 1992b) with similar results. The average maximal AG biomass was 147 g·m^{-2} in *Avenella flexuosa,* 128 g·m^{-2} in *Calamagrostis villosa* and 310 in *Luzula sylvatica* microcoenosis. A noteworthy fact is that the biomass stock was higher by *A. flexuosa* than by *C. villosa* in the Boubín locality. The grass growth in the Čertovo Lake catchment is probably limited by some site conditions. The limiting factor should be sought in a lack of some nutrients. Forests in the Čertovo Lake catchment had been cut in the history (Veselý 1994) and so nutrients were transported out of the ecosystem. Both the content of calcium in soils and the base saturation are higher near the Plešné Lake than in the Čertovo Lake catchment (Kopáček et al. 2002a,b).

Tree seedlings (*Picea abies*) were found in the biomass samples on plots CL and PJ4. Because the spruce seedlings are frequent on plot PJ4, the canopy regeneration would be probably intensive as it is common in similar conditions (Čížková et al. 2011), although the mortality of the youngest seedlings would be very high (Zenáhlíková et al. 2011). Similar intensive tree regeneration was also found in other Central European Norway spruce forests after wind disturbance (Jonášová et al. 2010). The present beech seedling on plot CL indicates natural potential vegetation of the *Calamagrostio villosae-Fagetum* association on this plot.

The aboveground plant biomass (AG biomass) differs among the investigated years. Several trends were found in the biomass data (Table 9). The most

Table 8. Dry aboveground biomass on plots P19, PJ3 and PJ4 near the Plešné Lake (all mass values in g·m^{-2}, for original data see Matějka 2011a)

Plot (MFC type)	P19(V)				PJ3(L)			PJ3(A)			PJ3(C-A)				PJ3(V)			PJ4(V)				PJ4(A)			
	2007	2008	2009	2010	2007	2009	2010	2008	2009	2010	2007	2008	2009	2010	2007	2008	2010	2007	2008	2009	2010	2007	2008	2009	2010
No. of samples	4	4	5	5	2	2	2	2	2	2	1	2	2	2	2	2	2	3	3	4	3	3	2	2	2
Standing dead mass					152.	156.	199.			11.4	49.2	16.4	17.8	29.2	8.76		0.00	0.00				2.20			5.24
Avenella flexuosa					0.16	32.2		121.	250.	215.	116.	0.56	104.	32.2	0.24		2.16	0.24				111.	114.	99.6	137.
Calamagrostis villosa					112.	28.9	10.7			6.36	117.	180.	225.	226.	2.00		3.68								
Dryopteris dilatata									0.44																
Luzula sylvatica					323.	314.	440.					73.6													
Oxalis acetosella						0.92		0.04		0.16			0.08	0.44		0.24	0.04								
Picea abies																		0.00	0.08	0.04	0.04	0.08	0.32	0.04	0.68
Trientalis europaea						1.04	0.36										0.40								
Vaccinium myrtillus	640.	468.	508.	856.											596	744.	1108.	248	358.	400.	788.			0.24	8.00
V. myrtillus – green	372.	288.	352.	600.											397.	564.	680.	204.	250.	343.	584.				8.00
V. myrtillus – wood	266.	181.	155.	253.											199.	180.	428.	43.6	108.	58.4	204.				
V. myrtillus green:total	*0.58*	*0.61*	*0.69*	*0.70*											0.67	0.76	0.61	0.82	0.70	0.85	0.74				*1.00*
Vaccinium vitis-idaea	11.96	85.2	28.3	40.8																11.4	52.4				
Total	652.	556.	536.	896.	588.	532.	652.	121.	250.	232.	283.	270.	346.	288.	608.	744.	1116.	248.	358.	412.	840.	113.	114.	99.6	150.
Total without wood	384.	374.	380.	644.											408.	564.	688.	204.	250.	354.	636.				

