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Stanislav Vacek, Zdeněk Vacek, Lukáš Bílek, Pavla Hejcmanová, Václav Štícha, Jiří Remeš*

The dynamics and structure of dead wood in natural spruce-beech forest stand – a 40 year case study in the Krkonoše National Park

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Abstract: The study deals with long-term dynamics of snags and fallen dead wood from 1970 to 2010 in an unmanaged forest ecosystem dominated by European beech in the Bažinky area, Krkonoše National Park (Czech Republic). The volume of dead wood was estimated from 1970 separately for fallen dead wood (logs) and standing dead wood (snags and stumps). Total dead wood volume on permanent research plot (PRP) 6 increased from 41.9 to 241.6 $m^3\ ha^{-1}$ and on PRP 7 from 27.7 to 170.0 $m^3\ ha^{-1}$. During 40 year case study the mean total volume of fallen dead wood was 193.3 $m^3\ ha^{-1}$ (± 29.8 S.E.) and 96.2 $m^3\ ha^{-1}$ (± 19.4 S.E.) and the mean total volume of standing dead wood was 17.4 $m^3\ ha^{-1}$ (± 3.4 S.E.) and 12.6 $m^3\ ha^{-1}$ (± 1.4 S.E.) on PRP 6 and PRP 7, respectively. Comparing tree species, the mean volume of fallen dead wood was significantly higher for Norway spruce than for beech in the decomposition class 1 ($F_{(1, 14)} = 5.7$, $P = 0.03$) and significantly higher for beech in the decomposition classes 4 ($F_{(1, 14)} = 20.4$, $P < 0.001$) and 5 ($F_{(1, 14)} = 25.5$, $P < 0.001$). Dead wood was distributed from randomly to aggregated spatial pattern. Despite the rapid decay of beech wood, the amounts of deadwood are likely to increase further during the next decades with continuing disintegration of the forest stand.

Additional key words: fallen and standing dead wood, natural forest, mixed stand, European beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* /L./ Karst.)

Addresses: S. Vacek, Z. Vacek, L. Bílek*, J. Remeš, V. Štícha, Czech University of Life Sciences, Prague, Faculty of Forestry and Wood Sciences, Kamýcká 129, 165 21 Prague, Czech Republic, e-mail: bilek@fld.czu.cz
P. Hejcmanová, Czech University of Life Sciences, Prague, Faculty of Tropical AgriSciences, Kamýcká 129, 165 21 Prague, Czech Republic

Introduction

Dead wood is an important element of forests both for biodiversity and ecosystem functions (Odor et al. 2006; Jakoby et al. 2010) and has an important impact on the stability and continuity of forest ecosystems (Harmon et al. 1986; Bobiec 2002). Dead wood provides valuable habitats for lichens, bryophytes, fungi, invertebrates, small vertebrates, birds, and mammals (Humphrey et al. 2004; Siitonen 2001) and it is also an important component for conserving carbon stock (Lombardi 2008; Pichler et al. 2013).

Decaying trees, snags and fallen dead wood are one of the key elements of natural or near-natural forests (Průša 1985; Korpeľ 1995; Holeksa 2001; Zielonka and Niklasson 2001; Krankina et al. 2002; Rouvinen et al. 2002) supporting higher biodiversity of saproxylic organisms in primary old-growth forests compared to secondary or managed forest stands (Grove 2002; Jankovský et al. 2004). On the contrary, forest harvesting and most other conventional silvicultural interventions do not normally aim to produce large amounts of dead wood typically found in old-growth forest. Larrieu et al. (2012) confirmed that management of montane beech-fir stands reduces the total volume of dead wood and the snag volume, modifies the pattern of decay stages and also reduces the tree species diversity and the diversity of tree microhabitats. Yet, in the framework of sustainable forest management, a better knowledge of the factor influencing the occurrence of dead wood would allow foresters to adopt scientifically-base practices to preserve biodiversity.

The amount of standing and lying dead wood, number and distribution of tree giants/veterans and eventually specific microhabitats are closely related to the development of forest ecosystem (Meyer and Schmidt 2011) and are often considered as an important structural indicator of old-growthness or naturalness in forests (Lindenmayer and Franklin 2006; Bauhus et al. 2009). In temperate forests for the development of forest stands the combination of frequent small-scale events such as mortality and competition and occasional large-scale disturbances caused by storms is decisive (Leibundgut 1982; Korpeľ 1995; Průša 1985; von Oheimb 2007). The biggest share of dead wood was found in forest stands in long-term established forest reserves and also in mountain areas (Christensen et al. 2005), nevertheless dead wood accumulation in man-made forests left to develop freely is a slow process, mainly in the absence of major disturbances. Moreover, their dynamics appeared to be more unidirectional and successional, rather than cyclical as in virgin forests (Vandekerkhove et al. 2009).

The necessity of management for certain amounts, types and dimensions of woody debris in managed forests is well known (Christensen et al. 2005; Müller-Using and Bartsch 2003). The implications for forest management and biodiversity conservation were already discussed in several scientific works. Variable techniques as density cutting, partial cutting and permanent retention of live trees as important tools of silvicultural approaches to maintain old-growthness and increase dead wood volumes attain more and more emphasis in modern forestry prescriptions and research works (Bebber et al. 2005; Götmark 2009; Franklin et al. 2007), nevertheless there is an urgent need for complementary studies to supply information from other forest sites and site conditions.

