

Structure of coarse woody debris in Lange-Leitn Natural Forest Reserve, Austria

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ABSTRACT: The amount, variability and quality of coarse woody debris (CWD) in an oak-dominated natural forest reserve in Austria were studied in 2006. The average volume of CWD (snags and logs) was 107.3 m³/ha, which accounted for 39% of the total living volume. Among the CWD, on average, 23.4 m³/ha (22%) were snags and 83.9 m³/ha (78%) were logs. According to quality aspects the CWD displayed a wide range of variation in tree species, tree size, stage of decay, and structural characteristics, creating a high diversity of CWD habitats for microorganisms. Among the three forest associations, the highest amount of CWD was found in the mesic *Galio sylvatici-Carpinetum* association. The results of this study are discussed as reference values for a close-to-nature management of oak-dominated broadleaved submontane forests emphasizing conservation management.

Keywords: forest association; habitat; fungi; oak; broadleaved forest

Coarse woody debris (CWD) plays a conspicuous role for both the functioning and the biodiversity of forest ecosystems (HARMON et al. 1986). It is an indicator that captures many elements of naturalness and is becoming a general reference for natural forests in Europe. In order to determine the naturalness of forest ecosystems, CWD has become an important indicator (GRABHERR et al. 1998). The volume of standing and fallen CWD is an important Pan-European indicator for sustainable forest management in Europe (criterion 4: maintenance, conservation and appropriate enhancement of biological diversity in forest ecosystems, MCPFE 2003). For the interests of conservation management, efforts are being made to raise levels towards those found in natural forests (HARMON 2001). In natural forests CWD can be found across a wide range of spatial and temporal scales (ROUVINEN, KUULUVAINEN 2001). CWD quantities are normally much lower in managed forests than in unmanaged old-growth forests, as most of the large-sized harvestable timber is extracted (GREEN, PETERKEN 1997; KIRBY et al. 1998; ÓDOR, STANDOVÁR 2001). Tree mortality in natural forests

is caused by natural disturbances (KARJALAINEN, KUULUVAINEN 2002) which largely differ in terms of quality and quantity (ENGELMARK 1999). The amount of CWD differs from one forest type to another, one species to another and one diameter class to another (KARJALAINEN, KUULUVAINEN 2002). On the other hand, the decomposition rate depends on several factors, such as tree species, tree size, wood quality, and climate, which control the activity of decomposing organisms (HARMON et al. 1986). In this context natural reserves, which have a long history of protection, may serve as a guideline for natural levels of CWD. The natural forest reserves network of Austria serves as a reference for biotype assessment and ecological monitoring (FRANK, MÜLLER 2003).

There is currently no scientific review of natural deadwood levels for oak forests in temperate Europe. However, suitable natural forest reference sites are scarce within the oak forest zone particularly in submontane areas where no untouched forests have survived and very few sites have been strictly protected for more than few decades. Researches on CWD structural diversity under absolute natural

Table 1. Decay classes of CWD

Decay class	Characteristics
A	Tree recently died, fresh cambium, no damage
B	Slight decay of sapwood but heartwood fresh, early phase of decaying
C	Heartwood starts to rot, intermediate phase of decaying
D	Heartwood fully decayed, advanced phase of decaying
E	Heartwood fully decayed, advanced phase of decaying

conditions in different forest associations are also scarce; especially the role of dead wood in coppice forests is unknown in Central and Northern Europe, where coppice forests take up just a small percentage of the total forest area. In Austria most coppice forests are located in the eastern parts of the country with prevailing oak-dominated vegetation covering about 2% of the total forest area. The present study conducted in Lange-Leitn Natural Forest Reserve, Austria, was aimed to estimate the amount of CWD in three oak-dominated forest associations managed as coppice forests in the past, to examine CWD quality and to find out the variability of CWD under absolute natural conditions.

MATERIALS AND METHOD

The study site in the Lange-Leitn Natural Forest Reserve consists of 29 ha forested land near to Neckenmarkt in Burgenland, at the borderline to Hungary. The natural forest reserve is located in the colline and submontane vegetation zone with prevailing oak-dominated vegetation. The forests have been used for coppice production but there have been only minimum human interventions in the forests since 1935. This forest was included in the Austrian *Natural Forest Reserves Programme* in 1996 and was assigned the first natural forest reserve by the Federal Office and Research Centre for Forests in compliance with the Helsinki Resolution H2 (MCPFE 1993). The sites are characterized by brown podzolic soils with an elevation ranging from 415 to 490 m a.s.l. The average temperature is about 9°C with annual precipitation including snowfall around 850 mm. The duration of snow cover varies from 60 to 80 days with a maximum of 50 cm snow thickness, which allows a length of 250 days of the growing season per year approximately. The forests are dominated by oak (*Quercus petraea*, *Quercus cerris* and *Quercus* sp.) with an admixture of hornbeam (*Carpinus betulus*), birch (*Betula pendula*) and European beech (*Fagus sylvatica*). Three forest associations were found according to WILLNER and GRABHERR (2007): (i) Mesic *Galio sylvatici-Carpi-*

netum (GSC); this association was found on humid lower slopes of comparatively deeper (20–30 cm deep) and alkaline soils taking up the area of 20 ha. (ii) Semi-dry *Luzulo-Quercetum-typicum* (LQT); this association was found on middle slopes of 10 to 20 cm deep and slightly acidic soils taking up the area of 7 ha. (iii) Dry *Luzulo-Quercetum-Calluna* (LQC); this association was found on dry slopes of 5–10 cm deep and acidic soils taking up the area of 1.7 ha.

