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When nature takes over from man: Dead wood accumulation in previously managed oak and beech woodlands in North-western and Central Europe

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ABSTRACT

The accumulation of dead wood and its characteristics are analysed in forests that have been withdrawn from regular silvicultural management and left unmanaged between 10 and 150 years ago. These forests are dominated by beech (*Fagus sylvatica*) and oak (*Quercus robur* and *Quercus petraea*) and located in the lowlands of North-western and Central Europe.

The total volumes of dead wood ranged from 6 to nearly 500 $m^3\ ha^{-1}$, with a median value of 53 $m^3\ ha^{-1}$. The average accumulation rate ranged from <0.1 to 19 $m^3\ ha^{-1}\ year^{-1}$. Variation was significantly higher in beech- than in oak-dominated forests. The variables and factors influencing dead wood volumes and accumulation rates were tree genus, stand age at the time of the onset of non-intervention, and the interaction between geographical location and tree genus. In beech-dominated stands, the ratio of lying to total dead wood was more or less constant at 75%; in oak-dominated stands, this ratio was related to the length of time non-intervention had occurred, rising from <50% in recently assigned areas to 75% in the long-established sites. It is concluded that in the absence of major disturbances, dead wood accumulation in man-made forests left to develop freely is a slow process. It may take a very long time to achieve the average amount and dynamic steady state of dead wood as described for virgin forests in Central Europe.

1. Introduction

Publications on base line or reference values for dead wood in primary forests which have never been subjected to silvicultural management (subsequently referred to as 'virgin forests' in this study) are numerous for Europe (a.o. Leibundgut, 1993; Korpel, 1995; Saniga and Schütz, 2001a,b). However, very little is published on the processes of dead wood accumulation in forests that have been withdrawn from regular silvicultural management and deliberately assigned to a non-intervention regime (subsequently referred to as 'unmanaged forest reserves'). This study comprises a meta-analysis of data (published and original) on dead wood volume (standing and lying) in these forests, focusing on oak and beech forests in the lowlands of Central and North-western Europe.

Over the last three decades, dead wood is increasingly recognised as an important component in the functioning of forest ecosystems. It plays an important role in biogeochemical cycles, trophic chains, natural regeneration, and is an important element in carbon storage as well as providing key niches for many species (Dajoz, 1974; Maser and Trappe, 1984; Harmon et al., 1986; Ferris-Kaan et al., 1993; Kirby and Drake, 1993; Rauh, 1993; Samuelsson et al., 1994; Falinski and Mortier, 1996; Økland et al., 1996; Esseen et al., 1997; Bücking, 1998; Denis, 1998; Köhler, 2000; Heilmann-Clausen, 2001; Siitonen, 2001; Grove, 2002; Vallauri et al., 2003; Vandekerkhove et al., 2003; Brustel, 2004; Brustel and Dodelin, 2005; Odor et al., 2006). A combination of forest fragmentation and forest management (including the removal of dead wood) has led to a substantial decline in species that are dependent on dead wood. Many species are threatened or have become extinct locally and regionally (Siitonen, 2001). This is especially true for highly fragmented and intensively treated forests in North-western Europe (Odor et al., 2006).

The amount of dead wood is often used as an important structural indicator in the context of Biodiversity Evaluation Tools (Larsson, 2001; Van Loy et al., 2003; Corona et al., 2003; Marchetti, 2004) and as a basic indicator of old growth characteristics and naturalness in forests (Peterken, 1996; Bobiec, 2002). It has become one of the primary indicators of sustainable forest management in Europe (MCPFE, 2002) and periodic reporting on this indicator is mandatory for all signatory states (MCPFE, 2003, 2007). Although its importance in practice and in policy has

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dramatically increased, amounts of dead wood in European forests, especially in the lowlands, are still extremely low. Average figures per country in Europe vary from <1 to 23 $m^3\ ha^{-1}$ (MCPFE, 2007). This is far below the amounts typically found in virgin forests (Green and Peterken, 1997; Kirby et al., 1998; Odor and Standovar, 2001; Winter and Nowak, 2001), and below the amount that may be required to safeguard the complete spectrum of species that rely on dead wood, which is widely agreed to be 20–30 $m^3\ ha^{-1}$ (Stokland, 2001; Siitonen, 2001; Angelstam et al., 2003; Humphrey et al., 2004).

Regional forest policies have an explicit goal to significantly increase both the quantity and quality of dead wood (Ammer, 1991; ONF, 1993; Hodge and Peterken, 1998). In order to achieve this objective a two-way policy has been developed incorporating an integrative and a segregative approach. An integrative approach aims to retain a certain quantity and quality of dead wood in regular multifunctional forest management. A segregative approach concentrates conservation efforts in protected forest areas. Both are necessary and complementary to attain the biodiversity conservation objective in forests generally (Frank et al., 2007).

In virgin forests and unmanaged forest reserves, the conservation policy objective on dead wood is realised through processes of spontaneous development. These types of forest cover <5% of the total forest area in Europe (Parviainen et al., 2000; MCPFE, 2007; Bücking, 2007). In the 19th century, the main objective for the assignation of reserves was aesthetic and ethical, namely to conserve the last remains of virgin forest in Central Europe (Welzholz and Johann, 2007; Bücking, 2007). Over time, the value of these 'virgin forest' reserves for nature conservation and scientific research became increasingly recognised (Parviainen et al., 1999; Bücking, 2007) and essential to the development of nature-based silviculture as they provide reference base-line values and ranges for structural parameters such as the amounts of living and dead wood, species composition and gap dynamics (Leibundgut, 1959, 1978; Korpel, 1992). Hence, scientific criteria such as representativeness became a focus in the selection of new reserves. The aim was to develop a network of unmanaged reference sites that represent all forest types and site conditions present in a certain area or country (Leibundgut, 1959; Mlinsek, 1976; Parviainen et al., 1999, 2000; Meyer et al., 2007). As a consequence, new reserves are and have been selected in managed forests, as there are no virgin forests remaining for many of the target forest types. Natural dynamics in these, previously managed forests are clearly different from virgin forests. Whereas the latter are considered in a dynamic equilibrium with respect to interchanging developmental phases (e.g. Leibundgut, 1978; Korpel, 1995; Saniga and Schütz, 2001a), the newly established unmanaged forest reserves are still developing in a more unidirectional way towards equilibrium. Indeed, they all start from a man-made structure that is more or less divergent from this equilibrium with generally lower stocking density than virgin forests and a species composition and dominance that has been influenced and altered by human intervention. Most of the semi-natural forests in the European lowlands are dominated by beech or oak. This dominance, especially where oak is concerned, is often the result of centuries-old management regimes. The structural difference however is most striking in the typical old growth elements, particularly ancient trees and dead wood volume (Bobiec, 2002; Korpel, 1997). This paper analyses the process of dead wood accumulation in unmanaged forest reserves in the lowlands of North-western and Central Europe.