Previous studies indicate that dead wood volumes are related to numerous factors such as forest type (Christensen et al. 2005; Mountford 2002), history of the particular area, mainly the past forest management (Castagneri et al. 2010; Von Oheimb et al. 2007), time since establishment of forest reserve (Christensen et al. 2005; Saniga and Schutz 2001a; Meyer and Schmidt 2011; Bílek et al. 2011) and natural disturbance types, development phase and live standing tree volume (Saniga and Schütz 2002; Von Oheimb et al. 2007; Vrška 2001a,b,c; Krejčí et al. 2013). Nevertheless very little is published about spatio-temproral dynamics of dead wood in areas without direct human interventions and the role of indirect human interventions such as air-pollution and worsened health status of forest stands.

The aim of this study was to evaluate the long-term changes of the amount of snags and fallen dead wood in unmanaged forest stands dominated by European beech in Bažinky area, National Park Krkonoše (Czech Republic), separately for Norway spruce (*Picea abies* /L./ Karst.) and for European beech (*Fagus sylvatica* L.) and the spatial pattern of standing and fallen dead wood. Another aim was to reveal mutual relationships and the dynamics of coarse woody debris parameters, living trees density and foliage and climatic parameters, namely average annual temperature, annual rainfall and aerial concentration of SO_2. We hypothesize that the volume of fallen and standing dead wood is increasing during the time irrespective of tree species and research plot and that the total volume of dead wood are closely related to the health status and development phase of the parent stand. In the case of European beech we expect faster decay process compared to Norway spruce.

Material and methods

Study area

The study area Bažinky was in 1960 declared to state nature reserve and now belongs to the I. zone of the Krkonoše National Park, Czech Republic. The protected area covers 33.4 ha of semi-natural forests at an altitude from 830 to 1 070 m a.s.l. Before 1960 forest harvesting and regeneration on tree-by-tree basis was only limited to the edge zones of the future protected area. Last historical records about selective forest logging in the core zone of the reserve is known from 1828. The main soil type is mesotrophic Cambisol with higher humus content, in the proximity of numerous water springs in mosaic with Gleysols or gley Cambisols. In higher parts Cryptopodsols are present. Main phytocenological associations are

Table 1. Stand and site characteristics on PRP 6 and 7

Stand	PRP 6		PRP 7	
Forest site type	7S1		6S1	
Age of tree layer 1970 2010	 226/42/20 185/2		 226/18 185	
Tree species	beech	spruce	beech	spruce
Volume (m³ ha⁻¹) 1970 2010	 268 274	 215 112	 404 401	 108 112
Volume (%) 1970 2010	 55 71	 45 29	 78 78	 22 22
DBH (cm) 1970 2010	 31.5 38.5	 46.9 52.1	 40.3 45.7	 58.1 65.1
Height (m) 1970 2010	 21.1 23.1	 29.7 29.7	 28.0 30.2	 34.5 37.9
Phytocen. association	*Calamagrosti villosae-Fagetum*		*Calamagrosti villosae-Fagetum*	
Altitude a.s.l (m)	1060		940	
Exposition	E		E	
Slope	22		24	
Soil	Cryptopodsol		Cambisol modal	
Parent rock	Gneiss, phyllite		Gneiss	
Geographical coordinates	50°43‘55“ N 15°32‘04“ E		50°44‘04“ N 15°32‘21“ E	

7S1 Piceeto-Fagetum oligomesotrophicum with *Oxalis acetosella; 6S1 Fageto-Piceetum oligomesotrophicum* with *Oxalis acetosella; Age, Height, DBH* mean values

Calamagrosti villosae-Fagetum, *Aceri-Fagetum* and *Equiseto-Abietetum*. In the overstorey dominant tree species are European beech (*Fagus sylvatica*) and Norway spruce (*Picea abies*), with admixture of sycamore maple (*Acer pseudoplatanus*), rowan (*Sorbus aucuparia*), silver fir (*Abies alba*) and Scotch elm (*Ulmus glabra*).

In 1968 Forest management institute established two permanent research plots in the locality: PRP 6 – Bažinky 2, area 50×100 m and PRP 7 – Bažinky 1, area 100×100 m. Basic characteristics of both plots are given in Table 1. Both PRP represent autochthonous stands with advanced break-up of the overstorey and abundant natural regeneration in the gaps.

Data collection

Within each permanent research plot (PRP) the occurrence of dead wood separately for standing and fallen dead wood was mapped. The volume of dead wood (diameter at the small end ≥ 7 cm) was estimated by complete enumerations within the permanent plots after the methodology of Harmon et al. (1986); only dead wood originating from the PRP was measured and evaluated, logs and coarse woody debris (CWD) lying outside the plot but originating from trees and snags included in the plot were also involved in the inventory. Fallen dead wood originating from stumps and snags from outside the PRP were omitted. For logs, the length and diameter of the butt, the small end and the middle section were measured. For snags the diameter at breast height (dbh) and the height were measured and for stumps the height and the diameter. Dead wood was classified according to decay classes (modified after Maser et al. 1998; Spetich et al. 2002): 1 = wood hard, without marks of decomposition; 2 = peripheral parts mostly soft, inner section hard (eventually conversely), share of soft rot less than 40%; 3 = peripheral parts mostly soft, inner section partially soft (eventually conversely), share of soft rot 40–80%; 4 = wood soft, share of soft rot more than 80%, contour partially deformed; 5 = wood soft, contour deformed or absent, wood covered with soil.

