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REVIEW

Deadwood volume in strictly protected, natural, and primeval forests in Poland

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Abstract

Standing and downed deadwood at different stages of decay provides a crucial habitat for a wide range of organisms. It is particularly abundant in unmanaged forests, such as strictly protected areas of national parks and nature reserves. The present work used the available data for such sites in Poland, analyzing a total of 113 studies concerning 79 sites to determine the causes contributing to variation in deadwood volume based on the duration of conservation, changes in deadwood volume over time (for those sites which were examined multiple times), elevation above sea level, forest type, stage of forest development, input of dead trees from the years preceding deadwood measurements, live tree volume, and the proportion of downed to standing deadwood). Depending on species composition and site altitude, most tree stands fell into one of four categories: subalpine spruce forests, montane beech-fir forests, low altitude beech-fir forests, or oak-hornbeam and riparian forests. The mean deadwood volume for all forest types amounted to 172.0 m^3/ha. The mean volume of deadwood in montane beech-fir forests (223.9 m^3/ha) was statistically significantly greater than in the other three forest types, for which it ranged from 103.5 to 142.5 m^3/ha. A direct effect of the duration of conservation on deadwood volume was not identified. Nevertheless, analysis of repeated measurements on the same sample plots at 10-year intervals showed a consistent rise in mean deadwood volume. A linear regression model for all the analyzed factors reported from montane beech-fir forests and subalpine spruce forests showed that in addition to site altitude, another statistically significant variable was the input of dead trees ($R^2 = 63.54\%$).

Keywords Old-growth forest · Volume · Coarse woody debris · Snags · Stumps · Biodiversity

Introduction

Surveys and monitoring of deadwood volume in forests provide useful indicators of habitat quality (Rondeux and Sanchez 2010). Previous research has shown that deadwood, whether standing or downed, constitutes an integral part of forest ecosystems, providing obligatory or facultative habitats for many organisms, such as bryophytes, lichens, fungi, and vascular plants (Dittrich et al. 2014; Preikša et al. 2015), as well as a variety of invertebrate and vertebrate animals (Bütler et al. 2004; Stokland et al. 2012). Of particular importance are nurse logs, which play a major role in the regeneration of tree stands under harsh climatic conditions (Zielonka 2006a). Deadwood is also a key factor in the nutrient cycle and a valuable carbon pool (Krankina and Harmon 1995; Merganičová and Merganič 2010).

Due to the significance of deadwood in contemporary forest management, efforts have been made to determine threshold values for biodiversity conservation. Review of data from European forests has revealed 36 thresholds ranging from 10 to 80 m^3/ha for boreal and lowland forests and from 10 to 150 m^3/ha for mixed montane forest, with the peak values being 20–30 m^3/ha for boreal forests, 30–40 m^3/ha for mixed montane forests, and 30–50 m^3/ha for lowland oak-beech forests (Müller and Bütler 2010). In addition to quantifying deadwood, it is also important to evaluate its degree of decay, species composition, and size distribution (heterogeneity of deadwood substrates) due to the diverse ecological requirements of saproxylic organisms (Stokland

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et al. 2012). Another crucial factor is the local climate of the site. In forest ecosystems, this is often linked to canopy openness, which determines the amount of light reaching the forest floor, modifying habitat conditions and affecting the species composition and population size of the organisms associated with deadwood (Seibold et al. 2016a, b). To ensure diversity of deadwood substrates and to foster natural dynamics in populations of species dependent on them, a constant supply of deadwood must be ensured over decades (Chećko et al. 2015).

One of the most effective ways of conserving endangered saproxylic species is the protection of their natural habitats by allowing dead trees to remain in the forest and gradually decompose (Gutowski 2006). This can be accomplished in strictly protected areas, and especially in sites from which deadwood has not been removed for decades. The number and size of such sites are affected by a range of biotic and abiotic factors, so differences among countries in this respect may be considerable.

In terms of both deadwood volume and other characteristics of tree stands (e.g. mean age and structure), managed forests differ significantly from natural and strictly protected ones (Bobiec 2002; Stachura-Skierczyńska and Bobiec 2008; WISL 2014). The forests of Poland constitute an important part of Central Europe's forests. The spatial distribution of different site conditions is largely reflected in the spatial structure of the dominant species. Except for montane areas, where *Picea abies* (L.) H. Karst., *Abies alba* Mill., and *Fagus sylvatica* L. are prevalent, in most tree stands across the country *Pinus sylvestris* L. is the most abundant species. According to data as of the end of 2013, the total forest area amounts to 9177.2 thousand ha (CSO 2014), or 29.4% of the country's area. As much as 81.2% of forests are state-owned, with 77.3% being managed by the State Forests National Forest Holding (SFNFH). In Poland the highest level of nature protection is afforded by 23 national parks occupying a total area of 314.6 thousand ha (individual parks ranging from 2.1 to 59.2 thousand ha). The average forest cover of national parks is 62%, varying from 4 to 95% for individual parks (CSO 2014; Jamrozy 2014). The average age of forests managed by the SFNFH is 58 years with a stand volume of 272 m^3/ha, while the corresponding figures for national parks are 74 years and 348 m^3/ha. Tree stands which are 100 years old or older account for 24.1% of forests in national parks (WISL 2014). Another type of nature conservation in Poland encompasses 1480 reserves with different protection statuses (strict, active, landscape), which occupy a total area of 165.7 thousand ha (CSO 2014).

The mean volume of deadwood for all European forests, including data from the Russian Federation, is currently estimated at 20.5 m^3/ha, while without the Russian Federation it amounts to approximately 10 m^3/ha. Over the past two decades, deadwood volume has slightly increased in most regions of Europe. The amount of deadwood varies considerably depending on forest type, stand volume, rate of decay, and vegetation zone and is also influenced by forest management regimes (Van Brusselen 2011).

According to 2009–2013 data from more than 28,000 sample plots located all over Poland, the mean deadwood volume is 5.8 m^3/ha, with the figure for national parks (irrespective of their protection status) amounting to 36.7 m^3/ha (WISL 2014). Depending on the national park type, tree stand, and conservation objectives, the percentage share of strictly protected areas in different national parks ranges from 1 to 64%. The total area subjected to strict protection in all national parks exceeds 712 thousand ha, or approximately 22% of their total area (Jamrozy 2014).

Deadwood in Polish forests has been systematically studied over the past years, leading to numerous reports on the subject. Some of them are part of wider research efforts, while others have not been released in electronic format or have not been published. However, to date no detailed overview of the existing, considerable body of data has been produced. Given that Polish forests occupy a large area in central Europe, such an overview would be interesting for scholars, practitioners, and environmental protection agencies. In view of the above, the objective of the present work was to:

- present comprehensive data on the volume of deadwood in natural and strictly protected forests;
- examine the relationship between deadwood volume and selected factors, such as site elevation a.s.l., forest type, live tree volume, duration of conservation, input of dead trees, and stage of forest development.

Methodology

Data

The review includes available data on deadwood volume in strictly protected forests ("Appendix"), some of which were reported as primeval. The term "forests of primeval character" was understood as forest complexes not affected by direct intervention of man (either entirely unharvested or only with individual trees removed—usually the largest ones), but possibly compromised by air pollution, road construction, etc. (Jaworski et al. 2002). The review includes data from many separate publications ("Appendix"), which vary depending on the methodology and detail of site description. Missing information has been either filled on the basis of other sources, or blank cells have been left. The reviewed data concern the volume of deadwood (standing and downed) as well as sampling methods, minimum diameters, live tree volume, elevation a.s.l., forest community characteristics, input of dead trees (the volume of trees that had died in the years preceding deadwood measurement), stage of forest development, measurement date, and the date when the national park was established or another form of conservation was instituted (subsequently operationalized as the "duration of conservation" variable). All the regions included in this paper are marked on the map in Fig. 1. The terminology used in this paper has the following meaning: a region is a national park, nature reserve, geographic region, etc., while a site is the exact place of study for which deadwood volume was reported for a given year. On some sites studies were carried out two or three times at intervals of up to more than a decade. In such cases, separate data are given for different years of measurement. The name of each site is provided in column 2 of "Appendix"; if several studies were conducted for a given site, the number of study is provided in parentheses. Finally, a study corresponds to an individual measurement, each presented as a separate line in "Appendix".

The data reported by individual studies (see "Appendix") were subsequently converted to standardized values for the purposes of the present work. The volumes have been standardized where the minimum diameter used to measure was > 5 cm diameter. The following regression was used: $\text{Volume}_{5\text{ cm}} = \text{Volume}_{x\text{ cm}} \cdot (0.0279 \times \text{diameter}_{x\text{ cm}} + 0.830)$ (Christensen et al. 2005).