2. Materials and methods

2.1. Selection criteria for study sites

This study comprised a meta-analysis of published and original data on standing and lying dead wood volume in unmanaged forest reserves. From a large dataset, sites were selected that met the following criteria:

- Before the adoption of a non-intervention management regime the forest was subject to regular forest management typical of current forest practice in the region, i.e. regular thinning, felling, planting, and removal of dead wood. Sites that are considered as 'virgin forest' were not included.
- Subject to non-intervention for at least 10 years.
- Within the natural range and typical site conditions of Beech woods, Birch-oak woods and Hornbeam-oak woods (*Fagion*, *Quercion robori-petraea* and *Carpinion* resp. sensu Jahn, 1991).
- Confined to the lowlands of North-western and Central Europe. The study included sites from the following countries: Belgium, Czech Republic, Denmark, France Germany, Hungary, the Netherlands, Poland and the United Kingdom. The altitudinal range only included lowlands and submontane ranges up to 700 m.
- Dominated by oak (*Quercus robur* and *Quercus petraea*) and beech (*Fagus sylvatica*). Oak or beech was considered 'dominant' if it comprised the greatest proportion of all tree species with respect to the living volume.
- Information had to be sufficient with data available on all response variables and the essential explanatory variables. Mensuration methodology had to be clearly described and had to comply with clear standards of quality and comparability (see below).

2.2. Assessment of response and explanatory variables

The response variables selected were (a) the total volume of dead wood ($m^3\ ha^{-1}$), (b) the accumulation rate of dead wood ($m^3\ ha^{-1}\ year^{-1}$), and (c) the ratio of the lying dead wood volume to the total volume of dead wood (%). Potential explanatory variables were the length of time of non-intervention, stand age at the time non-intervention management commenced, site fertility (poor versus rich), dominant tree genus (oak versus beech) and geographical location of the samples (North-western Europe versus Central Europe).

Total volume of lying and standing dead wood were sampled in a number of unmanaged forest reserves in Belgium and Germany. Sampling consisted of a systematic grid of circular plots of 500 or 1000 m^2 covering at least 10% of the area, or complete surveys of larger 'core area' plots of 1 ha. Threshold diameter for living and dead wood was 5 cm for Belgian sites and 7 cm for German sites (except for lying dead wood in the German circular plots where it was 20 cm). Volume calculations were made for living and fresh dead trees using regional tariffs based on DBH and height measurements. Volumes of wood fragments were calculated using formulas of truncated cones. The resulting volumes were converted and expressed in $m^3\ ha^{-1}$ (De Keersmaeker et al., 2005; Meyer et al., 2006). The dataset was further completed with published data that met the above criteria.

The ratio of lying to total dead wood volume was expressed as a percentage. Dead wood accumulation rate is the average net increase of dead volume divided by the number of years of non-intervention. The net increase of dead wood captures the balance between inputs and outputs (decay) of dead wood, and was calculated by subtracting the volume of dead wood at the moment the reserve was initiated from the recorded volume of dead wood at the time of measurement. For sites where this starting amount was unknown it was set at 2 $m^3\ ha^{-1}$. This is an average value for traditionally managed forests (Kappes and Topp, 2004). Sites where the volume was known to be much higher but not quantified, were omitted from the dataset.

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In order to evaluate the impact of the differences in diameter threshold applied in the different studies, we calculated the dead wood volumes in 5 cm classes for 10 Belgian samples (threshold diameter 5 cm; total dead wood volume ranging from 4 to 113 m^3 ha^{-1}, average 42.2 m^3 ha^{-1}), generating a correction factor for the 'missed fraction' in case of higher thresholds. We adjusted the dead wood volumes, accumulation rates and lying to total dead wood ratios, to a standard minimum threshold diameter of 5 cm, using this correction factor. This resulted in very marginal changes in recorded values as compared to the original dataset (e.g. mean total dead wood volume; 75.71 m^3 ha^{-1} versus 75.26 m^3 ha^{-1}; the median value was unaltered). The modified dataset was also tested using an identical statistical procedure as for the original dataset (see below), resulting in models which included the same explanatory variables and interactions, with minor changes for coefficients and significance levels as compared to the models on the original data. We concluded that the impact of the harmonisation process on the results and the statistics was marginal, and therefore preferred to maintain the original data for further analysis and discussion.

The length of time of non-intervention was postulated using reports or information derived from managers and/or researchers. Unlike Christensen et al. (2005) we did not derive the number of years of non-intervention from the official date of reserve establishment as these do not necessarily coincide. Some sites were, in practice, left unmanaged for many years before non-intervention was officially designated by means of a reserve statute. In other cases, reserve status still allowed or could not prevent human intervention such as the removal of dead wood, especially during World Wars I and II. Sites where this information was missing or unreliable, were omitted. Stand age at the time of assigning the reserve was determined as the average age of the dominant tree layer at the time of measurement subtracted by the length of time of non-intervention. The 'fertility' factor was derived from the phytosociological description of the sites; *Quercion, Luzulo-Fagetum* and *Milio-Fagetum* sites were classified as 'poor', and *Carpinion, Endymio-Fagetum* and *Asperulo-Fagetum* were classified as 'rich'. The dominant tree species was determined based on the proportion of a particular tree species to the total living volume. Only sites where beech or oak had the highest proportion of all tree species present were selected and were allocated to the genus classes 'beech' and 'oak' respectively. The geographical subdivision (North-western versus Central) was primarily based on the Atlantic and Continental regions as defined in Roekaerts (2002). These biogeographical regions are based on the natural vegetation map of Europe, and are discerned by means of indicator plant species for local climatic conditions such as temperature and annual rainfall. As this study was primarily concerned with the effects of windstorm conditions, we added information on windstorm regimes, derived from the Europe Windstorm Model for Extra-Tropical Cyclones (ETC) risk assessments (www.rms.com). As a consequence, a few sample sites were moved into new categories with respect to the biogeographical subdivision.

2.3. Data analyses

Linear models were developed in S-PLUS 8.0 to determine the variables that were significant in explaining the total volume of dead wood, the accumulation rate of dead wood and the ratio of lying to total dead wood volume. Exploratory data analyses revealed that data transformation was necessary for normalisation. A log transformation was applied to the total volume of dead wood and the accumulation rate. The ratio of lying to total dead wood was normalised by means of a quadratic function. The stepwise model building started with an upper model, which included all the above-mentioned potential explanatory variables and their interactions. The least significant term was removed and this procedure was repeated until all remaining terms were significant. The ratio of lying to total dead wood was modelled by means of a generalised linear model (GLM). The exploratory data analysis indicated that variance of dead wood volume and accumulation rate were related to tree genus and therefore a generalised least square model (GLS) was applied. The akaike information criterion (AIC) was used to select the most appropriate variance structure model. Significance of variables and interactions were tested by means of restricted maximum likelihood (REML), which can produce unbiased estimates of variance and covariance structures (Fitzmaurice et al., 2004).

3. Results

A total of 109 samples from 94 locations were represented in the dataset. Summary details of all sites are given in Appendix A. Seventy-four sites were dominated by beech and 35 by oak. The sites were well distributed with respect to the variables 'geographic region' and 'site fertility'. The average age of the dominant trees at the time of unmanaged forest reserve assignation varied between 3 and 178 years for the oak stands and 33 and 280 years for the beech stands. However in most sites, the dominant trees were between 100 and 150 years old, with very few less than 50 or over 200. Most sites in the dataset had only recently been withdrawn from ongoing regular management; the mean time of non-intervention was 35 years. More than half of the samples had been left unmanaged for 25 years or less. Only 22 sites had a history of non-intervention of more than 50 years and only 3 more than 100 years.

3.1. Total dead wood volume

Summary data on total dead wood volume are shown in Table 1 and illustrated in Figs. 1–3. The recorded total amount of dead wood ranged from 6 to nearly 500 m^3 ha^{-1}, with a mean value of

Table 1
Summary statistics on total dead wood volume, accumulation rate and ratio of lying to total dead wood volume for the complete dataset, and specific subsets (oak and beech in North-western and Central Europe).