The volume of dead wood was estimated separately for fallen dead wood (logs) and standing dead wood (snags and stumps). For logs, Newton's formula was used (Šmelko 2007). For dead standing trees volume tables of Lesprojekt Ltd. were used, where the volume of snags is calculated from the dbh and height. All measurements were repeated every fifth year from 1970 to 2010 (with the exception of the first 10-year period) with standard dendrometric methodology (Korf 1972; Šmelko 2007). In 2005 and 2010 the horizontal position of all evaluated entities was measured using the technology Field-Map (IFER-Monitoring and Mapping Solutions Ltd.). For snags, the shift from standing to fallen deadwood was recorded yearly.

Data analyses

The horizontal structure of snags and logs was tested using spatially explicit Clark-Evans aggregation index (Clark and Evans 1954), Pielou-Mountford aggregation index (Pielou 1959; Mountford 1961) and Hopkins-Skellam aggregation index (Hopkins and Skellam 1954). For the analyses the local coordinates of standing dead wood and fallen dead wood were used, for logs we calculated with the point characterising the middle of the log or of its part. Aggregated spatial structures are indicated by asterisk.

All data were log transformed in order to meet the assumption of normal distribution (tested by Kolmogorov-Smirnov test); therefore parametric tests were used for statistical treatment. Volume of standing dead wood was treated separately, since its dynamics is different from fallen dead wood. A series of Student's t-tests was used to test separately the difference in total volume of standing dead wood and fallen dead wood between research plots, than to test the difference in total volume of standing dead wood and fallen dead wood between Norway spruce and beech on each research plot separately. Finally, we tested the volume of fallen dead wood on each plot and for beech and Norway spruce separately; and this separately for all classes of wood decomposition.

To identify variables that affect the volume of fallen dead wood, general linear models were used for each class of wood decomposition separately. The categorical predictors in the models were research plot, tree species, year, and interactions 'research

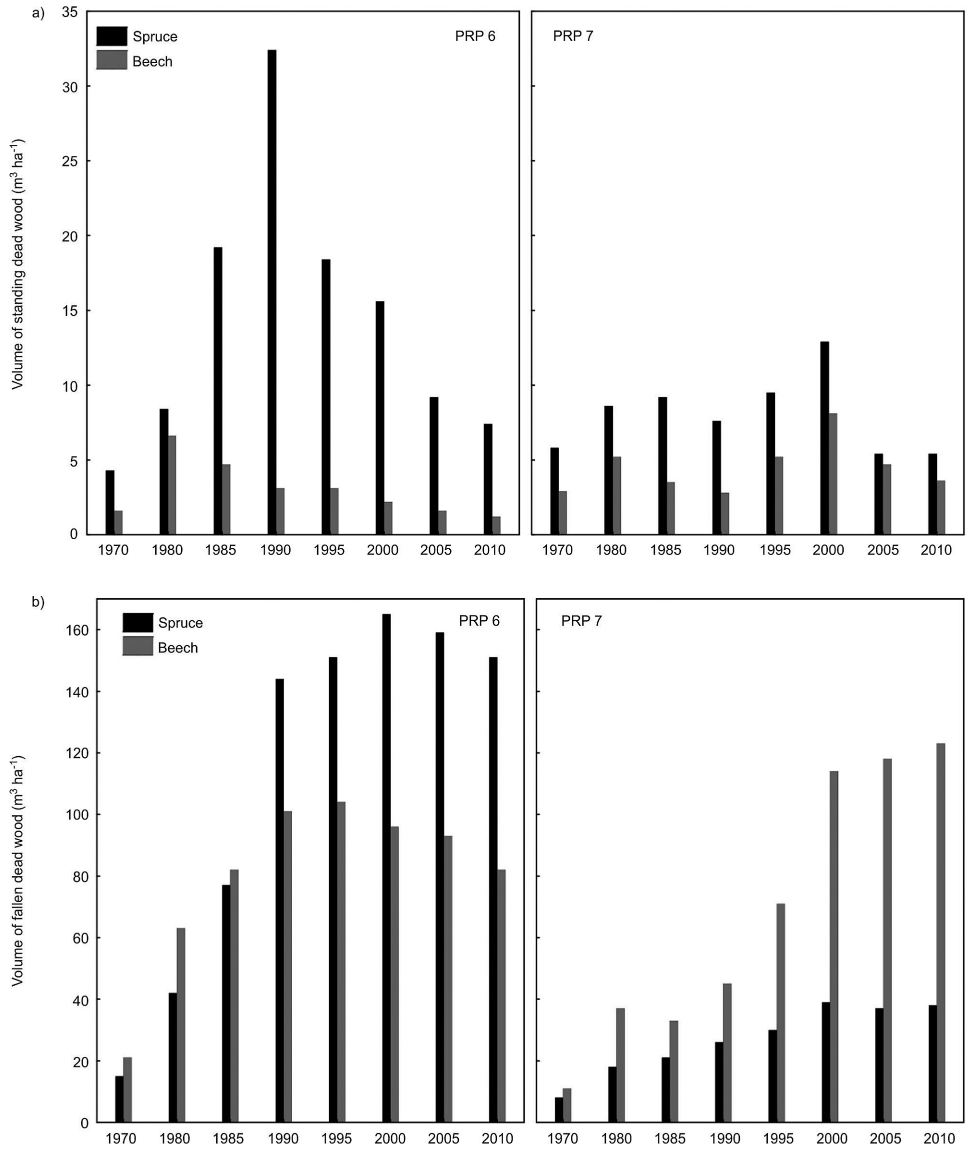

Fig. 1. Dynamics of a) standing dead wood and b) fallen dead wood volume of Norway spruce and beech on permanent research plots PRP 6 and PRP 7 during 40 years

plot*tree species' and 'tree species* year'. The data were collected on the same research plots repeatedly, hence the research plot was put as random factor in the model. Dependent variables in the models were the volume of fallen dead wood in relevant class of woody decomposition.