Data were collected on 24 circular permanent sample plots of an area 300 m² each on a regular grid with a distance of 100 m. The plots were distributed among the three forest associations as follows: 18 plots on GSC, 4 plots on LQT and 2 plots on LQC. Dead wood is defined in this study as standing deadwood or snags (≥ 5 cm dbh and ≥ 1.3 m height) and lying deadwood or logs (≥ 10 cm mid diameter). Deadwood was classified on the basis of structural characteristics (Table 2) and decay phase (Table 1). A height curve was developed for snags derived from PRODAN (1965) and the volume was calculated for logs considering a cylinder following Huber's formula.

RESULTS

Quantity of deadwood

The mean volume of CWD (snags and logs) was 107.3 m³/ha, of which 23.4 m³/ha (22%) were snags and 83.9 m³/ha (78%) were logs. On the GSC, LQT and LQC the mean volume of dead wood was 118.2 m³/ha, 83.1 m³/ha and 57.2 m³/ha, respectively. Among the associations LQT had the lowest amount of logs (62% of total volume) and GSC had the highest amount (81% of total volume) (Table 3).

Based on the total results the proportion of CWD in relation to the living tree volume was 39%. There were differences between the associations in the volume of CWD, in the proportion of CWD to the living tree volume and in the proportion of the log volume to the total CWD volume. The lowest proportion of CWD in relation to the living tree volume was found on LQC (31%) and the highest on GSC (40%).

Table 2. Structural class of CWD

Structural class	Characteristics
1	Recently died tree having leaves, twigs and branches with intact outline that is covered by bark
2	Dead tree having some leaves and branches, with smooth intact outline
3	Dead tree missing leaves and having small branches with smooth intact outline
4	Dead tree missing small branches with some lost outline
5	Standing dead tree with broken down trunk (>1.3 m height)
6	Uprooted dead tree or dead tree snapped at ground level
7	Stump (< 1.3 m height) with broken down trunk

Although the total amount of CWD in relation to the total volume of living trees is high, there were no statistically significant differences between the three forest associations due to the imbalanced number of sample plots for each association (Table 3).

According to the tree species oak accounted for 96.8 m³/ha CWD whereas hornbeam accounted for 4.6 m³/ha. There were huge variations between oak and hornbeam in the proportion of CWD in the total volume of living trees. A higher proportion was found with oak (42%) and a lower one with hornbeam (14%).

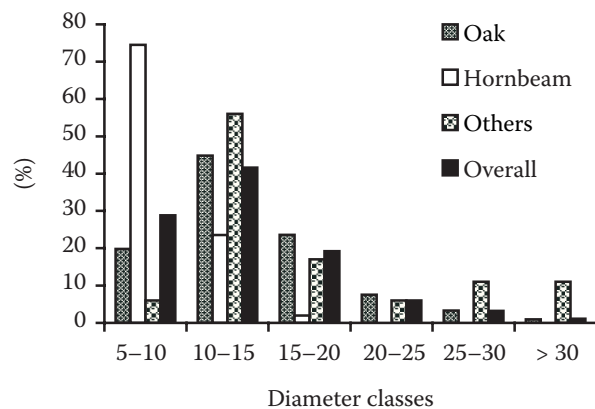


Fig. 1. Diameter distribution of CWD (by number) in different species

There were slight differences between oak and hornbeam in the proportion of logs and total deadwood volume. The proportion of logs and CWD volume was higher in oak than hornbeam (Table 3).

Quality of deadwood

The diameter distribution of logs showed a reverse J-shape pattern apparently (Fig. 1). The number of stems diminished with increasing diameter. There was a single exception with oak, which had more stems in the 10–15 cm diameter class than in the 5–10 cm diameter class. The largest diameter of hornbeam stem did not exceed 20 cm, where in oak it exceeded 30 cm diameter. Most of the hornbeam individuals (75%) were within the 5–10 cm diameter class. Considering all deadwood together the 10–15 cm diameter class comprised the highest number of individuals (42%), followed by 5–10, 15–20, 20–25, 25–30 and > 30 cm diameter class (Fig. 1). The height distribution classes also indicated a reverse J-shaped pattern having a similar single exception because a higher number of stems was found in the 5–10 m height class than in the < 5 m height class (Fig. 2).