Duration of conservation

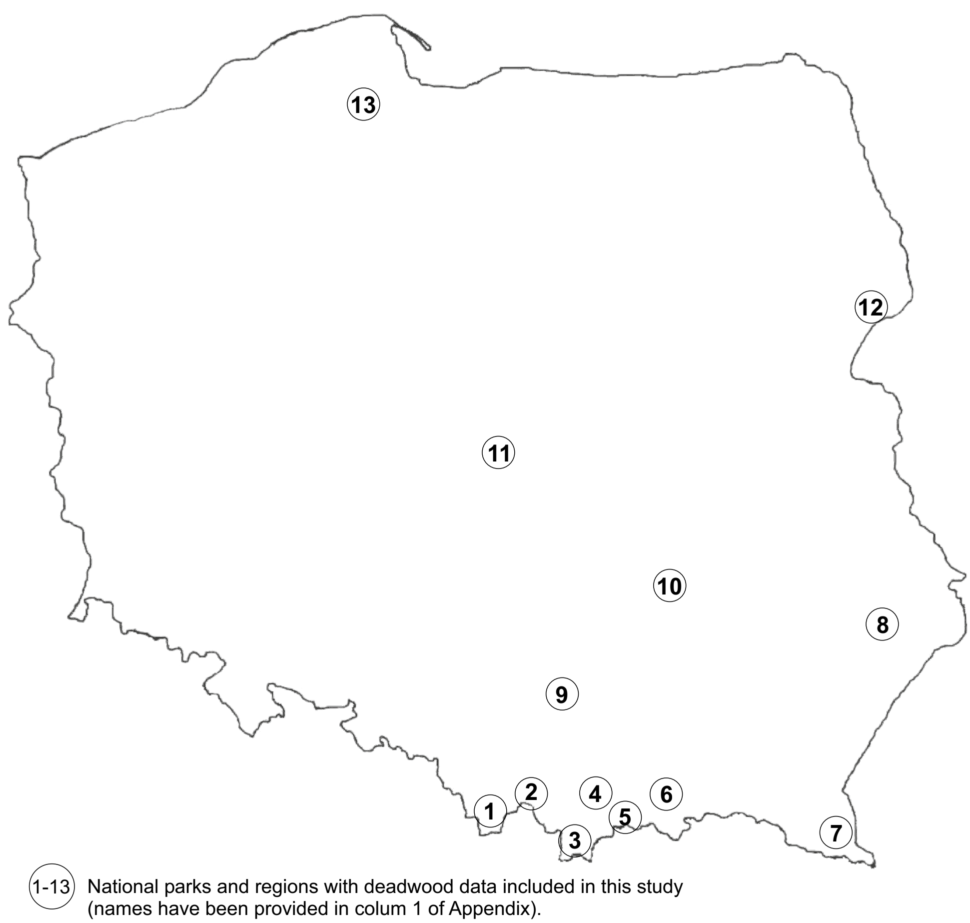
For the purposes of this paper, duration of conservation was defined as the difference between the year when strict protection was instituted (usually provided by the authors of the reviewed papers) and the year in which deadwood measurement was conducted. If the initial year of conservation was not specified, the year of establishing the national park or reserve was used instead. Alternatively, duration of conservation was defined as the period over which deadwood had not been removed from the site, if such data were provided. On 29 sites measurements were repeated two or three times at 10 or 11-year intervals. For such sites, all available data were included ("Appendix").

Forest elevation and forest type

Most of the reviewed works specified site elevation a.s.l. If that information was provided as a range, an arithmetic mean was calculated. In the absence of such data, elevation was determined based on maps or other publications concerning a given site.

Forest type was determined on the basis of several criteria: elevation a.s.l., species composition, and plant community. The following four basic types were adopted:

Fig. 1 Regions in which sites for deadwood study were located



- Subalpine spruce forest—tree stands located above 1100 m a.s.l. with the typical community being *Plagiothecio-Piceetum tatricum* (Szaf., Pawł. et Kulcz. 1923) Br.-Bl., Vlieg. et Siss. 1939 em. J. Mat. 1977 and with the dominant tree being *Picea abies*.
- Montane beech-fir forest—tree stands located from approximately 600 to 1150–1250 m a.s.l. (depending on the mountain range). The main communities include *Dentario glandulosae-Fagetum* W. Mat. 1964 ex Guzikowa et Kornaś 1969, *Abietetum polonicum* (Dziub. 1928) Br.-Bl. et Vlieg. 1939, and *Carici-Fagetum abietetosum* Pancer-Koteja 1973*, Abieti-Piceetum montanum* Szaf., Pawł. et Kulcz. 1923 em. J. Mat. 1978. The dominant trees are beech and fir, with some spruce and sycamore presence.
- Low altitude beech-fir forest—tree stands located below approximately 600 m a.s.l., with the typical communities being *Abieto-Fagetum* Kulczyński 1928, *Dentario glandulosae Fagetum, Luzulo pilosae-Fagetum* W. Mat. & A. Mat. 1973 and *Melico-Fagetum* Lohm. ap Seibert 1954.
- Oak-hornbeam and riparian forests—tree stands belonging to the communities *Tilio cordatae-Carpinetum betuli* Tracz. 1962 and *Circaeo-Alnetum* Oberd. 1953.

Only two sampling sites were located in pine-oak forests with *Querco roboris-Pinetum fagetosum* (W. Mat. 1981) J. Mat. 1988 communities, and so they were excluded from analysis of deadwood volume per forest type. Some studies encompassed larger and more phytosociologically varied areas; they were not assigned to any of the above-mentioned types, either.

Stage of forest development and input of dead trees

The stage of forest development was determined based on the classification proposed by Korpel (1989, 1995) for primeval forests, taking into account their structure and growth dynamics. It should be noted that the duration and trajectory of the three stages identified (growing up, optimum, and breakup) depended on site conditions and species composition.

The other factor describing changes in forest stands was the volume of trees which had died in the period immediately preceding deadwood measurements on site, which reflects the input of dead trees to the ecosystem. This pre-measurement period ranged from 5 to 21 years, and in the vast majority of cases amounted to 10 or 11 years. However, such data were available only for some of the sites, mostly for subalpine spruce forests and montane beech-fir forests. "Appendix" provides both the volume and period of time specified by the authors; the values used in the present analysis were converted into volume per decade.

Data analysis

Analysis of data concerning deadwood volume was carried out in two steps:

- selected individual factors (type of forest, elevation above sea level, share of standing deadwood in total deadwood volume, total deadwood to live tree volume ratio, duration of conservation) were studied to show present-day differences among strictly protected Polish forests;
- multiple regression analysis was used to identify those factors which have the greatest influence on deadwood volume variation in the studied sites.

The relationships between independent variables and deadwood volume were analyzed using different datasets, depending on the variable. The current values of the variables were taken from the latest studies from sites. Given that not all studies contained all the needed information, the number of data used for determining: total deadwood volume; live tree volume, deadwood volume in the various forest types, volume of downed deadwood, and volume of standing deadwood, ranged from 72 to 79. All available data were used to determine relationships between these variables, and in particular between: total deadwood volume and site elevation a.s.l; duration of conservation and total deadwood volume; combined volume of deadwood and live trees; deadwood to live tree volume ratio; and standing deadwood to total deadwood volume ratio. The number of data used in these analyses ranged from 101 to 110; the differences were again due to certain data missing from some studies.

In terms of the number of total deadwood measurements per site (which was also subjected to statistical analysis), among the total of 77 sites for which data were reported, 48 were investigated once, 25 twice, and 4 three times. This has resulted in an additional 33 data for the 29 sites with multiple measurements. These data are expressed as differences with respect to previous measurements and presented in a separate figure to illustrate temporal changes in deadwood volume.

Analysis of variance, Student's *t* test, Friedman's ANOVA and the Kruskal–Wallis test were used to determine the significance of differences. Relationships between variables were tested by means of Pearson's correlation coefficient and nonlinear regression. The above tests were conducted using STATISTICA 13 software.

In multiple regression analysis, models were constructed exclusively based on data from the latest measurements for the studied sites. Due to the absence of data on the input of dead trees in two forest types (low altitude beech-fir forest, oak-hornbeam and riparian forests) and the similarity of the variables "elevation a.s.l" and "forest type" (in this paper forest type is largely associated with site altitude), several different models were considered. The other variables, that is, live tree volume, duration of conservation, and stage of forest development, were present in all the analyzed models. Scatter plots were used to determine the dependence curves between the variables. The relationship between deadwood volume and elevation a.s.l. was a quadratic function.

Since the number of variables differed and models could not be estimated from the same data set, leave-one-out cross-validation was used, followed by calculation of the root mean squared error (RMSE):

$$\mathrm{RMSE} = \sqrt{\frac{1}{n}\sum_{i=1}^{n} e_i^2}$$

where e_i is the error for ith observation and n—the number of observations. Models with smaller RMSEs, with the best fit to data, were used in further analysis. Normal distribution of residuals and homoscedasticity of variances were analyzed using the Shapiro–Wilk and Breusch–Pagan tests. Calculations were made using R v. 3.4.3 software (R Core Team 2017).

Results

The mean deadwood volume was 172.0 m^3/ha (SD = 101.3 m^3/ha), with values for individual sites from 0 to 427 m^3/ha. The mean live tree volume on those sites was 526.4 m^3/ha (SD = 138 m^3/ha), ranging from 211 to 907 m^3/ha.

The deadwood to live tree volume ratio was from 0 to 172% (Fig. 2). In two cases, deadwood volume exceeded live tree volume. The average ratio was 34.0% (SD = 24.5%). The combined volume of deadwood and live trees was from 270 to 1093 m^3/ha, with a mean value of 701 m^3/ha (SD = 171 m^3/ha). The deadwood to combined volume of deadwood and live trees ratio was from 0 to 29.9% (Fig. 3). The average ratio was 5.0% (SD = 3.9%).

The duration of tree stand conservation was not significantly correlated with deadwood volume (Pearson's $r = 0.14$, $p > 0.05$), but significant differences were found for repeated (two or three) measurements of the same sites at 10–11 year intervals (Student's t test = 3.74, $p < 0.001$ for double measurements; Chi-square ANOVA = 6.50, $p < 0.05$ for triple measurements). Deadwood volume increased considerably over the years, on average by slightly more than 30 m^3/ha/decade between first and second measurements and by 57 m^3/ha/decade between the second and third measurements (Fig. 4). However, not all reports revealed an increase in deadwood volume after 10–11 years. Out of 33 measurements (Fig. 5), an increment was noted in 27 cases (by 0.4–155 m^3/ha/decade), and a decline in 6 cases (by 1–31 m^3/ha/decade).

Deadwood volume varied considerably throughout the entire range of elevations a.s.l., with rather low values observed at all elevations (approximately 50 m^3/ha). The highest deadwood volumes were found for the 600–1000 m a.s.l. range. The relationship was statistically signiicant (quadratic regression analysis, p < 0.05; Fig. 6). Also a comparison of sites by forest type (a variable associated with elevation) showed significant differences between deadwood volume in montane beech-fir forests (223.9 m^3/ha) and other forest types (ANOVA $F = 7.99$, $p < 0.001$). In the remaining three forest types, deadwood volume ranged from 103.5 to 142.5 m^3/ha (Fig. 7).