Unconstrained principal component analysis (PCA) in Canoco for Windows 4.5 program was used to analyze relationships among volumes of snags and fallen dead wood, average diameter at the breast height of snags, dead and living trees density, and foliage of living and all trees in order to reveal similarity of all records. Climate parameters, namely average annual temperature, annual rainfall, average and maximal concentrations of SO_2 in the air, and time (40 years of records) were entered as supplementary variables into the analysis. The methodology of measurements is described in Schwarz et al. (2009). Data were log-transformed, centered and normed before the analysis. The results of the PCA analysis were visualized in the form of an ordination diagram constructed by CanoDraw program.

Results

While total dead wood volumes on PRP 6 increased from 41.9 to 241.6 m^3 ha^{-1} and on PRP 7 from 27.7 to 170.0 m^3 ha^{-1}, the dynamics of snag volumes during the course of 40 years of development showed rather short-termed growth with following drop back to initial levels of standing dead wood volumes (Fig. 1). The mean total volume of standing dead wood from 1970 to 2010 on PRP 6 was 17.4 m^3 ha^{-1} (± 3.4 S.E.) with maximum in 1990 – 35.5 m^3 ha^{-1} and on PRP 6 was 12.6 m^3 ha^{-1} (± 1.4 S.E.) with maximum in 2000 – 21.0 m^3 ha^{-1}. Dead to live wood volumes ratio was ranged from 7.7 to 62.6% on PRP 6 and from 5.2 to 33.1 % on PRP 7 in 1970 and 2010, respectively. Standing to fallen dead wood volumes ratio on PRP 6 decreased from 14.1 to 3.6 % and on PRP 7 from 31.4 to 5.3% m^3 ha^{-1}.

While in 1970 on PRP 6 the volume of fallen dead wood was only 35.9 m^3 ha^{-1} (21.2 m^3 ha^{-1} for beech and 14.7 m^3 ha^{-1} for spruce), in 2010 it amounted to 233.2 m^3 ha^{-1} (81.8 m^3 ha^{-1} for beech and 151.4 m^3 ha^{-1} for spruce). On PRP 7 in the same period the volume of fallen dead wood increased from 19.1 m^3 ha^{-1} to 160.8 m^3 ha^{-1} (123.3 m^3 ha^{-1} for beech and 37.5 m^3 ha^{-1} for spruce). The mean total volume of fallen dead wood was 193.3 m^3 ha^{-1} (± 29.8 S.E.) and 96.2 m^3 ha^{-1} (± 19.4 S.E.) during 40 year period on PRP 6 and PRP 7, respectively. The mean total volume of fallen dead was across all classes of wood decomposition consistently higher on PRP 6 than on PRP 7 (for decomposition classes 1, 3, 4 and 5, $P < 0.05$) (Fig. 2). There was no difference in the volume of fallen dead wood between research plots for beech (Student's $t = 0.92$, $df = 78$, $P = 0.36$), the mean volume of fallen dead wood was 16.1 m^3 ha^{-1} (± 1.3 S.E.) and 13.8 m^3 ha^{-1} (± 2.1 S.E.) on PRP 6 and PRP 7. Beech however differed in the volume of fallen dead wood in decomposition classes 4 and 5. For Norway spruce, the mean volume of fallen dead wood was 22.6 m^3 ha^{-1} (± 4.0 S.E.) and 5.4 m^3 ha^{-1} (± 0.8 S.E.) on PRP 6 and PRP 7, respectively (Student's $t = 4.17$, $df = 78$, $P < 0.001$) and was significantly higher on PRP 6 in all classes of wood decomposition (all $P < 0.05$).

Comparing tree species, the mean volume of fallen dead wood was significantly higher for Norway spruce than for beech in the decomposition class 1 ($F_{(1, 14)} = 5.7$, $P = 0.03$), similar for both species in the decomposition classes 2 and 3 ($P > 0.05$), and significantly higher for beech in the decomposition classes 4 ($F_{(1, 14)} = 20.4$, $P < 0.001$) and 5 ($F_{(1, 14)} = 25.5$, $P < 0.001$). Total volume of snags was significantly higher for Norway spruce than beech on each PRP (PRP 6: Student's $t = 3.4$, $df = 14$ $P = 0.003$; PRP 7: Student's $t = 3.2$, $df = 14$, $P = 0.006$), but there was no significant difference between total volume of snags of each tree species separately between plots ($P > 0.05$ for both PRP 6 and PRP 7).

The changes in dynamics of the volume of fallen dead wood in the course of time was significant in all wood decomposition classes, except decomposition class 1 (for decomposition class 1 $P = 0.09$, other decomposition classes $P < 0.05$).

Fallen dead wood on PRP 7 was in years 1970 and 1980 distributed randomly, starting from 1990 the spatial pattern of logs changed toward more and more aggregated structures (year 2010 CEi 0.803*, PMi 2.738*, HSi 0.757*). Logs of beech were in 1970 and 1980 distributed randomly, from 1990 to 2010 in aggregations (year 2010 CEi 0.794*, PMi 2.398*, HSi 0.739*). Logs of spruce were during the whole study period distributed randomly, only in 2000 and 2010 Clark-Evans index indicated aggregated spatial pattern (year 2010 CEi 0.692*, PMi 1.857, HSi 0.713). Fallen dead wood on PRP 6 was from 1970 to 2010 distributed randomly, only in 2000 and 2010 Clark-Evans index signified aggregated spatial pattern (year 2010 CEi 0.917*, PMi 1.427, HSi 0.576). Logs of beech and spruce were both mostly distributed randomly (year 2010 for spruce CEi 1.019, PMi 1.357, HSi 0.504; year 2010 for beech CEi 1.125, PMi 1.171, HSi 0.440). The only exception were years 1990 and 2000 with Clark-Evans index indicating aggregated spatial pattern.