Taking into account the total CWD volume, decay class B was most abundant (51%), followed by class C

Table 3. Distribution of CWD for different species and forest associations

Items	Name	Snag vol. (m ³ /ha)	Log vol. (m ³ /ha)	Total CWD vol. (m ³ /ha)	Total living tree vol. (m ³ /ha)	Ratio of CWD and living tree vol. (%)	Proportion of snag vol. (%)	Proportion of log vol. (%)
Species	Oak	21.6	75.2	96.8	232.9	42	22	78
	Hornbeam	1.2	3.4	4.6	32	14	26	74
	Other	0.6	5.3	5.9	11.7	50	10	90
Associations	GSC	22.8	95.4	118.2	292.9	40	19	81
	LQT	31.6	51.5	83.1	248.4	34	38	62
	LQC	12.8	44.4	57.2	185.7	31	22	78
Overall		23.4	83.9	107.3	276.5	39	22	78

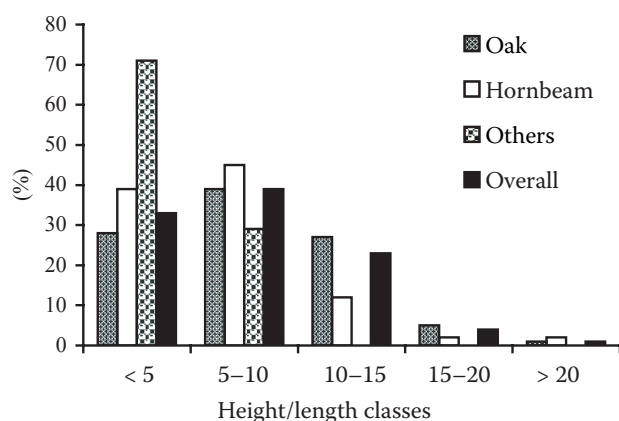


Fig. 2. Height/length distribution of CWD (by number) in different species

(43%), A (3%) and D (2%). Decay class E (fragmented heartwood and ill-defined wood) was only 1% of the total CWD volume. Comparing the tree species decay, class B was the most abundant for oak followed by decay class C whereas decay class C was the most abundant for hornbeam followed by decay class B (Table 4). In the GSC association all 5 decay classes were present whereas LQT and LQC lacked the advanced decay phases (Table 4). Structural class 4 was the most abundant in all associations followed by class 7 in GSC and LQT, and class 2 in LQC. In LQT and LQC only 3 structural classes out of 7 were present whereas in GSC, 6 classes out of 7 were found. Class 5 was absent in all associations. Structural class 4 was the most abundant followed by class 7 in all species (Table 4).

DISCUSSION

Quantity of deadwood

The mean volume of total CWD was 107.3 m³/ha in this natural forest reserve. A comparison of the results with other published data is hampered by the fact that most studies were conducted in beech-dominated natural reserves in the montane and submontane regions of Europe (CHRISTENSEN et al. 2005). SANIGA and SCHÜTZ (2001a) reported 102 m³/ha, 103 m³/ha and 108 m³/ha of CWD in Kyjov, Havesova and Rozok forest reserve of Slovakia and KORPEL (1997) found 108 m³/ha of CWD in Stuzica 4 and Stuzica 5 forest reserve. ÓDOR and STANDOVÁR (2003) reported 106 m³/ha of CWD in Kekes forest reserve of Hungary. All these forest ecosystems are beech-dominated submontane forests. However, the average amount of CWD of this natural reserve can be compared to old-growth oak-beech (*Quercus-Fagus grandifolia*) forests

in Tennessee reported in North America (HARMON et al. 1986). As the average volume of CWD in these *Quercus-Fagus grandifolia* forests ranged from 82 to 132 m³/ha, it could be assumed that the Lange-Leitn natural reserve tends to be classified as an old-growth forest though it was established as natural reserve one decade ago and the last intensive management activities took place in 1935. WILSON and MCCOMB (2005) reported 19.5 m³/ha volume of CWD in a study of 20 years dynamics of CWD in a New England oak forest whereas in the Lange-Leitn reserve 107.3 m³/ha of CWD were found. It can be assumed that a big proportion of snags and logs died during the last decade. A reason for this might be the fact that the advanced decay classes (class D and class E) contributed only 3% of the total CWD volume and the early decay stage (class B) and fresh stage (class A) contributed 54% of the total CWD volume. The mean volume of snags was 23.4 m³/ha (22% of total CWD) and that of logs was 83.9 m³/ha (78% of total CWD). A similar ratio of snags and logs was found by JAWORSKI et al. (1999), LABUDDA (1999), KÖLBEL (1999), MEYER (1999), SANIGA and SCHÜTZ (2001a) in submontane beech-dominated reserve forests of Slovakia, Poland and Germany.

The highest volume/ha of CWD was found in GSC (mesic) followed by LQT (dryish) and LQC (dry) association. In a study by UOTILA et al. (2001) in eastern Finland and Russian Karelia, the mean volume of total CWD was higher in mesic than in sub-xeric sites and in another study by KARJALAINEN and KUULUVAINEN (2002) in Eastern Fennoscandia, the mean volume was highest at the mesic site followed by dry and dryish sites. It could be assumed that the moist site produces a higher amount of CWD than the dry site. The proportion of logs and total CWD volume (81%) and the share of advanced decay phases (class D and E) were highest in the mesic association among the three forest associations. So, the decomposition rate is more rapid on the mesic site due to a possibly higher average temperature and higher humidity followed by a higher decomposition rate of CWD (STOKLAND 2001; HAHN, CHRISTENSEN 2004).

