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Dead wood in European beech (Fagus sylvatica) forest reserves

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Abstract

Data was analysed on the volume of dead wood in 86 beech forest reserves, covering most of the range of European beech forests. The mean volume was 130 m^3/ha and the variation among reserves was high, ranging from almost nil to 550 m^3/ha. The volume depended significantly on forest type, age since reserve establishment, and volume of living wood. More dead wood was found in montane (rather than lowland/submontane) reserves, longer-established reserves (time since designation), and reserves with higher volumes of living wood.

On average, fallen dead wood contributed more to the total dead wood volume than standing dead wood. The percentage of dead wood that was standing was almost twice as high in montane than in lowland/submontane forest reserves (45% versus 25%). The volume of dead wood volume at selected sites changed considerably over time. The fluctuations were significantly higher in lowland/submontane than montane reserves, possibly connected with differences in the disturbance regimes and especially damage caused by windstorms. In NW Europe the blow down of formerly managed, even-aged stands led to extraordinary high volumes of dead wood shortly after reserve establishment.

The implications for forest management and biodiversity conservation are discussed. An increase in dead wood volumes must be carried out in accordance with the local/regional forest type and disturbance regime. Thus, in order to fulfil the requirements of as many wood-depending organisms as possible, it is important to preserve not only larger amounts of dead wood, but also dead wood of different types and dimensions as well as securing a long-term continuity of dead wood.

Keywords: biodiversity, coarse woody debris, CWD, Fagus sylvatica L., indicator, nature-based forest management, sustainability

1. Introduction

Dead wood is an important component in natural forests. It is widely regarded as an important aspect of forest biodiversity forming key habitats for many species. For example invertebrates, fungi, bryophytes, lichens, birds and mammals depend on or utilise dead wood as a source of food or shelter (Maser and Trappe 1984, Harmon et al. 1986, Ferris-Kaan et al. 1993, Samuelsson et al. 1994, Esseen et al. 1997, Siitonen 2001). Fallen dead wood and stumps provide nurse logs for regeneration in cool temperate, boreal and sub-montane forest types (Eichrodt 1969, Hofgaard 2000, Takahashi et al. 2000). Dead wood influences the forest microclimate and can act as an important water-storing element during dry periods (Maser and Trappe 1984, Harmon et al. 1986). Dead wood is also an important long-term nutrient storage (Harmon et al. 1986, Keenan et al. 1993), the carbon content adds significantly to the overall carbon storage of forest ecosystems (Harmon 2001), and the humification process secures a continuous supply of organic material to the soil (Schaetzl et al. 1989). If dead wood is a management goal, the factors influencing the quantity, quality, and dynamics need to be identified (Rubino and McCarthy 2003).

Dead wood 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 and Peterken 1997, Kirby et al. 1998, Ódor and Standovár 2001, Winter and Nowak 2001). In addition, dead wood in managed stands typically consists only of small twigs and branches and short stumps, with few large logs or snags found (Kruys et al. 1999). In the interest of sustainable forestry and biodiversity conservation, efforts are being made to increase dead wood levels in managed forests (e.g. Hodge and Peterken 1998, Harmon 2001). In Europe, the volume of standing and fallen dead wood is one of nine pan-European indicators for sustainable forest management (Criterion 4: Maintenance, conservation and appropriate enhancement of biological diversity in forest ecosystems) (MCPFE 2003).

In contrast to North America and the boreal zone of Europe, where natural dead wood levels have been reviewed thoroughly (Harmon et al. 1986, Siitonen 2001), there is no such review for the beech and mixed-beech forests of temperate Europe, in which Fagus sylvatica L. is a dominant or co-dominant tree. Because beech forests are widespread and represent the potential natural vegetation of many areas of the lowlands of NW and NC Europe (up to S Sweden) and the mountains of C, S, and E Europe (Ellenberg 1996, Jahn 1991), it is of interest to analyse and estimate the natural dead wood volumes in these forests. However, suitable natural forest reference sites are scarce within the beech forest zone (Peterken 1996, Parviainen et al. 1999, Diaci 1999), particularly in the lowlands where no untouched forests have survived and very few sites have been strictly protected for more than a few decades. In contrast, in the mountains of C and E Europe there are several surviving ‘virgin’ reserves and strict forest reserves tend have a longer protection history and were less influenced by human activity before designation: these reserves therefore provide a better reference for the natural level of dead wood (Korpel 1995, Prusa 1985, Standovár and Kenderes 2003). This paper aims to redress this imbalance in knowledge by presenting a review of data on dead wood levels in ‘natural’ beech forests reserves from around Europe. Such information is of great interest for conservationists, forest managers and policy-makers.