The mean volume of downed deadwood was 105.8 m^3/ha (SD = 68.9 m^3/ha) and that of standing deadwood was

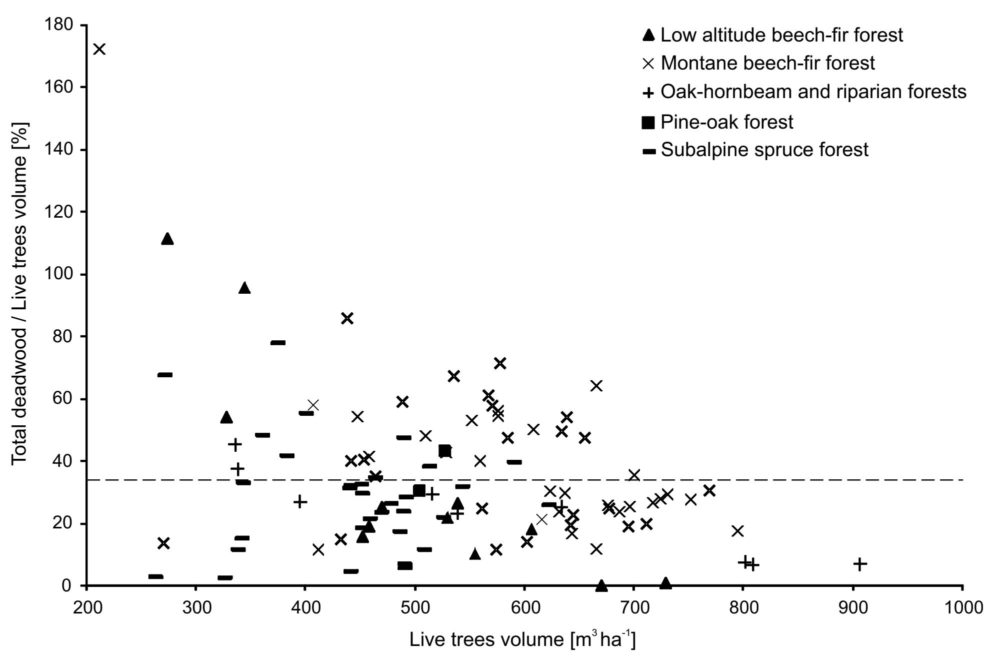


Fig. 2 Relationship between live tree volume and deadwood volume for the various studies (the dashed horizontal line indicates the mean total deadwood/live tree volume ratio (%), which is 34.0%)

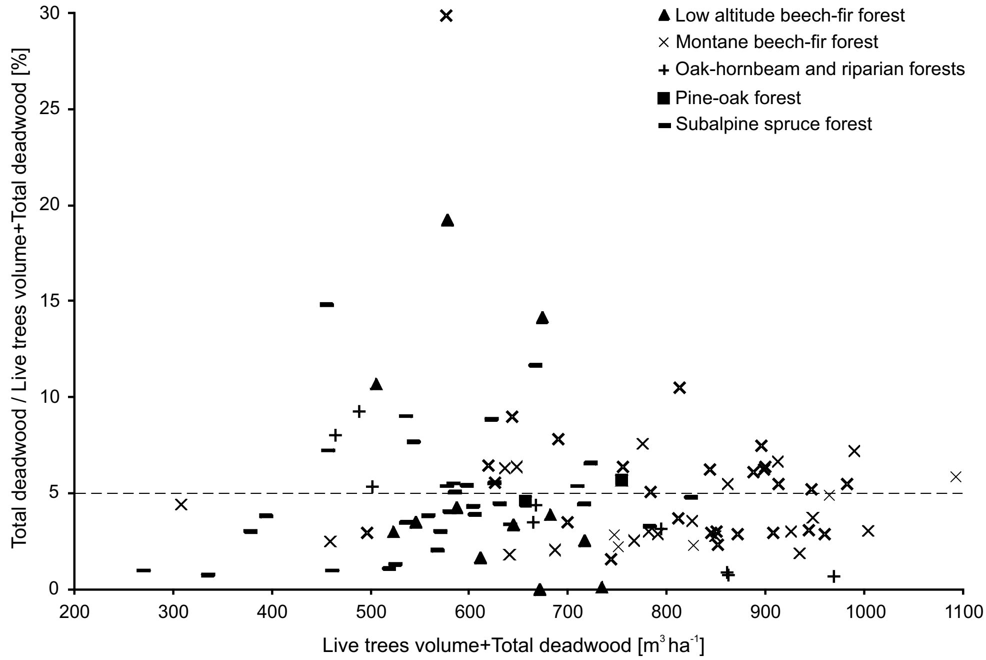


Fig. 3 Relationship between deadwood volume and combined volume of deadwood and live trees for the various studies (the dashed horizontal line indicates the mean total deadwood/combined volume of deadwood and live trees ratio (%), which is 5.0%)

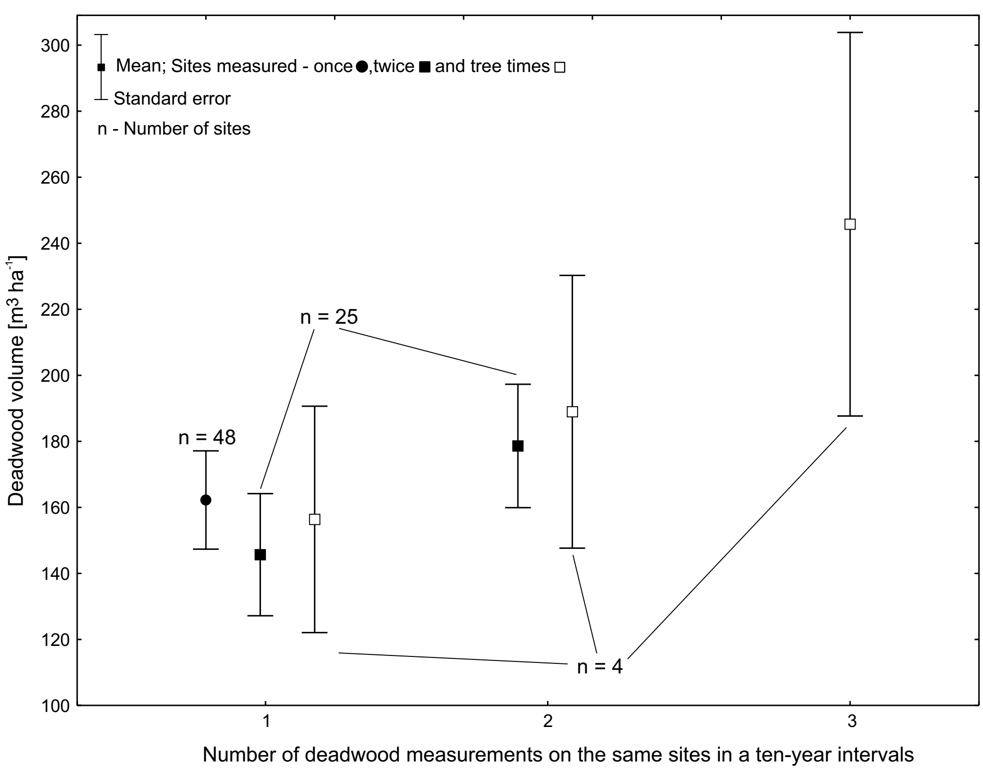


Fig. 4 Relationship between the number of measurements on the same sites and deadwood volume

65.3 m^3/ha (SD = 49.2 m^3/ha). In different studies, standing deadwood accounted for 0.4–100.0% of total deadwood volume, with the mean being 40.1% (SD = 17.9%). Significant differences in standing deadwood volume were found between different forest types (Kruskal–Wallis; $H = 30.8$; $p < 0.001$) (Fig. 8). No differences were identified between