For oak the relation of CWD and living tree volume was 42%, for hornbeam about 14% were found, which might indicate that the mortality of hornbeam is higher than that of oak. The overall relation of CWD to living trees was 39%. This result was similar to the results found by SANIGA and SCHÜTZ (2001b), VRŠKA et al. (1998), and KOOP and HILGEN (1987) in beech-dominated forest reserves in Slovakia, Czech Republic and France although those reserves were established a longer time ago compared with

Table 4. Distributions of CWD classes among different species and forest associations

Items	Name	Decay classes					Structural classes								
		A	B	C	D	E	Σ	1	2	3	4	5	6	7	Σ
Species	Oak	4	64	30	2	1	100	1	5	15	59	0	2	18	100
	Hornbeam	3	34	61	2	0	100	1	5	17	44	0	6	28	100
	Others	0	23	69	8	0	100	0	0	0	62	0	15	23	100
Associations	GSC	4	46	46	3	1	100	1	5	16	50	0	5	23	100
	LQT	0	66	34	0	0	100	0	0	15	58	0	4	23	100
	LQC	4	63	33	0	0	100	0	13	0	79	0	0	8	100
Overall	All	3	51	43	2	1	100	1	5	15	53	0	4	22	100

Lange-Leitn. CHRISTENSEN et al. (2005) reported that montane reserves established a longer time ago had a higher ratio of CWD and living tree volume than submontane reserves which have been established recently. The findings of this study are partly in line with this argument as the submontane coppice forests were established as a natural reserve one decade ago and the last intensive management activities were recorded some 60 years ago. So, absolute naturalness might be an important factor for a high ratio of CWD to living tree volume.

Quality of deadwood

In the overall diameter distribution of CWD small trees were the most abundant and within 5–20 cm diameter the CWD stems accounted for 90% of the total. Without a single exception (the number of CWD stems is higher in 10–15 cm than 5–10 cm) the density of dead trees decreased with larger diameter classes. Ignoring this single exception the findings were supported by BÖHL and BRÄNDLI (2007) in the third Swiss National Forest Inventory. Inter-competitions and lack of sunlight may lead to an increased mortality in the young trees compared to the older and mature trees. Within the 5–10 cm diameter class hornbeam had 75% of the dead stems of its total number whereas oak had only 20% of its total number of dead stems in this class, which indicates that the young stages of hornbeam are more vulnerable to mortality than oak.

Decay class B was the most abundant (on average 51% of total volume), followed by class C (on average 43% of total volume). On the other hand, structural class 4 (missing small branches) is the most abundant (on average 53% of total volume) in the Lange-Leitn reserve. Decay class E (fragmented heartwood and ill-defined wood) was the most infrequent (on average 1% of total volume) because of the short duration of naturalness which did not allow a sufficient time for full decomposition. Decay class A (dying recently, cambium still fresh) was also infrequent (on average 3% of total volume) and structural class 1 (intact freshly dead) was the most infrequent (on average 1% of total volume) because this class remains for less than a year only (KARJALAINEN, KUULUVAINEN 2002). Decay class D and decay class E are absent in LQT and LQC, but present in GSC. A more humid microclimate may be the cause of a comparatively higher proportion of advanced decay phases in GSC than in the other two associations (compare VASILIAUSKAS et al. 2004). As a whole, 10 years naturalness was not enough time for getting a good proportion of advanced decay phases.

Implications of this CWD level as reference for biodiversity conservation in temperate submontane broadleaved forests