	Beech			Oak			Total
	NW	C	All	NW	C	All	
N	24	50	74	12	23	35	109
Total volume (m^3/ha)							
Mean	130.4	64.9	86.1	24.8	66.8	52.4	75.3
Standard error of mean	23.2	8.2	9.9	4.3	9.8	7.4	7.3
Median	96.0	39.0	59.0	23.4	57.0	39.2	53.0
Lower quartile	53.2	20.8	26.9	15.9	38.6	25.2	26.4
Upper quartile	145.0	92.4	120.5	28.4	69.6	62.4	95.0
Accumulation rate (m^3 ha^{-1} $year^{-1}$)							
Mean	5.13	2.13	3.10	1.04	1.75	1.51	2.59
Standard error of mean	0.98	0.29	0.40	0.21	0.20	0.16	0.29
Median	3.44	1.26	1.89	1.00	1.72	1.24	1.64
Lower quartile	1.94	0.63	1.00	0.46	1.18	0.83	0.96
Upper quartile	6.62	2.87	4.03	1.25	2.31	2.07	3.00
Lying dead wood (%)							
Mean	75.6	70.1	71.7	42.3	54.9	50.9	65.2
Standard error of mean	3.6	2.5	2.03	5.9	5.5	4.3	2.1
Median	74.7	75.8	75.0	44.1	65.0	50.7	70.4
Lower quartile	70.0	63.2	65.5	31.3	31.3	31.2	53.4
Upper quartile	87.7	79.9	82.2	54.7	77.4	68.8	79.2
Missing values	4	1	5	2	2	4	9

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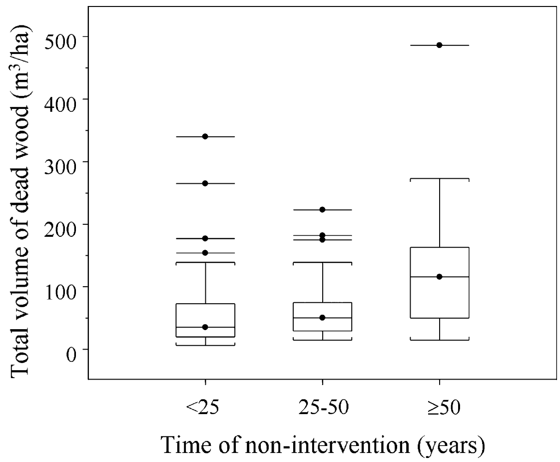

Fig. 1. Boxplots representing the total dead wood volume in forest reserves, subdivided in three classes, defined by the length of time of non-intervention.

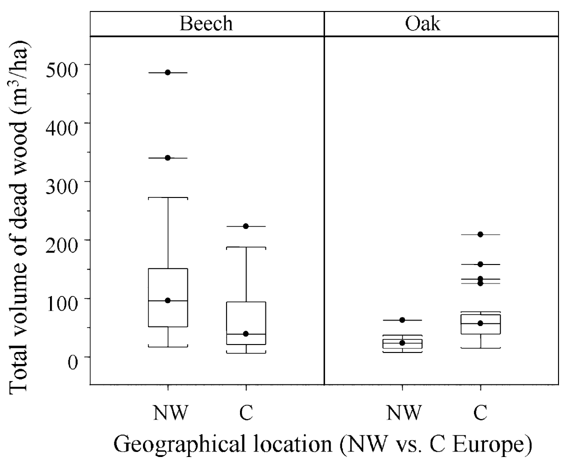

Fig. 2. Boxplots representing the total dead wood volume in forest reserves, subdivided by tree genus (beech versus oak) and geographical location (North-western versus Central Europe).

75 m^3 ha^{-1}. The results were not evenly distributed; three out of four sites contained <100 m^3 ha^{-1}. Mean and standard deviations are therefore not very indicative of the recorded range of values. Median, upper and lower quartiles are therefore better measures

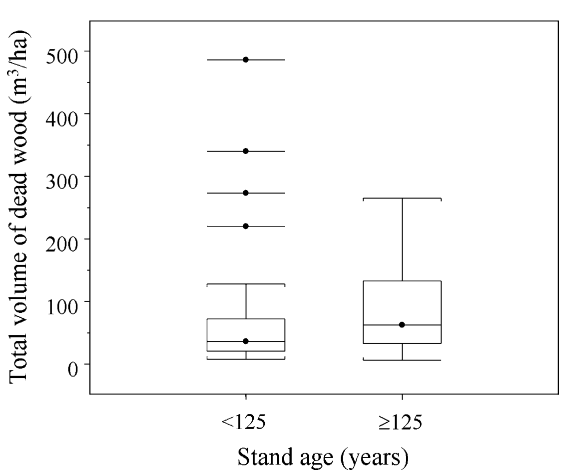

Fig. 3. Boxplots representing the total dead wood volume, subdivided in two classes of average stand age at the length of time of non-intervention.

and were 53, 95 and 26 m^3 ha^{-1}, respectively. A gradual increase in the amount of dead wood as the non-intervention time interval increased was evident (Fig. 1). The range of values was particularly high and unevenly distributed in the first 25 years of non-intervention. After 50 years and beyond, the distribution was more balanced and there were fewer outliers.

Both oak and beech showed strong differences between mean and median values illustrating a left-skewed distribution. The median value for oak was lower than for beech but of the same order of magnitude. However, the interquartile range was much higher in beech and was unequally distributed. The upper quartile and maximum values were quite different: 120.5 and 486.0 m^3 ha^{-1} for beech and 62.4 and 209.0 m^3 ha^{-1} for oak. Lower quartiles and minima on the other hand were comparable. The increase of the total dead wood volume appeared to be a more steady and balanced process for the oak-compared to the beech-dominated sites.

The GLS model (Table 2) confirmed that the variance of the total amount of dead wood was significantly larger in beech than in oak forests (beech = 1; oak = 0.663, respectively). As data was incomplete for some of the tested variables, only 87 of the 109 samples could be used in this analysis. Tree genus and stand age at the time of assignation of non-intervention, the length of time of non-intervention, and the interaction between tree genus and geographical location (North-western versus Central Europe) were significant variables which explain the total amount of dead wood. All other interactions and the site fertility factor did not appear to have a significant effect on the amount of dead wood recorded. The corresponding linear model (with a fixed variance structure) resulted in a multiple *R*-squared value of 0.51.

Tree genus and the interaction between tree genus and geographical location were significant factors affecting the total amount of dead wood. Total dead wood was significantly greater in beech than in oak stands. Median values for North-western beech stands were markedly greater than for beech stands in Central Europe and also the spread of values was clearly different (Fig. 2).

Table 2
GLS models for total dead wood amount and accumulation rate and GLM model for lying to total dead wood ratio.