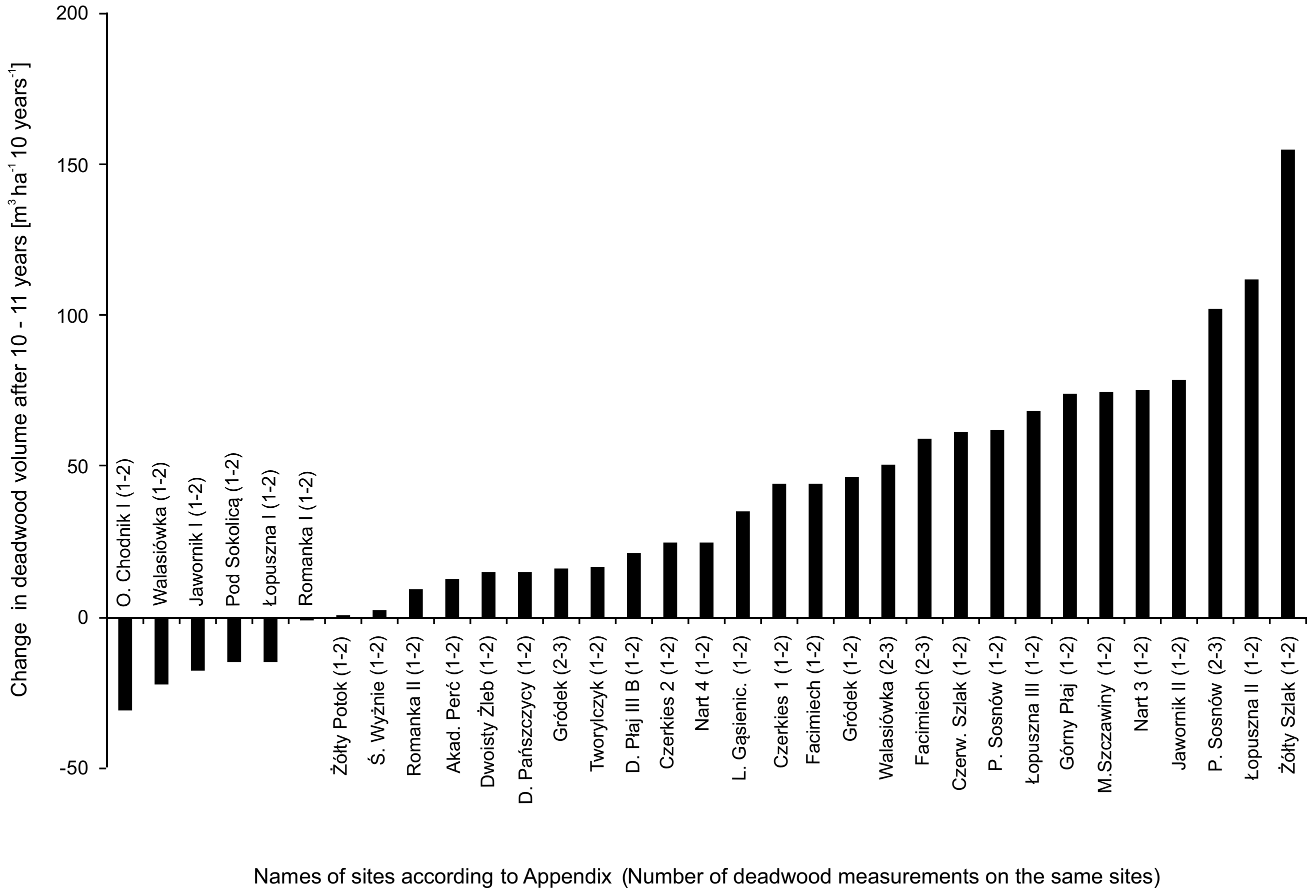


Fig. 5 Changes in deadwood volume between consecutive measurements on the same sites at 10–11 year intervals

low-altitude beech-fir forests and both high-altitude forest types. In the remaining cases, the differences were significant, with the highest average standing deadwood proportion being 50.1% in subalpine spruce forests and the lowest proportion being 16.0% in oak-hornbeam and riparian forests.

Among the studied models, the lowest RMSE (73.7) was exhibited by the one consisting of elevation a.s.l. and input of dead trees (Table 1). The linear regression model with the best fit showed that these two variables are independent predictors of the dependent variable ($p < 0.05$). An increase in the variable "elevation a.s.l." by x units, when all other predictive variables were kept constant, translated into a mean increment in the dependent variable by $1.037\ x - 0.001\ x^2$ units. The variable "input of dead trees," ranging from 2.0 to 148.4 m^3/ha/decade was also significant. In this case, an increase by 1 unit resulted in a mean increase in the dependent variable by 1.651 units, when all else being constant. However, the dependent variable was affected to the greatest degree by "elevation a.s.l," as indicated by the largest absolute values of beta coefficients. The R^2 coefficient for this model was 63.54%. Thus, the remaining 36.44% is attributable to variables that were not included in the model, as well as to random effects.

Models developed for all elevations a.s.l. (all forest types), but excluding the input of dead trees (due to a lack of data for low altitude beech-fir forest and oak-hornbeam and riparian forests) led to higher RMSE values (the lowest RMSE was 83.7, with the model consisting of the following variables: volume of living trees, duration of conservation, stage of forest development, and forest type)

Discussion

Deadwood volume and forest type

Numerous studies have addressed deadwood volume in Poland; however, they mostly focused on the southern and eastern regions of the country, where most natural forests and national parks with high forest cover are located. Relatively few papers have been devoted to *Pinus sylvestris* stands, which constitute the prevalent forest communities in Poland, but predominantly of managed character. The most substantial body of data is available for the Carpathian Mountains, and so tree stands from that area exert the greatest effect on the mean values obtained in this review. An

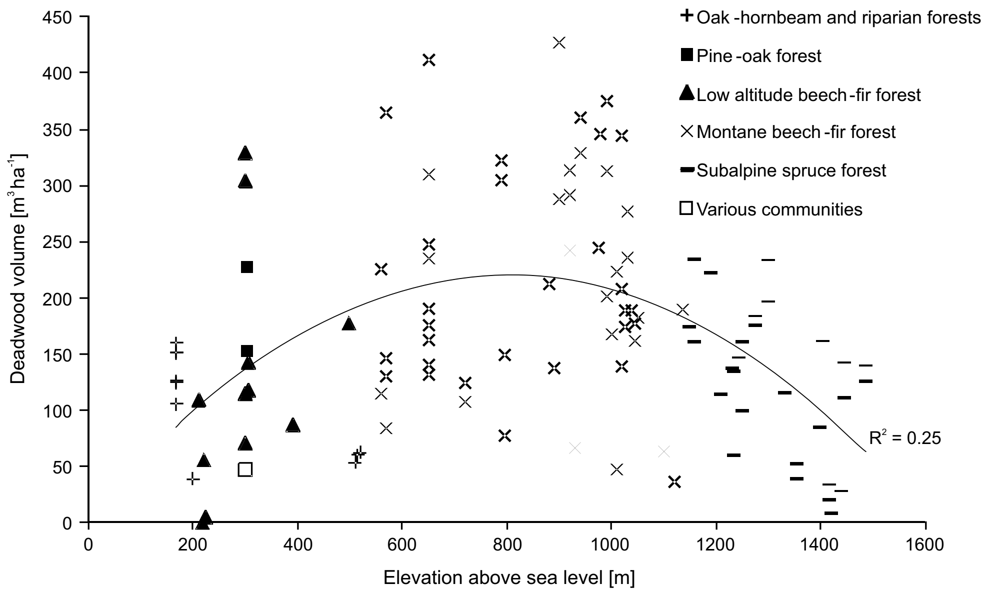
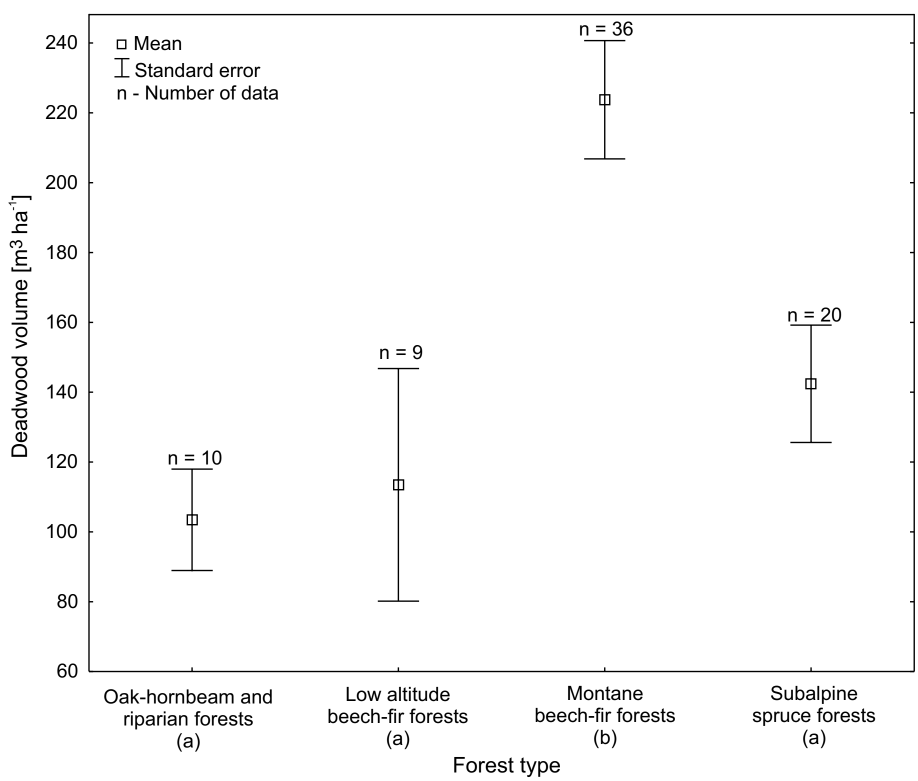


Fig. 6 Relationship between sites elevation a.s.l. and deadwood volume

Fig. 7 Deadwood volume in different forest types (values with different letters differ significantly at $p < 0.05$ as evaluated by the post hoc Scheffe test, only the latest measurements on sites were analyzed, $n = 75$)



important feature of the analyzed data is that they are derived from studies applying diverse methodologies, mostly differing in the number and size of sampling plots. The majority of studies used a single sampling plot, usually ranging from 0.25 to 1 ha, while a number of other studies used grids of several dozen to hundreds of sampling plots with a size of several hundreds m^2 each. Finally, in a few studies measurements were conducted along transects of varying lengths. The other aspect is the location of sites. In some studies, they were distributed randomly, but in most cases their location was not random. Nevertheless, researchers generally selected sites in fragments of forests of primeval character,

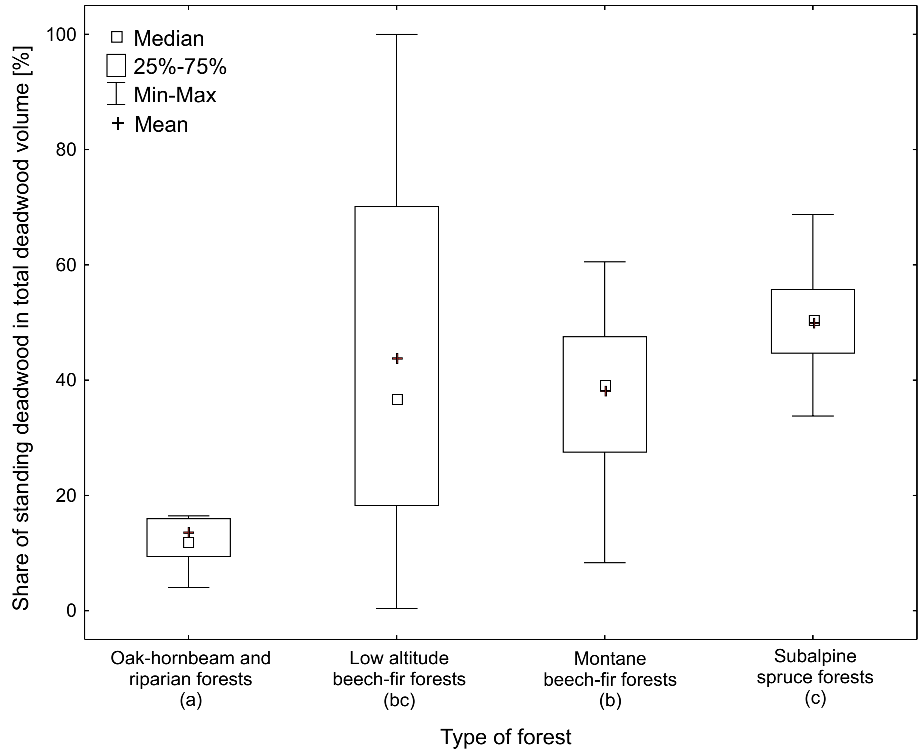


Fig. 8 Share of standing deadwood in total deadwood volume by forest type (values with different letters differ significantly at $p<0.05$ as evaluated by the nonparametric Kruskal–Wallis test and corrected with the post hoc test for number of comparisons)