CWD is an important component of forest ecosystems, reducing erosion and affecting soil development, storing nutrients and water, serving as a seedbed for plants and as a major habitat for decomposers and heterotrophic organisms (HARMON et al. 1986; FRANKLIN et al. 1987; KEY, BALL 1993; SAMUELSSON et al. 1994; MCCOMBE, LINDENMAYER 1999). They provide nesting, roosting, feeding, loafing, and storage sites for birds, small mammals, reptiles, and amphibians (SCOTT, PATTON 1989; DEGENHARDT et al. 1996; RABE et al. 1998). The number of directly available snags influences the population size for cavity breeding animals (HUNTER 1990; MIKUSINSKI, ANGELSTAM 1997). Fungi form a very diverse organism group and are essential for other organisms depending on CWD and ecosystem functioning. Decomposing logs are considered the most species rich and important type of CWD for wood-inhabiting fungi (RYDIN et al. 1997; SIPPOLA, RENVALL 1999). On the other hand, management history and substrate abundance influence fungal diversity at a site level (HØILAND, BENDIKSEN 1996; LINDBLAD 1997; STOKLAND et al. 1997; SIPPOLA, RENVALL 1999; LUMLEY et al. 2000; NORDEN, PALTTO 2001; EDMAN et al. 2004; PENTTILÄ et al. 2004; BERGLUND, JONSSON 2005; HEILMANN-CLAUSEN, CHRISTENSEN 2005; SCHMIT 2005; SIPPOLA et al. 2005; SIMILÄ et al. 2006; ÓDOR et al. 2006). Fungi and bryophytes have their highest diversity connected to fallen logs in certain decay classes (ÓDOR, STANDOVÁR 2002; HEILMANN-CLAUSEN, CHRISTENSEN 2003, 2005). Intermediate decay stage of logs is considered the most rich in fruiting species of fungi (RENVALL 1995; WILLIG, SCHLEGTE 1995; HØILAND, BENDIKSEN 1996). Logs in intermediate stage support the highest number of red listed fungi (HEILMANN-CLAUSEN, CHRISTENSEN 2003). Fungi are occurring at highest diversity in the intermediate decay stages and bryophytes have a preference for both medium and late decay stages and a special requirement for a constantly high level of air humidity (ANDERSSON, HYTTTEBORN 1991; SÖDERSTRÖM 1998; RAMBO, MUIR 1998; ÓDOR, STANDOVÁR 2001). 43% of the total volume of CWD in this reserve was at intermediate decay phase. So it can be assumed that a congenial environment exists in Lange-Leitn Natural Forest Reserve for different fungi including red listed fungi. Various insects and lichens have a strong preference for sun-exposed stumps, snags and standing decay columns. So, to conserve the biodiversity related to

deadwood, it is obvious to keep the right balance between logs and snags.

To enhance the biodiversity related to deadwood in Austrian broadleaved forests it is important to have knowledge of a reference value derived from absolute natural conditions. One of the objectives of establishing a natural reserve in Austria was to maintain forest biodiversity at the level of natural condition to put a landmark for sustainable forest management. In this context the discussion about reference values for CWD in conservation management should consider the outcomes of the recent study. Several studies from Europe reported that the volume of CWD did not exceed 10 m³/ha in managed forests where it originated from logging waste and stumps (ERDMANN, WILKE 1997; TABAKU 1999; FRIDMAN, WALHEIM 2000; UNECE/FAO 2000). The recent discussion in the Austrian forest dialogue about an average reference level of 3 m³/ha in managed forest ecosystems is even beyond this level (BMLFW 2007). On the other hand, GRABHERR et al. (1998) reported that in managed oak-hornbeam forests the amount of CWD ranged from 3 to 15 m³/ha and the amount of CWD for the trees having more than 10 cm dbh did not exceed 3 m³/ha. The level of CWD found in this study was 107 m³/ha, which is more than 10 times higher than that of managed forests and the ratio of CWD and living tree volume (39%) can serve as a preliminary reference for the near natural management of submontane broad-leaved forests. On many sites, 30–50 m³ snags and about 100 m³ logs were probably commonly occurring amounts before European forests were subjected to human exploitation (NILSSON et al. 2002).

In this context HARMON (2002) proposed the new paradigm “morticulture” along with silviculture for an active culturing of CWD. To increase the overall CWD volume in managed forests it is necessary to leave some merchantable timber in the forest and actively mark some trees as future CWD, so that in the course of time they may become snags and afterwards logs that decayed naturally. The volume of CWD in managed forests will be a vital indicator for the sustainability and biodiversity conservation (MCPFE 2003). Therefore, the CWD amount reported in the study may serve as a guideline for managers to meet the degree of naturalness and improve the overall biodiversity of CWD related organisms specially fungi in close-to-nature management as well.