GLS-model: LogDEADT ~ AGE + TIME + TREE + LOCATION + TREE:LOCATION
Parameter estimate of variance function: Fagus = 1; Quercus = 0.6633

Coefficients	Value	S.E.	*t*-Value	*p*-Value
Intercept	2.292000	0.269539	8.503422	<0.0001
AGE	0.007396	0.001612	4.587713	<0.0001
TIME	0.017120	0.002871	5.963933	<0.0001
TREE	0.206533	0.075403	2.739072	0.0076
LOCATION	0.071844	0.073190	0.981614	0.3292
TREE:LOCATION	0.351292	0.073519	4.778236	<0.0001

GLS-model: LogACCU ~ AGE + TREE + LOCATION + TREE:LOCATION
Parameter estimate of variance function: Fagus = 1; Quercus = 0.5952

Coefficients	Value	S.E.	*t*-Value	*p*-Value
Intercept	0.768236	0.202834	3.787505	0.0003
AGE	0.009498	0.001512	6.282741	<0.0001
TREE	0.203331	0.076483	2.658501	0.0094
LOCATION	0.207103	0.074234	2.789847	0.0066
TREE:LOCATION	0.366134	0.073957	4.950652	<0.0001

GLM-model: $LYING^2$ ~ TIME + TREE + TIME:TREE

Coefficients	Value	S.E.	*t*-Value	*p*-Value
Intercept	3534.0183	448.5739	7.8783	0.0000
TIME	23.6266	9.5450	2.4753	0.0156
TREE	2324.9926	448.5739	5.1831	0.0000
TIME:TREE	27.4825	9.5450	2.8792	0.0052

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In contrast, median values and variance for oak in the two geographical regions were similar and equivalent to beech in Central Europe.

The model confirmed that the total amount of dead wood was significantly influenced by the length of time of non-intervention and by the average age of the stand when regular silvicultural management ceased. Stands that were <125 years old when non-intervention was initiated had smaller amounts of dead wood than older stands (Fig. 3). However a wide variation in values occurred and some of the middle-age-range stands had high values that were associated with catastrophic storm events.

3.2. Average accumulation rate

Similar to the total amount of dead wood, the distribution of average accumulation rate over all sites was skewed, with many low values and a limited number of extremely high values. The average accumulation rate ranged between <0.1 and 19 $m^3\ ha^{-1}\ year^{-1}$, the median value was 1.64 $m^3\ ha^{-1}\ year^{-1}$; 75% of the sites had accumulation rates of ≤3 and one out of four sites <1 $m^3\ ha^{-1}\ year^{-1}$.

The GLS fit by REML after correction for differences in variance between tree genus (beech = 1; oak = 0.59) was applied to the same 87 samples as for total dead wood. The same variables were tested except for 'length of time of non-intervention', as it is directly related to accumulation rate. Tree genus, geographic location, and their interaction, and age of the stand at the time of non-intervention significantly affected the accumulation rate. The corresponding linear model with a fixed variance structure resulted in a multiple R-squared value of 0.48.

Dead wood accumulation was significantly faster in beech than in oak forests. In North-western Europe, the median accumulation rate for beech was markedly higher than in Central Europe; this difference was more pronounced for the higher accumulation rates, with upper quartile values of 6.62 and 2.87 $m^3\ ha^{-1}\ year^{-1}$, respectively. All outlying high values were situated in North-western Europe. For oak, accumulation rates were similar to those for beech in Central Europe; the median values and variance were similar in Central and North-western Europe. The average age of the oak and beech stands at the onset of non-intervention was positively related to the expected accumulation rate of dead wood. This pattern is somewhat blurred in the beech stands, as the dataset contains some middle-age beech stands in the UK that were severely damaged by an exceptional storm event in 1987.

3.3. Ratio of lying dead wood volume to the total dead wood volume

There was a difference in the ratio of lying to total dead wood volume with tree genus. In beech, this ratio was constant at about 75% regardless of the length of time of non-intervention and geographical location. In oak, the ratio increased from <50% in recently assigned to 75% in the long-established reserves (Fig. 4). The GLM confirmed that tree genus, length of time of non-intervention and the interaction between these two variables were the significant factors affecting this ratio; geographic location was not significant. The linear model gave a multiple R-squared value of 0.32.

4. Discussion

Virgin forests no longer exist in the North-western and Central European lowlands. Forests in these regions have been altered and intensively managed since prehistoric times. Their dynamics, when left unmanaged, are influenced by ageing, mortality, decay and catastrophic events, but also by their current structure as a result of management history. In this study, most sites had only recently been withdrawn from regular management (mean value 35 years). Their dynamics appeared to be more unidirectional and successional, rather than cyclical as in virgin forests.

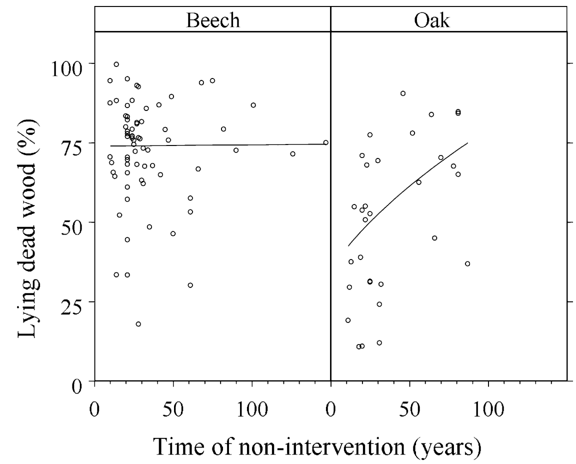

Fig. 4. Scatterplot of the ratio of lying to total dead wood subdivided for beech and oak-dominated forest reserves. The line represents the fitted linear model.

4.1. Limitations of this study

The dataset was compiled from different sources using different methodologies. This is often the case in such meta-analyses, and should not be problematic provided all sources produce reliable and comparable data (cfr. also Christensen et al., 2005). For inclusion in this study, the methodology had to conform with European standards on sample size and diameter thresholds (Hochbichler et al., 2000). However an important but unavoidable inconsistency was the threshold diameter for dead wood inventory that ranged from 5 to 20 cm. Compared to other variables such as stand density, dead wood volume is less affected by size thresholds. It is therefore considered a robust descriptor for comparisons between stands (Peterken, 1996; Nilsson et al., 2003; Piovesan et al., 2005) and it was considered that the differences in diameter thresholds between countries would not affect the results. A harmonisation of the diameter threshold (see Section 2) did not significantly change the outcomes from this study.

This study focused on quantity of dead wood and not qualitative aspects such as size distribution and decomposition classes. Dead wood of larger dimensions and advanced decomposition status has a greater capacity to support a variety of species and contains the majority of threatened species (Speight, 1989; Hekhuis et al., 1994; Rauh, 1993; Siitonen and Martikainen, 1994; Høiland and Bendiksen, 1997; Grove, 2002; Heilmann-Clausen and Christensen, 2003; Christensen et al., 2005; Odor et al., 2006). In the more recently assigned unmanaged forest reserves this type of dead wood was generally absent or underrepresented (Vandekerkhove et al., 2005; Odor et al., 2006).

Another limitation was the timeframe involved when considering deadwood accumulation. Most samples had a short non-intervention period of <30 years. This is well below the general lifespan of beech and oak trees that for Central European montane forests is estimated at 200–250 and 300–350 years, respectively (Korpel, 1995); in extreme montane conditions, beech may live for >500 years (Biondi, 1993; Bourquin-Mignot and Girardclos, 2001; Piovesan et al., 2003, 2005). In the more temperate Central and North-western European lowlands the life cycle of beech may extend to 300 years, but older stands are likely to collapse (Von Oheimb et al., 2007; Rademacher et al., 2001; Rademacher and Winter, 2003). As not all age classes were well represented in this study, and the covered timeframe was relatively small, conclusions regarding long term dynamics may be speculative to a certain degree (see also Pontailler et al., 1997) and the predictive value of the models limited, especially in the higher age and time-period classes.