Standing dead wood on PRP 7 showed mainly aggregated spatial pattern (year 2010 CEi 0.844* and HSi 0.646*, PMi 1.613). Snags of beech in 1970 and 1990 showed random and in 2000 – 2010 predominantly aggregated spatial pattern (v r. 2010 CEi 0.828*, PMi 1.773, HSi 0.682*). Snags of spruce

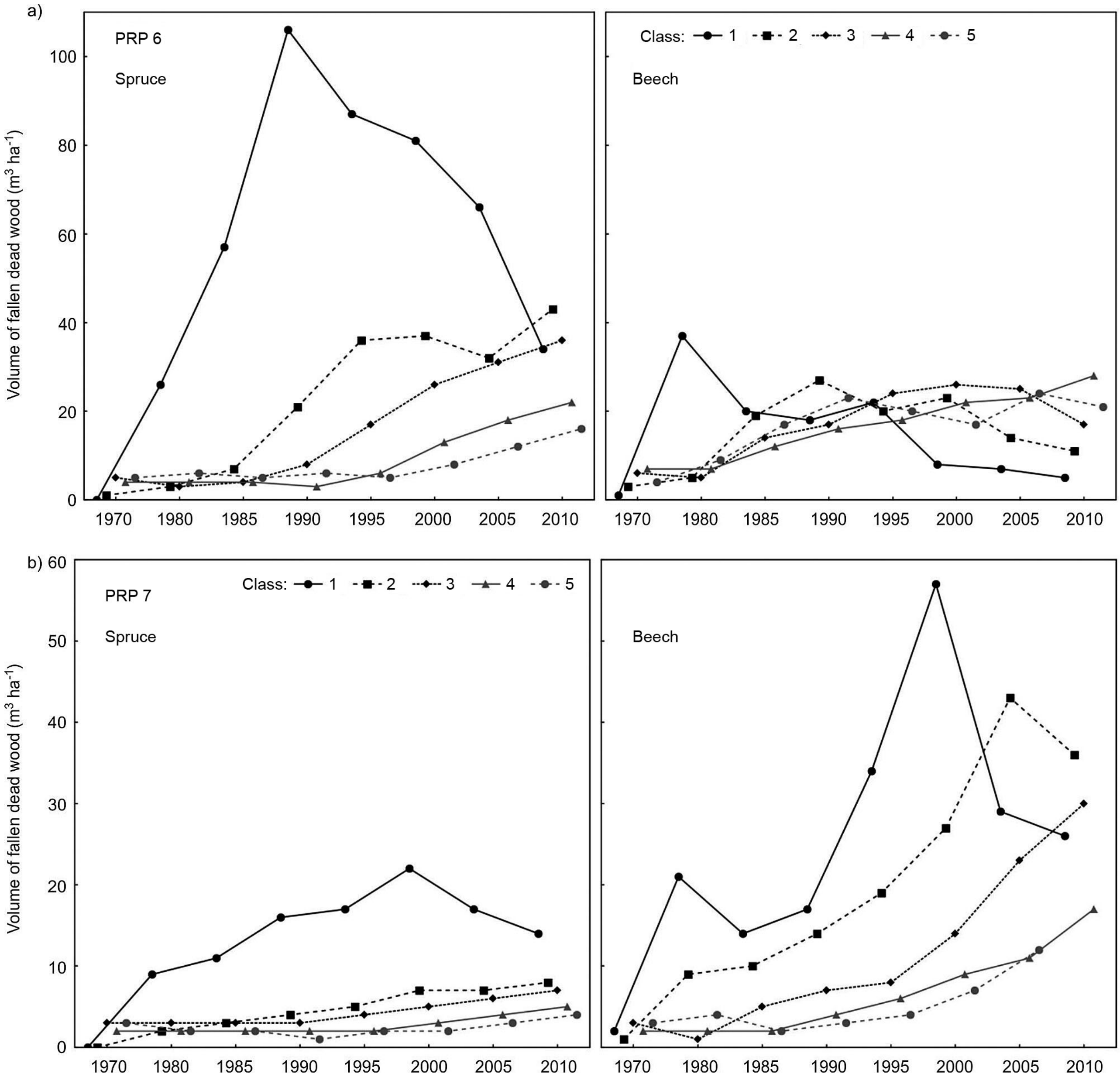

Fig. 2. Dynamics of fallen dead wood volumes of five decay classes of Norway spruce and beech during 40 year on a) PRP 6 and b) PRP 7. Decay classes: 1 = hard wood, without marks of decomposition; 2 = peripheral parts mostly soft, inner section hard, share of soft rot less than 40%; 3 = peripheral parts mostly soft, inner section partially soft, share of soft rot 40–80%; 4 = wood soft, share of soft rot more than 80%, contour partially deformed; 5 = wood soft, contour deformed or absent, wood covered with soil

were during the whole observation period distributed randomly (year 2010 CEi 0.602, PMi 1.601, HSi 0.751). Standing dead wood on PRP 6 was from 1970 to 2010 distributed randomly (year 2010 CEi 0.951, PMi 1.451, HSi 0.581). Snags of spruce had during the whole observation period strictly random spatial pattern (year 2010 CEi 0.685, PMi 1.381, HSi 0.723), while in the case of beech the spatial pattern was predominantly aggregated with occasional fluctuations towards random distribution (year 2010 CEi 0.820*, PMi 1.487, HSi 0.644*). The horizontal structure of fallen dead wood in 2010 on PRP 6 and 7 is shown in Fig. 3.