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References

- ANDERSSON L.I., HYTTBORN H., 1991. Bryophytes and decaying wood a comparison between managed and natural forest. *Holarctic Ecology*, 14: 121–130.
- BERGLUND H., JONSSON B.G., 2005. Verifying an extinction debt among lichens and fungi in Northern Swedish boreal forests. *Conservation Biology*, 19: 338–348.
- BMLFW (Hrsg.), 2007. Indikatoren, Ist-Größen und Soll-Größen-Vorschläge. Arbeitspapier, Stand 3, Oktober 2007: 101.
- BÖHL J., BRÄNDLI U.B., 2007. Deadwood volume assessment in the third Swiss National Forest Inventory: methods and first results. *European Journal of Forest Research*, 126: 449–457.
- CHRISTENSEN M., HAHN K., MOUNTFORD E.P., ÓDOR P., STANDOVÁR T., ROZENBERGAR D., DIACI J., WIJDEVEN S., MEYER P., WINTER S., VRŠKA T., 2005. Dead wood in European beech (*Fagus sylvatica*) forest reserves. *Forest Ecology and Management*, 210: 267–282.
- DEGENHARDT W.G., PAINTER C.W., PRICE A.H., 1996. *Amphibians and Reptiles of New Mexico*. Albuquerque, NM, University of New Mexico Press: 431.
- EDMAN M., GUSTAFSSON M., STENLID J., JONSSON B.G., ERICSON L., 2004. Spore deposition of wood-decaying fungi: importance of landscape composition. *Ecography*, 27: 103–111.
- ENGELMARK O., 1999. Boreal forest disturbances. In: WALKER L.R. (ed.), *Ecosystems of disturbed ground*. *Ecosystems of the World*, 16: 161–186.
- ERDMANN M., WILKE H., 1997. Quantitative und qualitative Totholzerfassung in Buchenwirtschaftswäldern. *Forstwissenschaftliches Centralblatt*, 116: 16–28.
- FRANK G., MÜLLER F., 2003. Voluntary approaches in protection of forests in Austria. *Environmental Science & Policy*, 6: 261–269.
- FRANKLIN J.F., SHUGART H.H., HARMON M.E., 1987. Tree death as an ecological process. The causes, consequences, and variability of tree mortality. *BioScience*, 37: 550–556.
- FRIDMAN J., WALHEIM M., 2000. Amount, structure, and dynamics of dead wood on managed forestland in Sweden. *Forest Ecology and Management*, 131: 23–26.
- GRABHERR G., KOCH G., KIRCHMEIR H., REITER K., 1998. *Hemerobie österreichischer Waldökosysteme*. Österreichische Akademie der Wissenschaften. Veröffentlichungen des österreichischen MaB-Programmes, 17: 493.
- GREEN P., PETERKEN G.F., 1997. Variation in the amount of dead wood in the woodlands of the Lower Wye Valley, UK in relation to the intensity of management. *Forest Ecology and Management*, 98: 229–238.
- HAHN K., CHRISTENSEN M., 2004. Dynamics of dead wood in European beech forests in relation to natural disturbances. *The Iceland Forest Research Bulletin*, 22: 5–8.
- HARMON M.E., 2001. Carbon sequestration in forests: addressing the scale question. *Journal of Forestry*, 99 (4): 24–29.
- HARMON M.E., 2002. Moving towards a new paradigm for woody detritus management. USDA Forest Service, General Technical Report PSW-GTR: 181.
- HARMON M.E., FRANKLIN J.F., SWANSON F.J., SOLLINS P., LATTIN J.D., ANDERSON N.H., GREGORY S.V., CLINE S.P., AUMEN N.G., SEDELL J.R., KIENKAEMPER G.W., CROMACK K. Jr., CUMMINS K.W., 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research*, 15: 133–302.
- HEILMANN-CLAUSEN J., CHRISTENSEN M., 2003. Fungal diversity on decaying beech logs-implications for sustainable forestry. *Biodiversity and Conservation*, 12: 953–973.
- HEILMANN-CLAUSEN J., CHRISTENSEN M., 2005. Wood-inhabiting macrofungi in Danish beech-forests – conflicting diversity patterns and their implications in a conservation perspective. *Biological Conservation*, 122: 633–642.
- HØILAND K., BENDIKSEN E., 1996. Biodiversity of wood-inhabiting fungi in a boreal coniferous forest in Sor-Trondelag County, Central Norway. *Nordic Journal of Botany*, 16: 643–659.
- HUNTER M.J., 1990. *Wildlife, Forests, and Forestry. Principles for Managing Forests for Biological Diversity*. Englewood Cliffs, New Jersey: Prentice Hall Career & Technology: 370.
- JAWORSKI A., PODLASKI R., WAGA T., 1999. Budowa i struktura drzewostanów o charakterze pierwotnym w rezerwacie Świąty Krzyż (Świątokrzyski park narodowy). *Acta Agraria et Silvicultura, Series Silvestris*, 37: 27–51.
- KARJALAINEN L., KUULUVAINEN T., 2002. Amount and diversity of coarse woody debris within a boreal forest landscape dominated by *Pinus sylvestris* in Vienansalo wilderness, eastern Fennoscandia. *Silva Fennica*, 36: 147–167.
- KEY R., BALL S.G., 1993. Positive management for saproxylic invertebrates. In: KIRBY K.J., DRAKE C.M., (eds), *Dead wood matters: the ecology and conservation of saproxylic invertebrates in Britain*. English Nature Science No. 7. Peterborough, English nature.
- KIRBY K.J., REID C.M., THOMAS R.C., GOLDSMITH F.B., 1998. Preliminary estimates of fallen dead wood and standing dead trees in managed and unmanaged forests in Britain. *Journal of Applied Ecology*, 35: 148–155.
- KÖLBEL M., 1999. Totholz in Naturwaldreservaten und Urwäldern. LWF aktuell 'Totes Holz-lebend(ig)er Wald', 18: 2–5.