As limited information was available on age structure, only the average age of the dominant tree layer was used in this analysis. However, as discussed later, age- and/or diameter distribution may play an important role in the dynamics of the system.

4.2. Dead wood volume and accumulation

Compared to virgin beech and oak forests in Europe and elsewhere, dead wood volumes were low as the accumulation process is still ongoing. Christensen et al. (2005) reported an average value of 132 $m^3 ha^{-1}$ for virgin and long-established lowland and montane European beech forest reserves; other studies in beech indicate a natural range of 50–200 $m^3 ha^{-1}$ (Koop, 1989; Leibundgut, 1993; Korpel, 1995; Saniga and Schütz, 2001a; Meyer et al., 2003). Virgin oak forests in Poland and Slovakia have values of between 70 and 160 $m^3 ha^{-1}$ (Bobiec, 2002; Korpel, 1997) and Tennessee oak-beech forests 82–132 $m^3 ha^{-1}$ (Harmon et al., 1986). In this study, sites left unmanaged for <50 years had 10 to 75 m^3 of dead wood. Only after approximately 60–80 years could unmanaged forest reserves accumulate volumes of dead wood comparable to virgin forests. Peterken (1996) postulates that accumulation of 'near natural' volumes of dead wood can occur within a century. On many sites however, the accumulation rate appeared to be much slower with <50 $m^3 ha^{-1}$ of dead wood accumulated after several decades of non-intervention.

The age of the stand at the onset of non-intervention, tree genus, geographic location and the interaction between the last two factors were significant in explaining the amount of dead wood and the accumulation rate. Mortality rate and dead wood recruitment increase as mature trees age and become more vulnerable to disease and physical instability (Harmon et al., 1986; Harcombe, 1987 in Peterken, 1996). The lowest mortality rates correspond with mature vigorous trees of around 40–70 cm DBH (Parker et al., 1985). Most samples in our study were dominated by mature trees within this age and DBH-range at the time of reserve assignation, hence their slow accumulation rate of dead wood. Sites in older age classes had higher accumulation rates and in some overmature stands near their natural age limit, dead wood amounts comparable to virgin forests were achieved within one or two decades of non-intervention (Vandekerkhove et al., 2005; Von Oheimb et al., 2005, 2007). However, there were also high values for mature-aged stands on steep chalk slopes in the UK that were severely damaged by an exceptional storm event in 1987 (Mountford and Ball, 2004; Mountford and Groome, 2004).

The process of dead wood accumulation differed between beech and oak forests. In oak forests, dead wood accumulation appeared to be a steady process; in beech forests, the process was more irregular with higher overall values, especially in North-western Europe. This interaction between tree genus and geographic location appears to be related to the effect and incidence of severe storm events. There is a greater frequency of windstorms in North-western than Central Europe (e.g. Leckebusch et al., 2006; Della-Marta et al., 2009), that may lead to more windthrow and larger gap sizes, especially in shallow-rooted trees such as beech. Conversely deep-rooted oak trees generally remain standing and only tend to shed crown branches during storm events (Peterken, 1996). Their stand dynamics are considered to be less influenced by different storm regimes. The assumption that differences in storm and windthrow frequency are the primary cause of differences in stand dynamics between North-western and Central Europe is also expressed in other studies (Koop and Hilgen, 1987; Pontailler et al., 1997; Parviainen et al., 2000; Christensen et al., 2005; Vandekerkhove et al., 2005), but may need reconsideration (see Section 4.4).

4.3. Ratio of lying dead wood volume to the total dead wood volume: just a matter of time

The ratio of lying to the total dead wood volume was specific to tree genus only and not influenced by geographic location and storm incidence. In beech forests this ratio was quite constant at about 75% irrespective of the period of time of non-intervention and geographical location, and similar to ratios of between 75 and 85% in virgin beech forests (Korpel, 1995, 1997; Meyer, 1999; Bobiec, 2002; Meyer et al., 2003). In Central Europe, the majority of beech trees die standing especially because of fungal attacks, and fall soon after with subsequent decay on the forest floor (Korpel, 1992; Borrmann, 1993; Peterken, 1996; Schmaltz and Lange, 1999; Saniga and Schütz, 2001a; Von Oheimb et al., 2007). In North-western Europe, death of the majority of beech trees is because of windthrow while still alive and vigorous (Mountford, 2004; Vandekerkhove et al., 2005). However, these different causes of death did not significantly influence the ratio of lying to total dead wood volume in these two regions. This is primarily determined by the total time of decay and the proportion of this time that is related to standing trees before they fall over. Trees that died standing, most often fall over within 10 years (Korpel, 1992; Schmaltz and Lange, 1999; Von Oheimb et al., 2007). The total decay time for beech is 25–50 years depending on site conditions (Koop, 1981; Korpel, 1995; Saniga and Schütz, 2001a; Müller-Using and Bartsch, 2003; Christensen et al., 2005). Thus the total decay process for beech takes up to four times longer than the period when the tree is dead but standing, resulting in this long term average ratio of 75–80%. A severe storm event may result in erratic pulses of lying deadwood (Peterken, 1996) and a temporary distortion of this ratio, but will not alter it in the long term. Christensen et al. (2005) obtained different lying to total dead wood ratios for montane (55%) and lowland (75%) beech forests and related this to different windstorm regimes. However, this difference may have been due to the presence of a larger proportion of dead but standing fir trees (*Abies alba*) in these montane beech forests (Saniga and Schütz, 2001b). If only the beech-tree component is considered, the ratios are comparable.

In oak forests, there was a steady rise in the ratio of lying to total dead wood volume from <50% in recently assigned unmanaged forest reserves to 75% in long-established reserves; geographic location did not affect the ratio. The higher values are similar to those found in virgin oak forests (Korpel, 1995, 1997; Bobiec, 2002) and the beech forests in this study. In oak forests the large majority of trees die standing (Peterken, 1996). Secure root anchorage and the slow, gradual decay process mean that standing trees take several decades to fall over. Trees of large diameter with a high amount of heartwood may then take >150 years before decay is complete (Schowalter et al., 1998). As with beech, oak trees that die standing will undergo at least 80% of their decay processes lying on the ground, resulting, in the longer term, in a similar ratio of lying to total dead wood volume. In the more recently assigned unmanaged oak forest reserves, the majority of the dead wood consists of standing trees. After several decades, initially the smaller, then the mature trees start to fall over. Although the recruitment ratio of standing versus lying dead wood remains constant, the proportion of lying dead wood will increase, as the standing dead trees fall to the forest floor. The model confirmed this steady increase of the ratio of lying to total dead wood volume for oak as a function of the length of time of non-intervention.

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4.4. Large-scale dynamics: a regional effect or otherwise?

The disturbance regime in temperate deciduous forests is characterised by a combination of frequent small-scale events caused by natural senescence, competition, disease, fungal attacks, drought, and occasional large-scale events predominantly caused by storms (Leibundgut, 1978, 1982; Prusa, 1985; Koop and Hilgen, 1987; Korpel, 1995, 1997; Mountford et al., 1999; Tabaku and Meyer, 1999; Emborg et al., 2000; Bobiec, 2002; Meyer et al., 2003; Christensen et al., 2005). In the absence of a large disturbance the death of individual or small groups of trees is the principal form of natural disturbance that provides a constant but limited supply of dead wood of different size and decay categories (Korpel, 1995; Peterken, 1996; Saniga and Schütz, 2001a; Standovar and Kenderes, 2003; Hahn and Christensen, 2004).