Table 1 Linear regression results for two forest types: montane beech-fir forest and subalpine spruce forest

Variable	Beta coefficient	Regression parameter	95% CI		*p*
Constant	–	−529.609	−914.249	−144.969	0.009
Elevation a.s.l (m)	3.192	1.037	0.438	1.635	0.001
Elevation a.s.l^2 (m)	−3.114	−0.001	−0.001	0	0.002
Volume of living trees (m^3/ha)	−0.161	0.116	−0.119	0.351	0.319
Duration of conservation (year)	0.275	1.472	−0.003	2.946	0.05
Input of dead trees (m^3/ha/decade)	0.689	1.651	0.7	2.603	0.001
Stage of forest development					
Growing up	–	Reference			
Optimum	−0.118	−22.736	−79.178	33.706	0.415
Breakup	−0.341	−69.361	−148.956	10.234	0.085

Normal distribution of residuals and homoscedasticity of variances were satisfied ($p>0.05$ Shapiro–Wilk's and Breusch–Pagan's tests)

making sure they varied in terms of the stage of development. In most studies deadwood was not the main focus of research, but rather one of many variables measured. In the future, it would be advisable to increase the studied areas and promote a more uniform methodology.

Deadwood volume in unmanaged forests often depends on forest type, which is in turn determined by climatic and site conditions, as they influence the distribution of plant communities (Lombardi et al. 2012; Karjalainen and Kuuluvainen 2002). However, this has not been corroborated by some studies. Larrieu et al. (2014) reported that deadwood availability remained more or less stable throughout the silvigenetic cycle, both in terms of quantity and diversity, and whether the forests were dominated by broadleaves or conifers. However, numerous studies from different geographic regions of the world showed large variation in the amount of deadwood depending on forest type and stage of forest development (Burrascano et al. 2008; Lombardi et al. 2008, 2012; Karjalainen and Kuuluvainen 2002; Mataji et al. 2014). For example, in natural spruce-beech forest stands in the Krkonoše National Park, Czech Republic deadwood measurements revealed from 27.7 to 241.6 m^3/ha depending on the site and year of survey. Higher deadwood volumes were reported from silver fir-beech forests in the Dinaric

Mountains, Slovenia, where the highest and lowest concentrations of CWD for virgin forests were found in the regeneration phase (626.0 m^3/ha) and the juvenile phase (248.3 m^3/ha), respectively (Debeljak 2006). The results obtained for different Carpathian regions generally indicated high deadwood volumes, which was also corroborated by Polish data. A primeval beech forest in the Ukrainian Carpathians had a deadwood volume of 162.5 m^3/ha (Hobi et al. 2015), while in a silver fir-beech virgin forest in the Southern Carpathians of Romania that value amounted to 134.9 m^3/ha (Petritan et al. 2015).

A review of deadwood volume in reserves representing almost the entire European range of beech was published by Christensen et al. (2005). On the basis of the data from 86 sites, they reported a mean deadwood volume of 130 m^3/ha, varying from almost nothing (6 m^3/ha) to 550 m^3/ha. Among lowland and montane forests with different duration of conservation, the highest amount of deadwood (220 m^3/ha) was found in mountain nature reserves that had been protected for more than 50 years, while the corresponding value for those protected for a shorter time was only 117 m^3/ha. The difference was much smaller for lowland nature reserves (132 vs. 99 m^3/ha, respectively). The Polish results are consistent with the above data, although in this case the duration of conservation was not found to have a direct effect on deadwood volume. In the present review, montane beech-fir forests were much richer in deadwood than low altitude beech-fir stands. It should also be noted that data from Poland are closer to the aforementioned results for forests with a 50-year conservation period. The differences between montane and low altitude beech-fir forests may be attributable to greater site productivity (live tree volume + total deadwood volume) in montane stands, as well as to the fact that they often contain a minor component of spruce, which may remain standing for many years after its death, slowly decomposing and adding to deadwood at a given site (Zielonka 2006b). Also dead trees already present before a conservation regime was introduced may contribute to the differences. In mountainous areas, the volume of remaining dead trees may be greater due to difficult terrain hindering their removal (Bujoczek et al. 2015).

The Polish results from montane forests are also similar to data from spruce stands in other countries. A deadwood inventory conducted in the montane zone in central Slovakia reported a mean volume of 143.5 m^3/ha (Holeksa et al. 2007). Data from the Czech Šumava National Park from the year 2002 indicated 311 and 156 m^3/ha (Svoboda and Pouska 2008), while a survey of a Japanese old-growth subalpine coniferous forest revealed 217.9 m^3/ha (Fukasawa et al. 2014). In boreal natural forests in the Petersburg region, deadwood volume ranged from 32 to 326 m^3/ha (Shorohova and Shorohov 2001). Much lower values were recorded in the Italian Alps (23 m^3/ha) in a reserve that had been established only 14 years prior to measurement (Motta et al. 2006).

In addition to the studies included in this work, in Poland there are other sites with considerable quantities of deadwood, but they are not always strictly protected (e.g., landscape parks with a lower protection status). Survey results indicating high deadwood volumes (33–166 m^3/ha) show that deadwood has not been removed from some of those areas for decades (Karczmarski and Bąk 2010; Maślak and Orczewska 2010). Some accumulations of deadwood (27 m^3/ha) are also found in certain areas of managed forests, far exceeding the mean value for Polish forests of 5.8 m^3/ha (WISL 2014; Bujoczek and Bujoczek 2016). Also protection zones with a radius of several hundred meters established temporarily around endangered species pursuant to the Polish law exhibit above-average deadwood volumes. In such zones, forest management treatments, including deadwood removal, are prohibited (Banaś et al. 2014).

The forests included in this study differ in terms of their development stages (Korpel 1989, 1995), which are linked to the proportion and size of trees dying in a given period. That in turn translates into the input of dead trees, a variable exerting a significant effect on the volume of deadwood identified on the studied sites. However, the input of dead trees was reported only for two forest types with the observation period typically amounting to approximately 10 years. Thus, regression models may be improved if information about tree mortality over a longer period of time is included. It would also be useful to take into account the species composition of the dying trees as this factor seems likely to affect the decay rates on the studied sites in view of the increasing body of knowledge on this subject (Kahl et al. 2017), but currently such data are not available.

Duration of conservation and the share of standing deadwood

The average deadwood volume for all the sites was 172.0 m^3/ha, ranging from 0 to 427 m^3/ha (with the highest results observed for a forest in the breakup stage of development). While the higher spectrum of results is uncontroversial, the lowest values are surprising as according to the cited authors deadwood had not been removed from the studied sites for at least 21 years (Karczmarski and Kunz 2010). The absence of deadwood could be partially explained by the small size of sample plots, whose distribution was often not random, or by the fact that some tree stands could have been in the optimum stage of development, in which few trees die (Korpel 1989, 1995). A similarly broad range of deadwood volume, including very low values for some sites, was reported in the review paper by Christensen et al. (2005). In that work, Christensen et al. found a significant correlation with the age of the reserve. Other reports also indicated that the duration of conservation significantly affects deadwood accumulation (Vandekerkhove et al. 2009; Bouget et al. 2014; Paillet et al. 2015). Although such a relationship was also expected to emerge in the present work, it was not confirmed directly, which is attributable to several factors. First, it is often very difficult to accurately determine the duration of strict protection. On some sites, it may not have been continuous, being interrupted by periods of sanitary thinning following insect outbreaks or windthrows (such data are often absent from publications). On other sites, forest management treatments may have been discontinued long before the initiation of strict protection (Some sites did not reveal signs of human intervention.) Furthermore, there are areas which were incorporated into national parks years after the latter had been established, while other conservation areas merged, which makes it impossible to precisely determine for how long they had been set aside. Second, the expected correlation between deadwood volume and conservation duration may have been disturbed by biotic and abiotic factors dramatically increasing the amount of deadwood soon after the introduction of strict protection.

However, a relationship between deadwood volume and the duration of conservation was identified on sites subjected to repeated measurements. An increase was found for more than ¾ of the sites, with a maximum of 155 m^3/ha/decade. The observed significant increments in deadwood volume were usually associated with a decline in stand volume. A decrease in the amount of deadwood is typically attributable to decay outpacing mortality. It should be noted that the decay rate is largely species-specific; for instance, beech decompose faster than spruce (Holeksa et al. 2008; Rock et al. 2008; Müller-Using and Bartsch 2009; Herrmann et al. 2015). Other contributing factors include local climatic conditions and the presence of organisms decomposing organic matter (Zhou et al. 2007). Furthermore, the wood decay rate may vary between the four analyzed forest types due to their different thermal and moisture conditions. In the present review, the maximum decrease in deadwood volume was 31 m^3/ha/decade. Similar decay-related changes in deadwood volume were described for the Krkonoše National Park by Vacek et al. (2015), who conducted measurements on a permanent research plot over a 40-year period at 5-year intervals. If any decreases in the amount of CWD were observed, they were relatively small for both dominant species, that is, spruce and beech. On the other hand, the dynamics of standing deadwood volume revealed a short-termed rise followed by a drop back to previous levels.