Results of the PCA analysis are presented in the form of the ordination diagram on Fig. 4. The first ordination axis explained 46%, the first two axes together 82% and the first four axes together 95% variability of dead wood and living trees data. Together with supplementary data (climatic parameters and 40 years of records), the first axis explained 7.5% and the first two axes together explained 74% of variability of data. The first axis x represented the tree species and second axis y represented the research plot, but also the development during the course of 40 years since 1970 till 2010. Volume and DBH of snags were positively correlated to one another and were higher in Norway

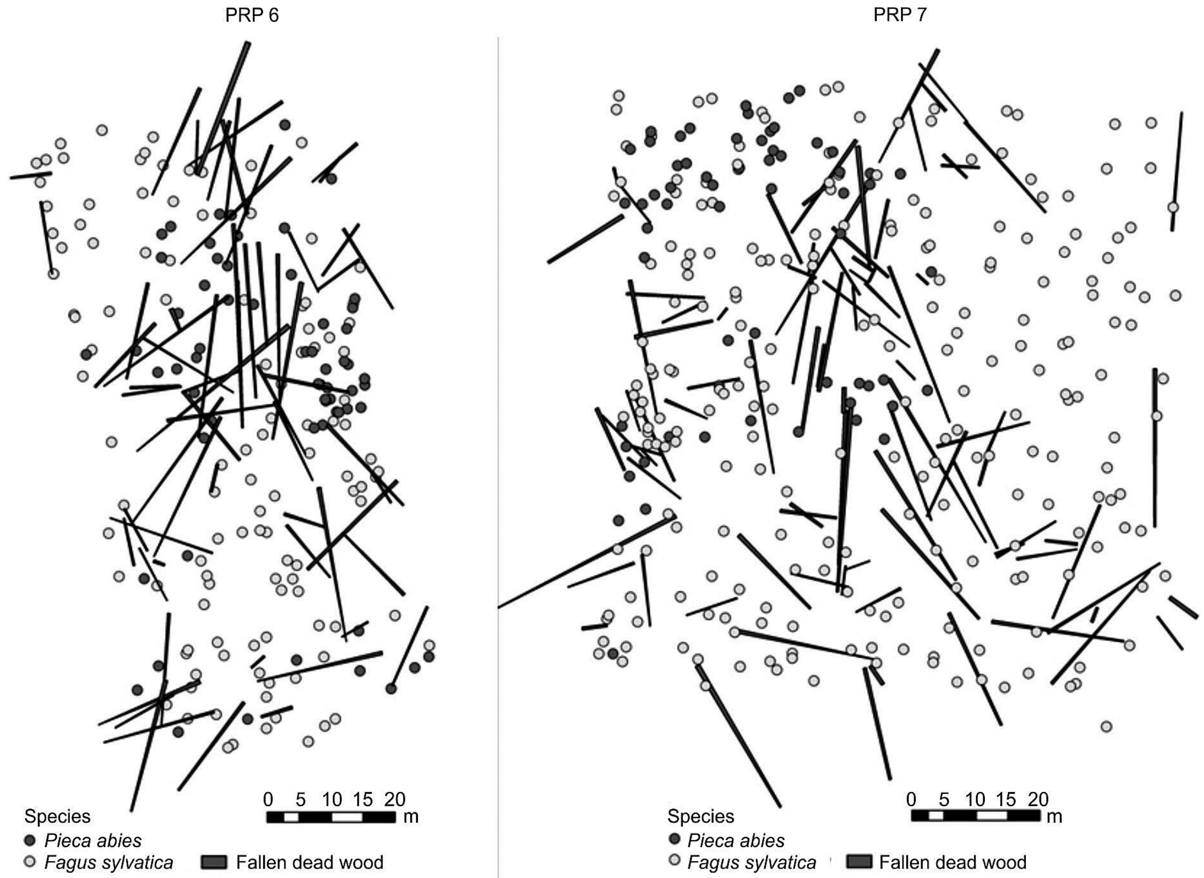

Fig. 3. Horizontal structure of fallen dead wood and standing trees of Norway spruce and beech and on PRP 6 and PRP 7 in 2010

spruce, while density of dead trees was positively correlated with the density of living trees and both were higher in beech. These parameters were independent from the time. Volume of fallen dead wood and partially density of snags were increasing in the course of time, while foliage of living and all trees were decreasing in the time. The contribution of rainfall, temperature and especially of SO_2 in the air was relatively small. The dynamics of parameters in the course of 40 years was remarkable especially for Norway spruce on the PRP 6 and on the PRP 7, and also for beech on the PRP 7 as marks of each record are relatively distant from one another whereas marks for beech on PRP 6 were relatively close together in the diagram.