Fluctuations and variability in dead wood recruitment is higher for lowland and submontane unmanaged forest reserves in North-western than in Central Europe, an observation that is often related to the more frequent storm and windthrow events in Western European lowlands (Koop and Hilgen, 1987; Pontailler et al., 1997; Parviainen et al., 2000; Mountford, 2001; Christensen et al., 2005; Vandekerkhove et al., 2005). Our study appears to support this conclusion, with higher and more irregular dead wood input in the beech sites of North-western Europe. However, recent analyses of gap size in unmanaged beech forest reserves throughout Europe show little difference between regions; in both montane and lowland beech forests small gaps were the rule; those over 1000 m^2 were the exception (Mountford, 2001). Over the last decade, Central European lowland and montane sites have also been subjected to large storm events and their incidence, like in North-western Europe, is likely to increase due to climate change (Dronia, 1991; Knippertz et al., 2000; Leckebusch & Ulbrich, 2004). This resulted in large-scale windthrow events (Steinfath, 2007; Diaci and Zeibig, 2001; Rozenbergar et al., 2003; Vrska, personal communication) that are not reflected in the dataset as most measurements were taken earlier. If the exceptional windthrow event of 1997 in the UK is excluded and new windthrow records from Central Europe are included, regional differences in windstorm-induced gap dynamics become less obvious. Stochasticity and stand-age structure related to stand management more likely explain the occurrence of large-scale stand disturbances than regional differences in windstorm events (Vandekerkhove et al., 2005; Von Oheimb et al., 2007).

Virgin montane forests in Central Europe have a relatively stable age and size distribution and balanced proportions of the different developmental phases (Korpel, 1995; Peterken, 1996; Saniga and Schütz, 2001a; Standovar and Kenderes, 2003; Hahn and Christensen, 2004; Westphal et al., 2006). Most unmanaged forest reserves in the North-western and Central European lowlands originate from relatively even-aged stands, resulting from regeneration cohorts and abandoned old wood pastures (Koop, 1981, 1989; Koop and Hilgen, 1987; Peterken, 1996; Mountford et al., 1999; Schmaltz and Lange, 1999; Emborg et al., 2000; Vandekerkhove et al., 2005; Meyer et al., 2006; Von Oheimb et al., 2007). These have a more bell-shaped or two-peaked age and size class distribution of the dominant tree layers, with disproportional fractions of the developmental phases (Schmaltz and Lange, 1999; Emborg et al., 2000; Vandekerkhove et al., 2005; Meyer et al., 2006; Von Oheimb et al., 2005, 2007). When average tree age is 100–150 years, mortality and dead wood input is often low. When average tree age is 200–300 years, high proportions of senescent trees are represented and mortality and dead wood accumulation rates become much higher than average (Van Den Berge et al., 1990; Vandekerkhove et al., 2005; Von Oheimb et al., 2005, 2007). At this stage, even-aged stands may attain even higher amounts of dead wood than virgin forests (Mountford, 2002; Von Oheimb et al., 2005). It is followed by a large-scale phase of rejuvenation, when dead wood accumulation is minimal and the total amount of dead wood declines. In unmanaged forest reserves, age structure rather than geographical location will tend to determine future small or large gap dynamics. Effects of past management are likely to survive for 200 years or more in the size- and age-distribution of the trees (Peterken, 1996). It may even continue over several tree generations and still be detectable after 500 years and more (Koop, 1989; Von Oheimb et al., 2007). The theoretical model of dynamic equilibrium and steady state over larger areas might not be realised in most of the unmanaged forest reserves even after many centuries of non-intervention. Instead, an undulating sequence of rejuvenation cycles and dead wood pulses can be expected.

Appendix A

See Table A1.

Table A1
Summary details for all sites included in this study.