- KOOP H., HILGEN P., 1987. Forest dynamics and regeneration mosaic shifts in unexploited beech (*Fagus sylvatica*) stands at Fontainebleau (France). *Forest Ecology and Management*, 20: 135–150.
- KORPEL Š., 1997. Totholz in Naturwäldern und Konsequenzen für Naturschutz und Forstwirtschaft. *Forst und Holz*, 52: 619–624.
- LABUDDA V., 1999. Die Bestandsstruktur des Bannwaldes Birkenkopf im Nordschwarzwald. *Berichte Freiburger Forstliche Forschung*, 5: 1–31.
- LINDBLAD I., 1997. Wood-inhabiting fungi on fallen logs of Norway spruce: relations to forest management and substrate quality. *Nordic Journal of Botany*, 18: 243–255.
- LUMLEY T.C., ABBOTT S.P., CURRAH R.S., 2000. Microscopic ascomycetes isolated from rotting wood in the boreal forest. *Mycotaxon*, 74: 395–414.
- MCCOMBE W., LINDENMAYER D., 1999. Dead, dying, and down trees. In: HUNTER M.L. (ed.), *Maintaining Biodiversity in Forest Ecosystems*. Cambridge, Cambridge University Press: 335–372.
- MCPFE, 1993. Ministerial Conference on the Protection of the Forests in Europe, 16–17 June, Helsinki. Conference Proceedings: 186.
- MCPFE, 2003. Improved Pan-European Indicators for Sustainable Forest Management as Adopted by the MCPFE Expert Level Meeting 7–8 October 2002. Vienna: 6.
- MEYER P., 1999. Totholzuntersuchungen in nordwestdeutschen Naturwäldern: Metodik und erste Ergebnisse. *Forstwissenschaftliches Centralblatt*, 118: 167–180.
- MIKUSINSKI G., ANGELSTAM P., 1997. European woodpeckers and anthropogenic habitat change: a review. *Vogelwelt*, 118: 277–283.
- NILSSON S.G.M., NIKLASSON J., HEDIN G., ARONSSON J.M., GUTOWSKI P., LINDER H., LJUNGBERG G., MIKUSINSKI-RANIUS T., 2002. Densities of large living and dead trees in old-growth temperate and boreal forests. *Forest Ecology and Management*, 161: 189–204.
- NORDEN B., PALTTO H., 2001. Wood decay in hazel wood: species richness correlated to stand age and dead wood features. *Biological Conservation*, 101: 1–8.
- ÓDOR P., STANDOVÁR T., 2001. Richness of bryophyte vegetation in a near-natural and managed beech stands: the effects of management-induced differences in dead wood. *Ecological Bulletin*, 49: 219–229.
- ÓDOR P., STANDOVÁR T., 2002. Substrate specificity and community structure of bryophyte vegetation in a near-natural montane beech forest. *Community Ecology*, 3: 39–49.
- ÓDOR P., STANDOVÁR T., 2003. Changes of physical and chemical properties of dead wood during decay (Hungary). *The NatMan Project, Working Report*, 23: 29.
- ÓDOR P., HEILMANN-CLAUSEN J., CHRISTENSEN M., AUDE E., VAN DORT K.W., PILTAVER A., SILLER I., VEERKAMP M.T., WALLEYN R., STANDOVÁR T., VAN HEES A.F.M., KOSEC J., MATOCEC N., KRAIGHER H., GREBENC T., 2006. Diversity of dead wood inhabiting fungi and bryophytes in seminatural beech forests in Europe. *Biological Conservation*, 131: 58–71.
- PENTTILÄ R., SIITONEN J., KUUSINEN M., 2004. Polypore diversity in managed and old-growth boreal *Picea abies* forests in southern Finland. *Biological Conservation*, 117: 271–283.
- PRODAN M., 1965. *Holzmesslehre*. Frankfurt am Main, J.D. Sauerlander's Verlag: 644.
- RABE M.J., MORRELL T.E., GREEN H., DEVOS J.C. Jr., MILLER C.R., 1998. Characteristics of ponderosa pine snag roosts used by reproductive bats in northern Arizona. *Journal of Wildlife Management*, 62: 612–621.
- RAMBO T.R., MUIR P.S., 1998. Bryophyte species association with coarse woody debris and stand ages in Oregon. *The Bryologist*, 101: 366–376.
- RENVALL P., 1995. Community structure and dynamics of wood-rotting basidiomycetes on decomposing conifer trunks in northern Finland. *Karstenia*, 35: 1–51.
- ROUVINEN S., KUULUVAINEN T., 2001. Amount and spatial distribution of standing and downed dead trees in two areas of different fire history in a boreal Scots pine forest. *Ecological Bulletin*, 49: 115–127.
- RYDIN H., DIEKMANN M., HALLINGBÄCK T., 1997. Biological characteristics, habitat associations, and distribution of macrofungi in Sweden. *Conservation Biology*, 11: 628–640.
- SAMUELSSON J., GUSTAFSSON L., INGELOG T., 1994. *Dying and Dead Trees a Review of Their Importance for Biodiversity*. Uppsala, Swedish Threatened Species Unit, Swedish University of Agricultural Sciences: 110.
- SANIGA M., SCHÜTZ J.P., 2001a. Dynamics of changes in dead wood share in selected beech virgin forests in Slovakia within their development cycle. *Journal of Forest Science*, 47: 557–565.
- SANIGA M., SCHÜTZ J.P., 2001b. Dynamik des Totholzes in zwei gemischten Urwäldern der Westkarpaten im pflanzengeographischen Bereich der Tannen-Buchen- und der Buchenwälder in verschiedenen Entwicklungsstadien. *Schweizerische Zeitschrift für Forstwesen*, 152: 407–416.
- SCOTT V.E., PATTON D.R., 1989. *Cavity-nesting birds of Arizona and New Mexico forests*. General Technical Report RM-10. Fort Collins, CO: Rocky Mountain Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture: 71.
- SIMILÄ M., KOUKI J., MÖNKKÖNEN M., SIPPOLA A.L., HUHTA E., 2006. Covariation and indicators of species diversity: can richness of forest-dwelling species be predicted in northern boreal forests? *Ecological Indicators*, 6: 686–700.
- SIPPOLA A.L., RENVALL P., 1999. Wood-decomposing fungi and seed-tree cutting. *Forest Ecology and Management*, 115: 183–201.