Discussion

Long term research on beech wood decomposition in Central Europe is rather sparse. In 2010, 50 years after the establishment of the reserve, total dead wood volume and the dead to live wood ratio amounted to 241.6 m^3 ha^{-1} and 62.6% on PRP 6 and 170.0 m^3 ha^{-1} and 33.1 % on PRP 7. These amounts and dead wood increment rates were confirmed from similar condition in European natural and semi-natural forests (Christensen et al. 2005; Meyer and Schmidt 2011; Saniga and Schütz 2001b). In most reserves, after three decades critical values for restoring the dead wood pool could be reached (Mountford 2002). Saniga and Schütz (2001a) published results from long term research in Havesova, Rozok and Kyjov beech forest, where maximal levels of dead wood ranging from 118 to 297 m^3 ha^{-1} were reached in the growing up stage. Study in beech-dominated forests in northwestern Germany showed that the average amount of dead wood almost doubled from 9.2 to 17.8 m^3 ha^{-1} within 10 years (Meyer and Schmidt 2011). Mountford (2002) estimates the development cycle of dead wood within 200–300 years with higher levels of coarse woody debris (CWD) following the rapid break-up of old-growth stands. After these events, the total volume of CWD can reach high values, as e.g. 550 m^3 ha^{-1} in virgin forest in Pecka, Slovenia (Debeljak 1999). Within this context Vandekerkhove et al. (2009) pointed out the difference between the cyclical development of dead wood pools in virgin forest and unidirectional accumulation in forests recently left unmanaged.

According to Korpeľ (1995) the volume of dead wood is closely related to the site and stand characteristics, terrain, age of the forest stand and the past

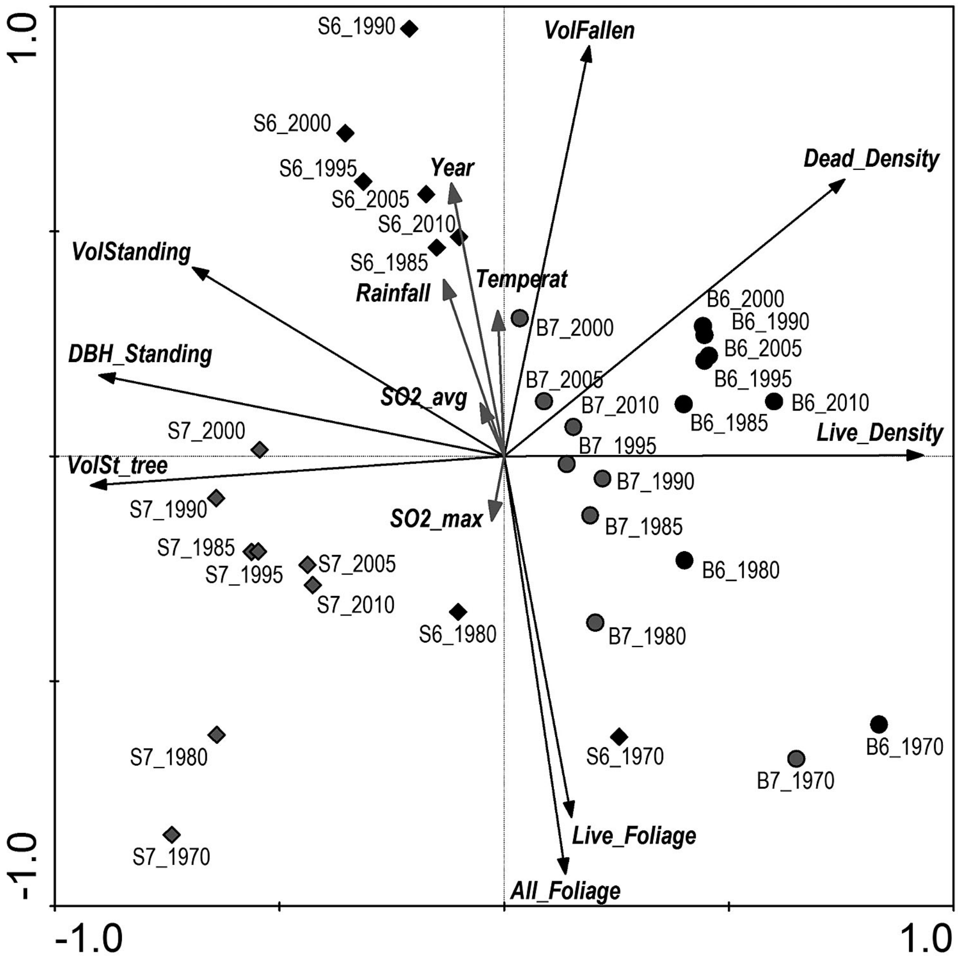

Fig. 4. Ordination diagram showing results of PCA analysis of relationships among dead wood characteristics (*VolStanding* volume of snags, *VolSt_tree* volume of wood per a snag, *DBH_Standing* average diameter at the breast height of snags, *VolFallen* volume of fallen dead wood, *Dead_Density* number of dead trees per hectare), living trees characteristics (*Live_Density* number of living trees per hectare, *Live_Foliage* average percentage of foliage of living trees, *All_Foliage* average percentage of foliage of all trees), climate parameters (*temperature, rainfall,* SO_2*_avg* average concentration of SO_2 in the air, SO_2*_max* maximal concentration of SO_2 in the air) and time (*year*). Codes indicate each record of data. Code abbreviation: S or B – Spruce or beech, 6 or 7 – identification of permanent research plot PRP 6 or PRP 7, and year of the record (1970–2010). ♦ and • indicate records of spruce and beech, respectively; black and grey colours indicate records on PRP6 and PRP 7, respectively