Reserve name	Country	Survey type	Date of recording	Lying dead wood (m^3/ha)	Standing dead wood (m^3/ha)	Total dead wood (m^3/ha)	Ratio lying dead wood (%)	Living volume (m^3)	TAB (m^3)	Ratio dead to TAB (%)	Accumulation rate (m^3/ha year)	Geographic location	Dominant tree species	Fertility	Elevation (m a.s.l.)	Average age (years)	Time of non-intervention (years)	Source
Bos Ter Rijst	B	CP	2005	14.8	12.1	26.9	55.0	493	520	5.2	1.13	NW	Q	R	70	128	22	Unpublished data
Bos Ter Rijst	B	CA	2005	31.8	30.9	62.7	50.7	628	690	9.1	2.76	NW	Q	R	70	128	22	Unpublished data
Bos Ter Rijst	B	LT	1996	9.8	16.6	26.4	37.1	267	293	9.0	1.88	NW	Q	R	70	137	13	Unpublished data
Hallerbos-Jansheide	B	CP	2006	2.3	5.5	7.8	29.5	424	431	1.8	0.48	NW	Q	R	100	58	12	Unpublished data
Jongenbos	B	CA	2006	9.0	8.0	17.0	47.1	305	322	5.3	1.15	NW	Q	P	60	147	13	Unpublished data
Kluisbos	B	CA	2006			35.0		500	535	6.5	3.00	NW	F	R	80	109	11	Unpublished data
Kolmont	B	CA	2006	19.0	36.0	55.0	65.5	375	430	12.8	2.04	NW	F	r	60	154	26	Unpublished data
Kolmont	B	LT	1994	16.0	31.9	47.9	33.4	327	375	12.8	3.28	NW	F	R	60	166	14	Unpublished data
Parikebos	B	LT	1993	14.0	3.0	16.8	83.3	360	377	4.5	1.14	NW	F	R	70	107	13	Unpublished data
Rodebos	B	CA	2001	3.0	5.0	8.0	37.5	422	430	1.9	0.46	NW	Q	P	80	87	13	Unpublished data
Wijnendalebos	B	CA	2003	3.6	29.4	33.0	10.9	392	425	7.8	1.55	NW	Q	P	30	130	20	Unpublished data
Wijnendalebos	B	CP	2003	12.2	10.5	22.7	53.7	406	429	5.3	1.04	NW	Q	P	30	130	20	Unpublished data
zonien kernvlakte 1991	B	CA	1991	112.5	6.6	119.1	94.5	634	753	15.8	11.71	NW	F	R	100	220	10	Van Den Berge et al. (1990)
zonien kernvlakte 2000	B	CA	2001	115.9	22.7	139.0	83.4	792	931	14.9	6.85	NW	F	R	100	205	20	De Keersmaeker et al. (2002)
Zonien-Harras	B	LT	1996	2.4	10.2	12.6	19.0	450	467	2.7	0.96	NW	Q	R	80	179	11	Unpublished data
Neunkirch	CH	LT	1999	51.0	6.0	57.0	89.5	470	527	10.8	1.12	C	F	R			49	Christensen et al. (2005)
Sihlwald	CH	CA	2000			8.0		516	524	1.5	0.60	C	F	R	650	140	10	Commarmot et al. (2005)
Cahnov-Soutok	CZ	CA	1994	93.5	39.5	133.0	70.3	549	682	19.5	1.87	C	Q	R	150	130	70	Vrška et al. (2006)
Jirina	CZ	CA	1999	71.0	87.0	158.0	44.9	588	746	21.2	2.36	C	Q	R	165	154	66	Vrška et al. (2006)
Ranspurk	CZ	CA	1995	105.3	20.3	125.6	83.8	586	711	17.7	1.93	C	Q	R	150	156	64	Vrška et al. (2006)
V kluci	CZ	CA	2000	169.0	54.0	223.0	75.8	681	904	24.7	4.70	C	F	R			47	Christensen et al. (2005)
Altes Gehege	D	CP	2003			12.0		494	506	2.4	0.24	C	Q	P	60	59	41	Meyer et al. (2006)
Bechtaler Wald	D	CP	1995	21.0	46.0	67.0	31.3	314	381	17.6	2.60	C	Q	R	170		25	Bücking (1996)
Braken	D	CP	2004	8.0	9.0	17.0	47.1	425	442	3.8	1.00	C	Q	R	40	135	15	Meyer et al. (2006)
Brand	D	CP	1997			30.0		530	560	5.4	1.22	C	Q	R	40	127	23	Meyer et al. (2006)
Buchheide-zechlin	D	CA	2005	59.4	28.3	87.7	67.7	445	533	16.5	2.32	C	F	P	100	233	37	Rüffer (2007)
eisgraben	D	CA	1999	139.0	38.0	177.0	78.5	774	951	18.6	8.33	C	F	R	700	159	21	Kölbel (1999)
Elsbach	D	CA	1999	19.0	10.0	29.0	65.5	562	591	4.9	1.29	C	F	R	600		21	Kölbel (1999)
Fauler Ort	D	CA	2005	126.0	33.0	159.0	79.2	363	522	30.5	1.91	C	F	R	200	238	82	Rüffer (2007)
Franzhorn	D	CA	1997	14.0	31.0	45.0	31.1	529	574	7.8	1.72	C	Q	P	40	115	25	Meyer et al. (2006)
Franzhorn	D	CP	1996	10.6	4.0	14.6	72.5	598	613	2.4	0.53	C	F	P	30	136	24	Unpublished data
Friedeholz	D	CA	1997	36.0	17.0	53.0	67.9	387	440	12.0	2.22	C	Q	R	45	177	23	Meyer et al. (2006)
Gitschger	D	CA	1999	94.0	41.0	135.0	69.6	640	775	17.4	6.33	C	F	R	650		21	Kölbel (1999)
Gr. Freden	D	CP	2004	7.1	4.8	11.9	59.6	814	826	1.4	0.31	C	F	R	225	98	32	Unpublished data
Grosser Staufenberg	D	CA	2000	18.7	1.5	20.2	92.6	588	608	3.3	0.65	C	F	R	520	112	28	Unpublished data
Grosser Staufenberg	D	CP	1999	25.9	6.8	32.7	79.2	503	535	6.1	1.14	C	F	R	520	113	27	Unpublished data
grubenhau	D	CP	1997	47.0	22.0	69.0	68.1	604	673	10.3	2.48	C	F	R	530		27	Christensen et al. (2005)
Hainich	D	CP	2002	42.0	22.0	64.0	65.6	567	631	10.1	5.17	C	F	R			12	Christensen et al. (2005)
Hasbruch – altes Reservat	D	CA	1994	56.1	61.9	62.0	90.5	401	463	13.4	1.30	C	Q	R	20	94	46	Meyer et al. (2006)
Heilige Hallen	D	CP	1999	97.0	88.0	185.0	52.4	506	691	26.8	3.00	C	F	R	130	279	61	Tabaku and Meyer (1999)
Herrenholz	D	CA	2004	14.0	32.0	46.0	30.4	422	468	9.8	1.38	C	Q	R	46	128	32	Meyer et al. (2006)
Herrenholz	D	CP	1991	13.0	25.0	38.0	34.2	486	524	7.3	1.89	C	Q	R	46	141	19	Meyer et al. (2006)
Hoher Knuck	D	CA	1999	79.0	16.0	95.0	83.2	576	671	14.2	4.43	C	F	R	450		21	Kölbel (1999)
Hoxfels	D	CP	2000	10.0	46.0	56.0	17.9	360	416	13.5	1.93	C	F	R	300		28	Christensen et al. (2005)
Hühnstollen	D	CA	1996	13.7	5.3	19.0	72.3	576	595	3.2	0.65	C	F	R	400	109	26	Unpublished data
Junkerwerder	D	CP	2002	16.0	17.0	33.0	48.5	428	461	7.2	1.24	C	Q	R	12	145	25	Meyer et al. (2006)
Kalkberg	D	CA	1999	8.0	6.0	14.0	57.1	734	748	1.9	0.57	C	F	R	700		21	Kölbel (1999)
Karlswörth	D	CP	1990	41.0	18.0	59.0	69.5	623	682	8.7	2.85	C	Q	R	80	160	20	Althoff et al. (1993)
Kitschenthalrangen	D	CA	1999	21.0	6.0	27.0	77.8	655	682	4.0	1.19	C	F	R	450		21	Kölbel (1999)
Königsbuche	D	CA	1996	57.5	17.2	74.7	77.0	616	691	10.8	3.03	C	F	R	230	86	24	Unpublished data
Landwehr	D	CP	1996	50.7	23.7	74.4	68.1	434	509	14.6	2.41	C	Q	P	15	110	30	Unpublished data