Deadwood volume and diversity are often used as biodiversity indicators (Gao et al. 2015). From the point of view of organisms living in and feeding on deadwood, of great importance is the position of dead trees. Thus, one of the main parameters of deadwood is the relative proportion of its standing and downed forms, which is largely determined by the species composition of tree stands and the causes of tree mortality. High percentages of snags are reported from areas affected by insect outbreaks or fires (Pedlar et al. 2002; Bujoczek et al. 2015; Franklin et al. 2015). Insect outbreaks, which often cause a die-off of spruces, increase the quantity of snags, leading to a higher proportion of standing deadwood in subalpine spruce forests as compared to other types of tree stands (Bobiec 2002; Bujoczek et al. 2015). Indeed, dead spruces may remain standing for dozens of years. Holeksa et al. (2006, 2008) reported that 40% of such snags may still be found in the third decade after dying. In the present study, the largest mean volume of standing deadwood was found for tree stands with a higher presence of spruce. On the other hand, spruce may also contribute to rapid changes in the standing to downed deadwood ratio due to the high susceptibility of this species to strong winds. For instance, a study from the lowland tree stands of the Białowieża Forest indicated that approximately 50% of spruces were dead at the time of falling, in contrast to almost all deciduous trees (Faliński 1978).

Conclusions

The results of studies included in the present review indicate very high variation in the volume of deadwood in strictly protected forests and forests of primeval character in Poland. This is mostly attributable to differences in the dynamics of tree mortality between sites in the years preceding deadwood measurements. It should also be noted that 63.54% of the variation of the dependent variable was explained by the factors included in the model, with the remaining variation being linked to other factors, random effects, or methodological discrepancies between studies. Due to this, future research should include more variables concerning the studied sites. In addition, it would be beneficial to standardize deadwood measurement methods.

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Appendix

See Table 2.

Table 2 Basic details concerning the strictly protected, natural, and primeval forests in Poland included in the study

Studied national park, region etc. and number on Fig. 1	Name of site; (1) (2) (3) - first, second and third measurement on the same site	Number and size of sampling plots or transect length	Sampling method	Commencement of protection of the site	Elevation a.s.l.	Type of forest or community	Stage of forest development	Live trees volume [m^3/ha]	Minimum diameter (cm)	Year of measurement	Standing deadwood [m^3/ha]	Downed deadwood [m3/ha]	Total deadwood [m3/ha]	Standing deadwood / Total deadwood ratio [%]	Total deadwood / Live trees volume ratio [%]	Total deadwood + Live trees volume [m^3/ha]	Input of dead trees m^3/ha/time	References
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Beskid Sądecki (6)	Obrożyska I	1x0.25 ha	CS	1919	510	OH RF	GUS/OS	768	8	2000	18	33	50	35.0%	6.5%	818		Jaworski et al. 2005
Beskid Sądecki (6)	Obrożyska II	1x0.5 ha	CS	1919	520	OH RF	OS	861	8	2000	9	50	59	15.4%	6.9%	920		Jaworski et al. 2005
Beskid Sądecki (6)	Obrożyska III	1x0.5 ha	CS	1919	515	OH RF	GUS	761	8	2000	9	48	57	15.9%	7.5%	819		Jaworski et al. 2005
Białowieski NP (12)	370B	1000 m	LIS	1921[1]	134-202	OH RF	Various stages	336	4	1998-2000	25	127	152	16.4%	45.2%	488		Bobiec 2002
Białowieski NP (12)	370C	900 m	LIS	1921[1]	134-202	OH RF	Various stages	539	4	1998-2000	5	120	125	4.0%	23.2%	664		Bobiec 2002
Białowieski NP (12)	371C	2000 m	LIS	1921[1]	134-202	OH RF	Various stages	395	4	1998-2000	5	101	106	4.7%	26.8%	501		Bobiec 2002
Białowieski NP (12)	317D	2000 m	LIS	1921[1]	134-202	OH RF	Various stages	516	4	1998-2000	18	133	151	11.9%	29.3%	667		Bobiec 2002
Białowieski NP (12)	Pow. I (1)	1x1 ha	CS	1921[1]	170[1]	OH RF	Various stages			1964		60						Faliński 1978
Białowieski NP (12)	Pow. I (2)	1x1 ha	CS	1921[1]	170[1]	OH RF	Various stages			1974		71						Faliński 1978
Białowieski NP (12)	Rp1	1000 m	LIS	1921[1]	134-202	OH RF	Various stages	338	4	1998-2000	14	112	126	11.1%	37.3%	464		Bobiec 2002
Białowieski NP (12)	Rp2	1000 m	LIS	1921[1]	134-202	OH RF	Various stages	634	4	1998-2000	15	145	160	9.4%	25.2%	794		Bobiec 2002
Łódź (11)	P. Konstan.	5x0.25 ha	LIS	1930	200	OH RF			5	2010	14	25	39	35.9%				Pawicka and Woziwoda 2011
Roztoczański NP (8)	Nart 3 (1)	1x0.5 ha	CS	1957	265-345	POF		492	7	1994			149		30.3%	641		Maciejewski 2006; Maciejewski and Szafraniec 2014
Roztoczański NP (8)	Nart 3 (2)	1x0.5 ha	CS	1957	265-345	POF		514	7	2004	107	115	221	48.2%	43.1%	735		Maciejewski 2006; Maciejewski and Szafraniec 2014
Kaszuby (13)	I	1x0.25 ha	CS	1985	208–213	LA BFF	BUS	576	8	2006	39	65	104	37.9%	18.0%	680		Karczmarski and Kunz 2010
Kaszuby (13)	II	1x0.25 ha	CS	1985	217–221	LA BFF	OS	637	8	2006	0	0	0		0.0%	637		Karczmarski and Kunz 2010
Kaszuby (13)	III	1x0.25 ha	CS	1985	223–225	LA BFF	OS/BUS	692	8	2006	5	0	5	100.0%	0.7%	697		Karczmarski and Kunz 2010
Kaszuby (13)	IV	1x0.25 ha	CS	1985	218–221	LA BFF	GUS	527	8	2006	0	53	53	0.4%	10.1%	580		Karczmarski and Kunz 2010
Ojcowski NP (9)	I	53x0.04 ha	SP	1956[1]	300-480	LA BFF	OS	447	7	2011	20	65	85	23.5%	19.0%	532	63,5/ 5 years	Bąk 2012
Roztoczański NP (8)	Czerkies 1 (1)	1x0.5 ha	CS	1957	255-345	LA BFF		441	7	1994			69		15.7%	510		Maciejewski 2006; Maciejewski and Szafraniec 2014
Roztoczański NP (8)	Czerkies 1 (2)	1x0.5 ha	CS	1957	255-345	LA BFF		517	7	2004	69	43	112	61.6%	21.8%	629		Maciejewski 2006; Maciejewski and Szafraniec 2014
Roztoczański NP (8)	Czerkies 2 (1)	1x0.5 ha	CS	1957	255-345	LA BFF		267	7	1994			297		111.3%	564		Maciejewski 2006; Maciejewski and Szafraniec 2014
Roztoczański NP (8)	Czerkies 2 (2)	1x0.5 ha	CS	1957	255-345	LA BFF		336	7	2004	43	285	327	13.0%	97.2%	664		Maciejewski 2006; Maciejewski and Szafraniec 2014

Table 2 (continued)