- SIPPOLA A.L., MÖNKKÖNEN M., RENVALL P., 2005. Polypore diversity in the herb-rich woodland key habitats of Koli National Park in eastern Finland. *Biological Conservation*, 126: 260–269.
- SÖDERSTRÖM L., 1988. The occurrence of epixylic bryophyte and lichen species in an old natural and managed forest stand in Northeast Sweden. *Biological Conservation*, 45: 169–178.
- STOKLAND J.N., LARSSON K.H., KAUSERUD H., 1997. The occurrence of rare and red-listed fungi on decaying wood in selected forest stands in Norway. *Windahlia*, 22: 85–93.
- STOKLAND J.N., 2001. The coarse woody debris profile: an archive of recent forest history and an important biodiversity indicator. *Ecological Bulletin*, 49: 71–83.
- TABAKU V., 1999. Struktur von Buchen-Urwäldern in Albanien im Vergleich mit deutschen Buchennaturwaldreservaten und Wirtschaftswäldern. Göttingen, Cuvillier: 206.
- UNECE/FAO, 2000. Forest Resources of Europe, CIS, North America, Australia, Japan and New Zealand (Industrialized Temperate/Boreal Countries). UN-ECE/FAO Contribution to the Global Forest Resources Assessment 2000. Main Report. Geneva Timber and Forestry Study Papers, No. 17. United Nations, New York and Geneva: 445.
- VASILIAUSKAS R., VASILIAUSKAS A., STENLID J., MATELIS A., 2004. Dead trees and protected polypores in unmanaged north temperate forest stands of Lithuania. *Forest Ecology and Management*, 193: 335–370.
- VRŠKA T., 1998. Prales Salajka po 20 letech (1974–1994). *Lesnictví-Forestry*, 44: 153–181.
- UOTILA A., MALTAMO M., UUTTERA J., ISOMÄKI A., 2001. Stand structure in semi-natural and managed forests in eastern Finland and Russian Karelia. *Ecological Bulletin*, 49: 149–158.
- WILLIG J., SCHLEGTE G.B., 1995. Pilzsukzession an Holz nach Windwurf in einem Buckennaturwaldreservat (Fungal succession on wood after windthrow in a natural beech-forest reserve). *Allgemeine Forstzeitschrift*, 15: 814–818.
- WILLNER W., GRABHERR G., 2007. Die Wälder und Gebüsche Österreichs. Elsevier, Spektrum Akademischer Verlag: 302.
- WILSON B.F., McCOMB B.C., 2005. Dynamics of dead wood over 20 years in New England oak forest. *Canadian Journal of Forest Research*, 35: 682–692.

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Charakteristika tlející dřevní hmoty v přírodní lesní rezervaci Lange-Leitn (Rakousko)

ABSTRAKT: V přírodní rezervaci Lange-Leitn v Rakousku s dominantním zastoupením dubu bylo v roce 2006 provedeno šetření objemu, variability a kvality tlející dřevní hmoty. Průměrný objem tlející dřevní hmoty, zahrnující ležící kmeny a zlomy, byl 107,3 m³/ha, což činí 39 % z celkového objemu dřevní zásoby porostu. Z tohoto objemu tlejícího dřeva zahrnovalo 23,4 m³/ha (22 %) zlomy a 83,9 m³/ha (78 %) ležící kmeny. Z hlediska kvality tlející dřevní hmota zahrnuje široké spektrum druhů dřevin, velikost kmenů v různých stádiích rozkladu s odlišnými strukturálními znaky. Tlející dřevní hmota zde zároveň vytváří přirozené prostředí pro mikroorganismy. V porovnání tří zkoumaných lesních společenstev bylo největší množství tlející dřevní hmoty zaznamenáno v asociaci *Galio sylvatici-Carpinetum*. Výsledky této studie budou použity jako referenční hodnoty pro nastavení přírodě blízkého hospodaření v listnatých lesích v pahorkatinách s dubem jako převažující dřevinou.

Klíčová slova: lesní společenstva; přírodní stanoviště; houby; dub; listnatý les

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