Leitenwies	D	CA	1999	50.0	21.0	71.0	70.4	737	808	8.8	3.29	C	F	P	400		21	Kölbel (1999)
Limker Strang	D	CA	2003	15.6	5.7	21.3	73.2	500	522	4.1	0.62	C	F	P	400	119	31	Unpublished data
Limker Strang	D	CA	2003	17.1	10.4	27.6	62.1	545	572	4.8	0.82	C	F	P	400	119	31	Unpublished data
Lohn	D	CA	1996	27.9	7.3	35.2	79.2	707	742	4.7	1.38	C	F	R	70	96	24	Unpublished data
Lösershag	D	CA	1999	25.0	16.0	41.0	61.0	651	692	5.9	1.86	C	F	R	650		21	Kölbel (1999)
Lüssberg	D	CA	1996	4.9	1.5	6.4	76.4	337	343	1.9	0.18	C	F	P	130	146	24	Unpublished data
Meinsberg	D	CP	2003	16.3	4.3	20.6	79.0	815	836	2.5	0.62	C	F	R	320	105	30	Unpublished data
Meinsberg	D	CA	2002	20.5	6.4	26.9	76.2	799	826	3.3	0.86	C	F	R	320	106	29	Unpublished data
Neuenburg	D	CA	2000	163.0	46.0	209.0	78.0	488	697	30.0	3.98	C	Q	R	7	128	52	Meyer et al. (2006)
Nordahner Holz	D	CA	2003	9.5	29.8	39.2	24.1	609	648	6.1	1.20	C	Q	P	6	109	31	Unpublished data
Nordahner Holz	D	CA	2003	8.6	63.6	72.2	12.0	518	591	12.2	2.27	C	Q	R	6	109	31	Unpublished data
Platzer Kuppe	D	CA	1999	105.0	49.0	154.0	68.2	638	792	19.4	7.24	C	F	R	650	159	21	Kölbel (1999)
ruppiner Schweiz	D	CA	2005	30.3	7.6	37.9	79.9	627	665	5.7	1.80	C	F	R	200	80	20	Rüffer (2007)
Schlossberg	D	CA	1999	4.0	5.0	9.0	44.4	554	563	1.6	0.33	C	F	R	600		21	Kölbel (1999)
Schneetal	D	CA	1999	13.0	2.0	15.0	86.7	655	670	2.2	0.62	C	F	R	550		21	Kölbel (1999)
Seeben	D	CA	1996	7.0	58.0	65.0	10.8	603	668	9.7	3.50	C	Q	R	530	122	18	Kölbel (1999)
Serrahn	D	CA	2002	61.0	33.0	94.0	64.9	603	697	13.5	2.19	C	F	P	100	158	42	Von Oheimb et al. (2007)
sommerberg	D	CP	1995	24.0	7.0	31.0	77.4	333	468	6.6	1.16	C	Q	R	350	145	25	Bücking (1998)
Stechpalmenwald	D	CP	2005	18.7	3.6	22.2	83.9	370	392	5.7	0.61	C	F	P	110	127	33	Unpublished data
Stöberhei	D	CA	2000	36.0	21.0	57.0	63.2	622	679	8.4	1.83	C	F	R			30	Christensen et al. (2005)
Süsing	D	CP	1996	4.0	8.0	12.0	33.3	416	428	2.8	0.20	C	F	R	100	70	50	Meyer et al. (2006)
swartzwihrberg	D	CA	1999	60.0	13.0	73.0	82.2	876	949	7.7	3.38	C	F	R	650		21	Kölbel (1999)
Vilm	D	CP	1997	44.0	109.0	153.0	28.8	561	714	21.4	2.48	C	F	P	5	239	61	Schmaltz and Lange (1999)
Vogelherd	D	CA	1999	32.6	2.5	35.1	93.0	480	515	6.8	1.22	C	F	P	490	133	27	Unpublished data
Vogelherd	D	CP	1996	21.4	3.2	24.6	86.9	443	468	5.3	0.94	C	F	P	490	136	24	Unpublished data
Waldhaus	D	CA	1999	115.0	6.0	121.0	95.0	780	901	13.4	5.67	C	F	R	400	159	21	Kölbel (1999)
Wasserberg	D	CA	1999	4.0	8.0	12.0	33.3	518	530	2.3	0.48	C	F	R	400		21	Kölbel (1999)
Weichel	D	CP	2002	8.0	10.0	18.0	44.4	514	532	3.4	1.00	C	F	P	30	124	16	Meyer et al. (2006)
Weiherbuchet	D	CA	1999	20.0	6.0	26.0	76.9	646	672	3.9	1.14	C	F	R	600		21	Kölbel (1999)
Fauler Ort	D	CA	1968	53.0	14.0	67.0	79.1	335	402	16.7	1.44	C	F	R	200	235	45	Rüffer (2007)
Knagerne	DK	LT	2003	56.0	31.0	87.0	64.4	449	536	16.2	6.54	NW	F	P	80	237	13	Christensen et al. (2005)
Moens klinteskoven	DK	LT	2001	48.0	24.0	72.0	66.7	201	273	26.4	1.06	NW	F	R	90	134	66	Christensen et al. (2005)
Stroedam	DK	LT	1983	101.0	38.0	139.0	72.7	490	629	22.1	4.03	NW	F	R	20	166	34	Christensen et al. (2005)
Suserup Skov	DK	LT	2002	154.0	9.0	163.0	94.5	674	837	19.5	2.15	NW	F	R	20	155	75	Christensen et al. (2005)
velling	DK	LT	2001	68.0	31.0	99.0	68.7	489	588	16.8	8.82	NW	F	P	75	264	11	Christensen et al. (2005)
Fontainebleau	F	CA	2000	165.0	55.0	220.0	75.0	260	480	45.8	1.48	NW	F	R	130	33	147	Christensen et al. (2005)
La Massane	F	CA	1998	25.0	8.0	33.0	75.8				1.24	NW	F	R			25	Christensen et al. (2005)
alsohegy	HU	LT	2001	23.0	17.0	40.0	57.5	284	324	12.3	0.62	C	F	R			61	Christensen et al. (2005)
kekes	HU	LT	2001	92.0	14.0	106.0	86.8	454	560	18.9	1.03	C	F	R	700	49	101	Christensen et al. (2005)
öserdö	HU	LT	2001	152.0	23.0	175.0	86.9	765	940	18.6	4.22	C	F	R	700	159	41	Christensen et al. (2005)
dassenberg	NL	LT	2000	43.0	18.0	61.0	70.5	402	463	13.2	5.90	NW	F	R		140	10	Christensen et al. (2005)
Gortel	NL	LT	2000	56.0	8.0	64.0	87.5	507	571	11.2	6.20	NW	F	R		140	10	Christensen et al. (2005)
Pijpebrandje	NL	LT	2000	32.0	11.0	43.0	74.4	457	500	8.6	1.64	NW	F	R	50	125	25	Christensen et al. (2005)
Vijlenerbos	NL	CP	1996			34.8		304	338	10.3	2.52	NW	F	P	250	107	13	Mountford (2004)
Bieszczady	PL	CA	2000	148.0	34.0	182.0	81.3	596	778	23.4	6.67	C	F	R			27	Christensen et al. (2005)
Las lipowy Obrozyska KV1	PL	CA	2000	32.5	17.5	50.0	65.0	768	818	6.1	0.59	C	Q	R	550	99	81	Jaworski et al. (2005)
Las lipowy Obrozyska KV2	PL	CA	2000	50.0	9.0	59.0	84.7	860	919	6.4	0.70	C	Q	R	550	99	81	Jaworski et al. (2005)
Las lipowy Obrozyska KV3	PL	CA	2000	48.0	9.0	57.0	84.2	761	818	7.0	0.68	C	Q	R	550	99	81	Jaworski et al. (2005)
Clairinsh	UK	LT	2000	7.0	12.0	19.0	36.8				0.20	NW	Q	P	10	3	87	Mountford (2004)
Dendles wood	UK	LT	2000	62.0	66.0	128.0	48.4				3.60	NW	F	p	50	115	35	Mountford (2004)
Denny Enclosure – New Forest	UK	LT	1996	195.0	78.0	273.0	71.4				2.15	NW	F	P	30	124	126	Christensen et al. (2005)
Lady Park Wood – old growth	UK	LT	1995	67.5	25.5	93.0	72.6				1.01	NW	F	R	50	50	90	Green and Peterken (1997)
Langley wood	UK	LT	1996	15.0	9.0	24.0	62.5				0.39	NW	Q	R	50	24	56	Mountford et al. (1998)
Monks Wood	UK	LT	1998	25.0	9.2	37.0	67.6	160	197	18.8	0.45	NW	Q	R	30	12	78	Mountford (2004)
Noar Hill Hanger	UK	CA/LT	2001	300.0	40.0	340.0	88.2	113	453	75.0	16.79	NW	F	R	200	106	14	Christensen et al. (2005)
Ridge Hanger, Ashford Hangers	UK	CA/LT	2001	264.0	1.0	265.0	99.6	66	331	80.0	18.79	NW	F	R	200	121	14	Christensen et al. (2005)
Scords wood, Toy's Hill	UK	CA	1998	456.0	30.0	486.0	93.8	50	536	90.7	7.12	NW	F	P	220	52	68	Christensen et al. (2005)
The Mens	UK	LT	1998	88.0		115.0	76.5				4.04	NW	F	R	35	142	28	Mountford (2004)

TAB = total aboveground biomass; LT = line transect; CA = core area; CP = circular plot sampling; C = Central Europe; NW = North-western Europe; F = beech (Fagus); Q = oak (Quercus); P = poor; R = rich.

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