Roztoczański NP (8)	Nart 4 (1)	1x0.5 ha	CS	1957	265-345	LA BFF		458	7	1994			115		25.2%	573		Maciejewski 2006; Maciejewski and Szafraniec 2014
Roztoczański NP (8)	Nart 4 (2)	1x0.5 ha	CS	1957	265-345	LA BFF		526	7	2004	50	89	139	35.8%	26.3%	665		Maciejewski 2006; Maciejewski and Szafraniec 2014
Świętokrzyski NP (10)	Św. Krzyż PZ	41x0.05 ha	SP	1924	400-595	LA BFF	GUS	320	7	1989	136	37	173	78.6%	54.1%	493		Poznański 1998
Babiogórski NP (2)	Czatoża	30x0.05 ha	SP	1954[1]	880-1070	M BFF		460	10	1995-2003	64	157	222	29.1%	48.2%	681		Pasierbek 2007; Pasierbek et al. 2007
Babiogórski NP (2)	D. Płaj III B (1)	1x0.5 ha	CS	1933	920	M BFF	GUS	552	6	1986	126	166	292	43.1%	53.0%	844		Jaworski and Kaczmarski 1990; Jaworski and Paluch 2001
Babiogórski NP (2)	D. Płaj III B (2)	1x0.5 ha	CS	1933	920	M BFF	GUS	576	6	1996	115	198	313	36.8%	54.3%	888	47,1/ 10 years	Jaworski and Paluch 2001; Jaworski and Paluch 2002
Babiogórski NP (2)	O. Chodnik I (1)	1x0.5 ha	CS	1933	940	M BFF	OS	536	6	1986	154	206	360	42.8%	67.1%	896		Jaworski and Kaczmarski 1990; Jaworski and Paluch 2001
Babiogórski NP (2)	O. Chodnik I (2)	1x0.5 ha	CS	1933	940	M BFF	OS	571	6	1996	115	214	329	34.9%	57.5%	900	29,3/ 10 years	Jaworski and Paluch 2001; Jaworski and Paluch 2002
Babiogórski NP (2)	Pod Sokolicą (1)	1x0.5 ha	CS	1933	1045	M BFF	GUS	442	6	1986	84	93	177	47.7%	40.1%	619		Jaworski and Kaczmarski 1990; Jaworski and Paluch 2001
Babiogórski NP (2)	Pod Sokolicą (2)	1x0.5 ha	CS	1933	1045	M BFF	GUS	464	6	1996	68	94	162	42.1%	34.8%	626	13,3/ 10 years	Jaworski and Paluch 2001; Jaworski and Paluch 2002
Babiogórski NP (2)	Żarnówka P	30x0.05 ha	SP	1954[1]	920-1120	M BFF		576	10	1995-2003	109	201	311	35.2%	53.9%	886		Pasierbek 2007; Pasierbek et al. 2007
Babiogórski NP (2)	Żarnówka S	1x1 ha	CS	1934	964-994	M BFF			7	1992	196	141	337	58.2%				Szewczyk and Szwagrzyk 1996
Beskid Sądecki (6)	Łabowiec I	1x0.75 ha	CS	1924	840-960	M BFF	BUS	666	6	1990	205	222	427	48.0%	64.2%	109 3		Jaworski et al. 1994
Beskid Sądecki (6)	Łabowiec II	1x0.70 ha	CS	1924	840-960	M BFF	GUS	489	6	1990	98	189	288	34.1%	58.8%	776		Jaworski et al. 1994
Beskid Żywiecki (1)	Oszast I	1x0.33 ha	CS	1971	1030	M BFF	OS	555	8	1999	94	169	263	35.7%	47.3%	818		Jaworski et al. 2001b
Beskid Żywiecki (1)	Oszast II	1x0.33 ha	CS	1971	990	M BFF	GUS	416	8	1999	79	277	355	22.1%	85.4%	772		Jaworski et al. 2001b
Beskid Żywiecki (1)	Oszast III	1x0.33 ha	CS	1971	1000	M BFF	OS	643	8	1999	75	84	159	47.2%	24.7%	802		Jaworski et al. 2001b
Beskid Żywiecki (1)	Śrubita I	1x0.33 ha	CS	1957	920	M BFF	GUS	425	8	2000	102	128	230	44.3%	54.1%	654		Jaworski et al. 2001a
Beskid Żywiecki (1)	Śrubita II	1x0.33 ha	CS	1957	890	M BFF	GUS	533	8	2000	54	77	131	41.3%	24.5%	664		Jaworski et al. 2001a
Beskid Żywiecki (1)	Śrubita III	1x0.25 ha	CS	1957	880	M BFF	OS	694	8	2000	78	124	202	38.7%	29.1%	895		Jaworski et al. 2001a
Bieszczady (7)	Jawornik I (1)	1x0.33 ha	CS	1973[1]	780-800	M BFF		547	8	1988	101	205	307	33.0%	56.0%	854		Jaworski et al. 1991; Jaworski et al. 2002
Bieszczady (7)	Jawornik I (2)	1x0.33 ha	CS	1973[1]	780-800	M BFF	GUS	578	8	1998	63	226	289	21.7%	50.0%	867	58,3/ 10 years	Jaworski et al. 2002; Jaworski and Kołodziej 2002
Bieszczady (7)	Jawornik II (1)	1x0.5 ha	CS	1973[1]	780-810	M BFF		632	8	1988	17	57	74	22.5%	11.7%	706		Jaworski et al. 1991; Jaworski et al. 2002
Bieszczady (7)	Jawornik II (2)	1x0.5 ha	CS	1973[1]	780-810	M BFF	OS	600	8	1998	12	130	142	8.3%	23.7%	742	71,3/ 10 years	Jaworski et al. 2002; Jaworski and Kołodziej 2002
Bieszczady (7)	Tworylczyk (1)	1x0.5 ha	CS	1973[1]	720	M BFF		611	8	1988	47	55	101	46.0%	16.6%	713		Jaworski et al. 1991; Jaworski et al. 2002
Bieszczady (7)	Tworylczyk (2)	1x0.5 ha	CS	1973[1]	720	M BFF	GUS	610	8	1998	29	89	117	24.3%	19.2%	727	76,0/ 10 years	Jaworski et al. 2002; Jaworski and Kołodziej 2002
Bieszczadzki NP (7)	Moczarne I	1x0.25 ha	CS	1991	1010	M BFF	OS	391	8	1993	18	27	45	39.9%	11.5%	436		Jaworski et al. 1995
Bieszczadzki NP (7)	Moczarne II	1x0.33 ha	CS	1991	930	M BFF	OS	545	8	1993	12	51	63	19.0%	11.6%	608		Jaworski et al. 1995
Bieszczadzki NP (7)	Rabia Skała I	1x0.25 ha	CS	1989	1120	M BFF	BUS	257	8	1993	5	30	35	14.0%	13.5%	292		Jaworski et al. 1995
Bieszczadzki NP (7)	Rozsypaniec	39x0.04 ha	SP	1973[1]	1000-1200	M BFF	OS	422	7	2012	21	41	62	33.9%	14.8%	485	60,0/ 18 years	Kuźnik 2013 Bujoczek et al. 2017

Table 2 (continued)

Gorczański NP (4)	D. Łopusznej TB	62x0.05 ha	SP	1970	900-1200	M BFF	BUS	442	7	2007	66	112	178	37.2%	40.2%	620	105, 5/ 15 years	Bujoczek 2010
Gorczański NP (4)	D. Łopusznej TS	11x0.05 ha	SP	1970	980-1080	M BFF	BUS	397	7	2007	111	119	229	48.3%	57.8%	626	190,1/ 15 years	Bujoczek 2010
Gorczański NP (4)	Łopuszna	1x1 ha	CS	1950	964-1112	M BFF	OS	562	10	2005	80	90	170	47.2%	30.3%	733		Cieślik 2006; Pawlaczek 2010
Gorczański NP (4)	Łopuszna I (1)	1x0.6 ha	CS	1970	1025	M BFF	GUS	605	8	1991	44	135	179	24.6%	29.6%	784		Jaworski et al. 2006
Gorczański NP (4)	Łopuszna I (2)	1x0.6 ha	CS	1970	1025	M BFF	GUS	642	8	2001	35	130	165	21.2%	25.8%	807	48.4/ 10 years	Jaworski et al. 2006; Jaworski et al. 2007
Gorczański NP (4)	Łopuszna II (1)	1x0.5 ha	CS	1970	990	M BFF	OS	688	8	1991	98	93	191	51.3%	27.8%	879		Jaworski et al. 2006
Gorczański NP (4)	Łopuszna II (2)	1x0.5 ha	CS	1970	990	M BFF	BUS	602	8	2001	155	142	297	52.2%	49.4%	899	140,9/ 10 years	Jaworski et al. 2006; Jaworski et al. 2007
Gorczański NP (4)	Łopuszna III (1)	1x0.5 ha	CS	1970	1020	M BFF	OS	755	8	1991	71	61	132	53.8%	17.5%	887		Jaworski et al. 2006
Gorczański NP (4)	Łopuszna III (2)	1x0.5 ha	CS	1970	1020	M BFF	BUS	714	8	2001	99	98	196	50.2%	27.5%	910	104,9/ 10 years	Jaworski et al. 2006; Jaworski et al. 2007
Gorczański NP (4)	Turbacz	25x0.05 ha	SP	1927	900-1120	M BFF	GUS	546	7	2007	57	161	218	26.0%	39.9%	764	88,6/ 21 years	Bujoczek 2010
Pieniński NP (5)	Facimiech (1)	1x0.25 ha	CS	1932[1]	650	M BFF	OS	660	8	1987	56	69	125	44.6%	19.0%	785		Jaworski and Karczmarski 1991; Jaworski and Podlaski 2007b
Pieniński NP (5)	Facimiech (2)	1x0.25 ha	CS	1932[1]	650	M BFF	OS	661	8	1997	101	66	167	60.5%	25.2%	827	93,8/ 10 years	Jaworski and Podlaski 2007a; Jaworski and Podlaski 2007b
Pieniński NP (5)	Facimiech (3)	1x0.25 ha	CS	1932[1]	650	M BFF	OS	730	8	2007	80	143	223	35.9%	30.5%	953	70,8/ 10 years	Jaworski and Jakubowska 2011; Jaworski and Jakubowska 2012
Pieniński NP (5)	Gródek (1)	1x0.25 ha	CS	1932[1]	570	M BFF	GUS	572	8	1987	64	16	81	79.5%	14.1%	652		Jaworski and Karczmarski 1991; Jaworski and Podlaski 2007b
Pieniński NP (5)	Gródek (2)	1x0.25 ha	CS	1932[1]	570	M BFF	GUS	585	8	1997	40	84	124	32.6%	21.2%	709	38,8/ 10 years	Jaworski and Podlaski 2007a; Jaworski and Podlaski 2007b
Pieniński NP (5)	Gródek (3)	1x0.25 ha	CS	1932[1]	570	M BFF	GUS	612	8	2007	25	114	139	18.0%	22.7%	751	30,7/ 10 years	Jaworski and Jakubowska 2011; Jaworski and Jakubowska 2012
Pieniński NP (5)	P. Sosnów (1)	1x0.33 ha	CS	1932[1]	650	M BFF	OS	665	8	1987	111	124	235	47.3%	35.4%	901		Jaworski and Karczmarski 1991; Jaworski and Podlaski 2007b
Pieniński NP (5)	P. Sosnów (2)	1x0.33 ha	CS	1932[1]	650	M BFF	GUS	622	8	1997	161	133	294	54.8%	47.2%	915	134,9/ 10 years	Jaworski and Podlaski 2007a; Jaworski and Podlaski 2007b
Pieniński NP (5)	P. Sosnów (3)	1x0.33 ha	CS	1932[1]	650	M BFF	GUS	549	8	2007	72	319	390	18.4%	71.1%	939	126,2/ 10 years	Jaworski and Jakubowska 2011; Jaworski and Jakubowska 2012
Pieniński NP (5)	Walasiówka (1)	1x0.4 ha	CS	1932[1]	650	M BFF	GUS	652	8	1987	79	75	153	51.4%	23.5%	805		Jaworski and Karczmarski 1991; Jaworski and Podlaski 2007b
Pieniński NP (5)	Walasiówka (2)	1x0.4 ha	CS	1932[1]	650	M BFF	GUS	676	8	1997	61	72	133	45.7%	19.6%	809	53,9/ 10 years	Jaworski and Podlaski 2007a; Jaworski and Podlaski 2007b
Pieniński NP (5)	Walasiówka (3)	1x0.4 ha	CS	1932[1]	650	M BFF	GUS	681	8	2007	63	118	181	34.8%	26.6%	862	77,7/ 10 years	Jaworski and Jakubowska 2011; Jaworski and Jakubowska 2012
Świętokrzyski NP (10)	Św. Krzyż PD	50x0.25 ha	SP	1922	560[1]	M BFF			7	2000-05			112					Podlaski 2014
Świętokrzyski NP (10)	Św. Krzyż I	1x0.5 ha	CP	1922	560	M BFF	GUS	502	8	1992	109	105	214	50.9%	42.6%	716		Jaworski et al. 1999
Świętokrzyski NP (10)	Św. Krzyż II	1x0.5 ha	CS	1922	570	M BFF	BUS/GUS	201	8	1992	163	183	346	47.1%	172.3%	547		Jaworski et al. 1999
Tatrzański NP (3)	Suchy Żleb	1x1 ha	CS	1955[1]	1115-1155	M BFF		447	7	2003-04	26	159	185	14.1%	41.4%	632		Burczak 2005; Szwagrzyk et al. 2006
Babiogórski NP (1)	Akad. Perć (1)	1x0.5 ha	CS	1928	1350-1360	SSF	OS	322	8	1984	24	13	37	64.9%	11.5%	359		Jaworski and Karczmarski 1995
Babiogórski NP (2)	Akad. Perć (2)	1x0.5 ha	CS	1928	1350-1360	SSF	OS	325	8	1994	32	17	50	64.9%	15.3%	375	20,8/ 10 years	Jaworski and Karczmarski 1995
Babiogórski NP (2)	Babia Góra	14.4 ha	CS	1928	1188-1300	SSF	Various stages	407	10		59	73	131	44.6%	32.2%	538		Holeksa 1998
Babiogórski NP (2)	Czerw. Szlak (1)	1x0.5 ha	CS	1928	1240-1265	SSF	GUS/OS	436	8	1984	47	47	94	50.4%	21.6%	530		Jaworski and Karczmarski 1995