and present forest management. Temporal dynamics of dead wood in unmanaged forests is particularly dependent on the forest ecosystem development with higher dead wood volumes after the break-up stage of the particular forest stand. On both plots, total dead wood volumes mainly in the 1st decay class steeply increased as result of disintegration of the overstorey of the parent stand. Less information is available about the influence of air-pollution with following worsened health status of forest stand on the accumulation of dead wood volumes (Schwarz et el. 2007). Vacek et al. (2007) reports from the Krkonoše Mts. in altitudes above 1000 a.s.l. a steep increase of mortality in spruce stands as combined effect of air-pollution, lower average annual temperature, shorter vegetation period and more frequent ice and wind disturbances. Schwarz et al. (2009) has shown that the dead wood volumes in bilateral biospherical reserve Krkonoše/Karkonosze vary strongly according to forest type: highest dead wood volumes were confirmed in the 8th vegetation zone; in the Czech part of the reserve mainly in forest types 8Y (*Calamagrostio villosae-Piceetum typicum*), 8F (*Calamagrostio villosae-Piceetum filicetosum*), 8V (*Calamagrostio villosae-Piceetum filicetosum*), 8Q (*Calamagrostio villosae-Piceetum sphagnetosum*), 8Z (*Calamagrostio villosae-Piceetum typicum*) and 8T (*Calamagrostio villosae-Piceetum sphagnetosum*) decreasing in the same order from 25.7 m^3 ha^{-1} to 14.5 m^3 ha^{-1}. However, irrespective of different site conditions, highest dead wood levels are reached within I. zone of NP (from 30 m^3 ha^{-1} to 450 m^3 ha^{-1}).

In our study on both plots the share of beech on the live standing tree volume was very similar (71% on PRP 6 and 78% on PRP 7), there was also no difference in mean volume of fallen dead wood for beech – 16.1 m^3 ha^{-1} (± 1.3 S.E.) and 13.8 m^3 ha^{-1} (± 2.1 S.E.) on PRP 6 and PRP 7, respectively. Nevertheless, despite 29% of live standing tree volume for spruce on PRP 6 the volume of dead wood for this tree species amounted to 61%. Comparing decomposition classes, the mean volume of dead wood was significantly higher for Norway spruce than for beech in the 1^{st} decomposition class and conversely significantly higher for beech in the decomposition classes 4 and 5 on both plots. On PRP 6 this pattern of dead wood accumulation was further accelerated due to bark beetle infestation, which substantially increased the share of spruce in the total dead wood pool. Moreover Norway spruce produces higher dead wood volumes than European beech under similar climatic conditions because of its less pronounced decomposition rates (Vacek 1982; Korpeľ 1995; Vacek et al. 1994, 1996; Saniga and Schütz 2001b). According to different authors (Müller-Using and Bartsch 2003; Von Oheimb et al. 2007; Saniga and Schütz 2001a) time span for complete decomposition of a beech trunk is between 30 to 40 years, whereas the decomposition of most conifers takes some decades longer (Korpeľ 1995; Saniga and Schütz 2001b). On the contrary Lombardi at al. (2008) showed that silver fir and beech tend to decompose at the same rate. Mean time since tree death for beech trees in central Apennines was 17 years for the first class, 29 years for the second class and 40 years for the third class. In our study area for beech the duration of the first decay class was 5–10 years, of the second, third and fourth decay class equally 5–15 years, and of the fifth decay class 5–10 years. For spruce the period of the first decay class is 5–30 years, of the second and third class 10–25 years, of the fourth decay class 10–30 years and for the fifth decay class 5–25 years.

Climatic and site environmental factors probably play very important role in decaying process. Therefore the decay process of beech and spruce logs among and within localities is highly variable. Average time for complete decay of beech log was in given conditions 20–40 years, on water springs 15–25 years. Only two beech logs without direct contact with the soil surface did not decomposed during the observation period of 40 years and are still in the fourth decay class. Only spruce logs and CWD with a diameter < 35 cm on water-logged sites decomposed completely after 35–40 years. Complete decay of the majority of logs and CWD on the remaining sites is expected after 50–85 years after tree or log fall, without soil contact even up to 85 years. Thus, decay of beech is two times shorter than that of spruce. Decay process of lower snags or stumps of beech shaded by ground vegetation or natural regeneration was by one fourth up to one half faster than that of logs. In the case of spruce it was one fourth up to one third.

Even higher variability was observed in the case of snags: in some cases parts of beech trunks persisted more than 25 years without apparent marks of decay process on its surface before they fell to ground, some of spruce snags even persisted the whole observation period of 40 years without pronounced decay process. As noted Lombardi et al. (2008) to understand better the relation between the time of death and the class of decay better, the cause of death should be known. For example, in a Norway spruce killed by bark beetle the main part of the snag remains solid for a long time with very limited uptake of humidity and thus in general slower decomposition rates. Opposite situation may be expected in the case of fungal infestation.

For logs very important role played the moisture characteristics of the microsite. Faster decay process was observed on logs with direct contact with the soil surface. On the contrary, when this contact is hampered by other logs or terrain irregularities, the decay process is less intensive. Important feature in the locality is the presence of small spring areas with higher soil moisture accelerating the decay process of CWD. This is also truth for logs, which are located in areas with abundant herb layer, mainly grass species such as *Calamagrostis villosa*. Also spruce logs with bark or rests of bark retain more humidity and therefore decay faster compared with logs without bark, which is often the result of previous infestation by *Ips typographus*.

Conclusions

At present, the amount of dead wood on PRP 6 and 7 are comparable to average dead wood volumes reported from other authors. On both plots, total dead wood volumes mainly in the 1^{st} decay class steeply increased as result of disintegration of the overstorey. The contribution of rainfall, temperature and especially of SO_2 in the air was relatively small. Mainly in the second half of the observation period we see decrease of dead wood volumes in the 1^{st} decay class and general shift from random to aggregated dead wood accumulation. Decomposition process and subsequent shift into higher decay classes continually increased dead wood levels in decay class 2–4 from 1970 to 2010. Despite generally faster decay of beech wood compared to spruce wood, the decay process of both tree species among and within localities is highly variable as result of heterogeneous microsite condition.

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