microphytocoenosis (MFC) type according to dominant species : V – *Vaccinium myrtillus*, L – Luzula sylvatica, A – *Avenella flexuosa*, C – *Calamagrostis villosa*), in italics – ratios

Fig. 5. Development of the green biomass to total aboveground biomass ratio of *Vaccinium myrtillus* on plot P19 during 2007–2010

noticeable biomass increase was recorded on all plots near the Plešné Lake in the *Vaccinium myrtillus* microcoenoses. Although the woody biomass increase was found on all plots near the Plešné Lake, an increase of the blueberry biomass was found on plot P19 with an older *V. myrtillus* population. The biomass increase started after 2008, following the initial population damage between 2007 and 2008 – compare regression results in the periods 2007–2010 and 2008–2010 (Table 9). This increase was connected with significant changes in the green biomass to total biomass ratio (Fig. 5), which indicated a regeneration process in the population. A different situation was described in a younger population on plot PJ4, where the biomass growth resulted in the rapid increase of woody biomass stock and the decrease of the green biomass to total biomass ratio. It can be elucidated by the tree canopy disturbance and change in environmental (mainly light) conditions. The *V. myrtillus* dynamics differs on plot CL, where a blueberry disturbance was observed between 2007 and 2008. The disturbance was followed by regeneration (biomass increase) since 2009, but the woody biomass has still the lower stock compared to the initial value (Table 9). The process is synchronized with plot P19, but the reason is not clear. The blueberry dynamics in forest ecosystems under canopy disturbance was described in some other studies (e.g. Cudlín, Vávrová 2010), where an AG biomass increase after the tree canopy disturbance was also reported. A change in the green biomass to total biomass ratio depends on initial conditions in the blueberry population, mainly on the population age as results from differences between the studied plots.

Table 9. Linear regression during 2007–2010 between the year of sampling and aboveground biomass of the separate compartments

Biomass partition	Plot	*N*	b (g·m^{-2}·year^{-1})	*r*	*p*
Avenella flexuosa	CU	27	12.9	0.3508	0.073
	PJ3	22	18.7	–	n.s.
	PJ4	10	15.1	–	n.s.
Calamagrostis villosa	CU	27		–	n.s.
	PJ3	21		–	n.s.
Luzula sylvatica	PJ3	19		–	n.s.
Vaccinium myrtillus–green	CL	20	–90.6	–0.6325	0.003
		15[1]	*29.6*	*0.3879*	*0.153*
	P19	18	–35.0	–	n.s.
		14[1]	*9.7*	–	n.s.
	PJ3	6	–	–	n.s.
	PJ4	14		–	n.s.
Vaccinium myrtillus–wood	CL	20	–	–	n.s.
		15[1]	*53.2*	*0.6813*	*0.005*
	P19	18	110.	0.6882	0.002
		14[1]	*40.1*	*0.7034*	*0.005*
	PJ3	6	146.	0.8799	0.021
	PJ4	14	92.9	0.4609	0.072

[1]regression parameters for the period 2008–2010 (respective values are given in italics), *N* – number of samples, all coefficients in Matějka (2011a), n.s. – not significant

Grass biomass was probably influenced mainly by climate variability in the particular growth seasons (Table 10; Matějka 2014). The highest biomass of both *Avenella flexuosa* and *Calamagrostis villosa* was found in the most favourable year 2009 with high precipitation, sufficient temperature and average daily sunshine time. Plot CU with *Avenella flexuosa* microcoenoses represents an example of the correlation between average daily precipitation in the vegetation period (Table 10) and *A. flexuosa* AG biomass (r = 0.719, P = 0.006; number of samples N = 13). Therefore, an increase of AG biomass during the period of observation (Table 9) would probably be a pseudo-effect caused by an increase of precipitation during this period. The grass biomass maximum in 2009 was recorded on all plots except for PJ4, where significant changes had been found regarding the tree canopy disturbance. Although *Avenella flexuosa* biomass grew on this plot, the total cover of this species decreased (Matějka 2011a) and the *A. flexuosa* microcoenosis started to be invaded by expanding *V. myrtillus*. This process cannot probably be elucidated by a decrease in nutrient availability (Cudlín, Vávrová 2010) because it occurred at the time of the canopy dieback. The increase of grass representation following the