Table 2 (continued)

Babiogórski NP (2)	Czerw. Szlak (2)	1x0.5 ha	CS	1928	1240-1265	SSF	BUS	364	8	1994	73	79	151	47.9%	41.6%	516	87,7/ 10 years	Jaworski and Karczmarski 1995
Babiogórski NP (2)	Górny Płaj (1)	1x0.5 ha	CS	1928	1150-1170	SSF	GUS	591	8	1984	79	73	152	51.9%	25.7%	743		Jaworski and Karczmarski 1995
Babiogórski NP (2)	Górny Płaj (2)	1x0.5 ha	CS	1928	1150-1170	SSF	GUS	561	8	1994	114	108	223	51.4%	39.7%	783	70,5/ 10 years	Jaworski and Karczmarski 1995
Babiogórski NP (2)	M.Szczawiny (1)	1x0.5 ha	CS	1928	1227-1242	SSF	OS	483	8	1984	26	30	56	46.0%	11.6%	539		Jaworski and Karczmarski 1995
Babiogórski NP (2)	M.Szczawiny (2)	1x0.5 ha	CS	1928	1227-1242	SSF	BUS	429	8	1994	57	70	127	44.8%	29.6%	556	73,7/ 10 years	Jaworski and Karczmarski 1995
Babiogórski NP (2)	Żółty Szlak (1)	1x0.5 ha	CS	1954	1225-1240	SSF	GUS	418	8	1984	15	115	129	11.3%	30.9%	547		Jaworski and Karczmarski 1995
Babiogórski NP (2)	Żółty Szlak (2)	1x0.5 ha	CS	1954	1225-1240	SSF	GUS	356	8	1994	118	159	277	42.5%	77.9%	633	99,4/ 10 years	Jaworski and Karczmarski 1995
Babiogórski NP (2)	Pow. 1-5	Total area of 4.3 ha	CS	1928	1250-1350	SSF		463	10		73	104	177	41.1%	38.2%	640		Zielonka 2006a
Tatrzański NP (3)	Pow. 6-9		CS	1955	1250-1350	SSF		442	10		117	93	210	55.7%	47.5%	652		Zielonka 2006a
Tatrzański NP (3)	D.Pańszczycy (1)	1x0.5 ha	CS	1955[1]	1480–1497	SSF	OS	454	8	1991	67	52	119	56.5%	26.1%	573		Karczmarski 2007
Tatrzański NP (3)	D.Pańszczycy (2)	1x0.5 ha	CS	1955[1]	1480–1497	SSF	OS	467	8	2002	67	65	132	50.6%	28.3%	599	36,8/ 11 years	Karczmarski 2007
Tatrzański NP (3)	Dwoisty Żleb (1)	1x0.5 ha	CS	1955[1]	1410–1427	SSF	OS	419	8	1990	9	10	19	47.6%	4.5%	439		Karczmarski and Zygarowicz 2007
Tatrzański NP (3)	Dwoisty Żleb (2)	1x0.5 ha	CS	1955[1]	1410–1427	SSF	OS	466	8	2001	17	15	32	53.7%	6.9%	498	12,3/ 11 years	Karczmarski and Zygarowicz 2007
Tatrzański NP (3)	Jarząbcza	1x0.5 ha	CS	1955[1]	1430-1450	SSF	OS	479	7	2006	17	10	27	63.0%	5.6%	506		Karczmarski and Bryniarska 2012
Tatrzański NP (3)	L. Gąsienic. (1)	1x0.5 ha	CS	1955[1]	1440–1453	SSF	BUS	446	8	1991	37	68	104	35.3%	23.4%	551		Karczmarski 2007
Tatrzański NP (3)	L. Gąsienic. (2)	1x0.5 ha	CS	1955[1]	1440–1453	SSF	BUS	419	8	2002	69	66	135	51.0%	32.2%	554	72,7/ 11 years	Karczmarski 2007
Tatrzański NP (3)	Pyszna	1x0.25 ha	CS	1955[1]	1390-1420	SSF	BUS	453	7	2006	116	41	157	73.9%	34.7%	610		Karczmarski and Bryniarska 2012
Tatrzański NP (3)	Ś. Wyżnie (1)	1x0.5 ha	CS	1955[1]	1412–1430	SSF	GUS	250	8	1990	2	4	7	33.8%	2.7%	257		Karczmarski and Zygarowicz 2007
Tatrzański NP (3)	Ś. Wyżnie (2)	1x0.5 ha	CS	1955[1]	1412–1430	SSF	GUS	310	8	2001	4	4	8	51.7%	2.6%	319	2,1/ 11 years	Karczmarski and Zygarowicz 2007
Tatrzański NP (3)	Tatry I	1x0.25 ha	CS	1955[1]		SSF		750	10	1998		59						Zielonka and Niklasson 2001
Tatrzański NP (3)	Żółty Potok (1)	1x0.5 ha	CS	1955[1]	1388–1413	SSF	GUS	429	8	1991	38	42	80	47.3%	18.6%	509		Karczmarski 2007
Tatrzański NP (3)	Żółty Potok (2)	1x0.5 ha	CS	1955[1]	1388–1413	SSF	GUS	462	8	2002	34	46	80	42.1%	17.4%	542	32,1/ 11 years	Karczmarski 2007
Beskid Żywiecki (1)	Romanka I (1)	1x0.5 ha	CS	1963[1]	1320–1345	SSF	OS	465	8	1993	61	49	110	55.8%	23.7%	575		Karczmarski and Kowalczuk 2007
Beskid Żywiecki (1)	Romanka I (2)	1x0.5 ha	CS	1963[1]	1320–1345	SSF	OS	500	8	2004	51	58	109	47.0%	21.9%	609	31,2/ 11 years	Karczmarski and Kowalczuk 2007
Beskid Żywiecki (1)	Romanka II (1)	1x0.5 ha	CS	1963[1]	1270–1280	SSF	BUS	343	8	1993	83	83	166	50.0%	48.5%	509		Karczmarski and Kowalczuk 2007
Beskid Żywiecki (1)	Romanka II (2)	1x0.5 ha	CS	1963[1]	1270–1280	SSF	BUS	258	8	2004	77	97	174	44.3%	67.3%	432	111,9/ 11 years	Karczmarski and Kowalczuk 2007
Gorczański NP (4)	D. Łopusznej O	18x0.05 ha	SP	1979	1160-1260	SSF	OS	335	7	2007	76	35	111	68.7%	33.1%	446	72,3/ 15 years	Bujoczek 2010
Gorczański NP (4)	D. Łopusznej TS	10x0.05 ha	SP	1970	1120-1260	SSF	BUS	391	7	2007	135	81	216	62.4%	55.2%	607	136,4/ 15 years	Bujoczek 2010
Gorczański NP (4)	D. Łopusznej TG	20x0.05 ha	SP	1970	1060-1240	SSF	OS	530	7	2007	87	82	170	51.4%	32.0%	700	81,9/ 15 years	Bujoczek 2010
Świętokrzyski NP (10)	-	250x250x 0.05 ha grid	SP	1957[1]	300[1]	Various communit ies	Various stages		7	2010-12[1]	7	39	46	15.2%				Figarski et al 2014

The table provides raw data. In actual analyses, the volumes have been standardized where the minimum diameter used to measure was >5 cm diameter, according to the formula given by Christensen et al. (2005). [1] – data taken from other sources; commencement of protection was defined as the date of establishment of the national park or nature reserve; OH RF – Oak-hornbeam and riparian forests, LA BFF - Low altitude beech-fir forests, M BFF – Montane beech-fir forest, SSF – Subalpine spruce forest, POF - Pine-oak forest. Sampling methods: CS – complete survey; LIS - line transect sampling method; SP – systematic grid plot sampling; BUS - break up stage; OS - optimum stage; GUS - growing up stage.

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