Table 10. Average basic climate features at the Churáňov station (data of Czech Hydrometeorological Institute) in the vegetation period (April–August) of the sampling years compared with two long-time averages

Year	Precipitation		Sunshine	Temperature (°C)
	(mm·day^{-1})	(mm)	(h·day^{-1})	
2007	3.19	488	7.3	12.6
2008	3.04	465	6.9	12.6
2009	5.78	884	6.6	12.3
2010	5.06	774	5.1	12.2
$Avg_{1983-1994}$	3.22	493	6.7	11.6
$Avg_{1995-2006}$	3.88	594	6.6	12.4

tree canopy dieback, which has been mentioned by some foresters, is not documented by the actual data. The situation in the Bohemian Forest with low air pollution and the canopy damage caused by bark beetle is not comparable with clear-cuts in air-polluted regions like the Beskydy Mts., where sites completely overgrown by *Avenella flexuosa* or *Calamagrostis villosa* have been described (e.g. Fiala 1996; Fiala, Tůma 2003).

The Norway spruce forests (mainly in the 8th FAZ) are often influenced by bark beetle (*Ips typographus*) gradations. Grodzki et al. (2004) suggested that the spruce bark beetle dynamics is driven by a complex interaction of biotic and abiotic factors and not by a single parameter such as air pollution. The climate extremes have the main effect in this dynamics. Very warm and dry periods can cause the gradation of bark beetle population. Climate variability connected with suitable stand conditions in the region can be a source of large-area forest dynamics (Matějka 2011c).

The composition of herb layer in climax Norway spruce forests (in the 8th FAZ) is very similar to the species structure of some grassland communities in parallel site conditions. Species such as *Avenella flexuosa*, *Calamagrostis villosa*, *Homogyne alpina*, *Nardus stricta*, *Solidago virgaurea*, *Trientalis europaea* and *Vaccinium myrtillus* are common or diagnostic for *Festuco supinae-Nardetum strictae* Šmarda 1950 (alliance *Nardion strictae* Br.-Bl. 1926). The second type of non-forest communities very similar to spruce forest is included in the alliance *Genisto pilosae-Vaccinion* Br.-Bl. 1926 with common species *Calluna vulgaris*, *Vaccinium myrtillus*, *V. vitis-idaea*. The moss layer has several species growing in both ecosystems, under tree stand and in subalpine grassland, e.g. *Pleurozium schreberi* and *Ptilidium ciliare* (Husová et al. 2002; Chytrý 2007). It is a possible reason why the species composition of spruce forest following the stand damage can be stable (Matějka 2011c) as has been demonstrated in this paper. The boreal forests are similar from the aspect of the presence of shade intolerant species in the ecosystem during the long time (e.g. Bradshaw 1993).

CONCLUSIONS

The Norway spruce canopy disturbance caused by the bark beetle gradation in ecosystems of the near-to-nature plant species composition would be of slight importance in the composition of vegetation as has been demonstrated comparing both catchments. The changes are rather quantitative (e.g. increase of biomass of some species) than qualitative (change of the species composition). The blueberry (*Vaccinium myrtillus*) biomass is sensitive to changes in tree canopy. Its biomass can increase after disturbance. This process is accompanied by changes in the green biomass to total biomass ratio because woody biomass can be accumulated.

The climate variability was the second most significant factor influencing between-year variability in the plant biomass stock. It was observed mainly for grass species (*Avenella flexuosa* and *Calamagrostis villosa*). The grass growth can probably be limited by water availability during the vegetation season. Such a wet season (like that in 2009) was connected with the rapid grass growth and high biomass stock.

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