2. Materials and Methods

Information about dead wood was gathered in two ways. Firstly, measurements of dead wood were made in 18 beech forest reserves in Denmark, England, France, The Netherlands, Hungary and Slovenia, during 2000-2002. The volume of dead wood was estimated by one of three sampling methods: line-intersect sampling (see Warren and Olsen 1964 and Kirby et al. 1998 for description of the method), grid point sampling (systematic or randomised grid with complete inventories in concentric circles at grid intersections), or complete enumerations within permanent plots. Data on the living volume of trees based on diameter and height measurements were similarly collected for most sites. Secondly, a literature review was made of other studies of dead wood levels in European beech forest reserves. These two sets of information were combined in a database of 86 reserves covering most of the distributional range of beech forests in Europe (Figure 1).

For each sample (some sites had more than one sample), information on climatic conditions, species composition, forest type, sampling methods, minimum diameters, recent disturbance, standing volume of live trees, snag volume (dead standing trees), and log volume (dead fallen trees and stumps) was compiled. Only reserves where beech made a major contribution (at least 17%) to the standing volume were included in the analyses. Newly established forest reserves with a dead wood volume of <5 m^3/ha were also excluded. Summary details of all sites and methods used are given in Table 1.

The minimum diameter used to measure dead wood differed between the sites, and this appeared to have substantially influenced the estimate of the dead wood volume (see Figure 2). Therefore, the volume for each site was adjusted to a standard minimum diameter of 5 cm using of the regression: $Volume_{5\ cm} = Volume_{x\ cm} * (0.0279*diameter_{x\ cm}+0.8301)$ (Figure 2). This equation was based on data from a total of 11.9 km line transects with 2,783 intersections from 13 forest reserves in Denmark, England, France and Hungary (Christensen et al. 2003). The living wood volume was not standardised due to difficulties in obtaining detailed information on the effect of various minimum diameters.

All of the reserves included were classified as either: 'Lowland/submontane beech forests (F5a)' or 'Montane beech/mixed beech-fir-spruce forests (F5b)' based on the BEAR-classification (Larsson 2001) and the General Map of Natural Vegetation of Europe (Bohn & Katenina 1996). The forest reserves were also classified as either 'recently-established' (< 50 years ago) or 'long-established' (> 50 years ago), based on the time since official protection as a strict forest reserve managed by minimum-intervention and without removal of dead wood. Dividing the reserves in these two ways produced: 16 long-established montane reserves; 20 long-established lowland/submontane reserves; 6 recently-established montane reserves; and 42 recently-established lowland/submontane reserves.

We first analysed the relative influence of reserve age (recently-established versus long-established) and forest type (lowland/submontane versus montane) on the total dead wood volume (m^3/ha), snag volume (m^3/ha), and log volume (m^3/ha). Based on the presence of interactions we described the pattern of total dead wood volume and that in snags and logs across forest types and reserve classes. We then tested the relationship between living and dead wood volume using general linear models (proc glm, SAS 1999-2000). A model predicting the response of dead wood volume, snag volume, and log volume to the explanatory variables that included forest type, living wood volume, reserve age and their interactions was tested. For certain analyses, some sites could not be included because, for example, the dead wood volume was not separated into snags and logs. Finally we analysed changes in dead wood over time, using measurements from twenty of the oldest reserves that had two or more measurements of dead wood over at least a ten year period. The mean and variation of relative changes in dead wood volume were tested using a student t-test and Cochran Q test for approximate variance probabilities for datasets with unequal variances.

3. Results

3.1 Description of forest reserves

The 86 forest reserves in the database represented a wide range of forests types in which beech is an important tree. The lowland and submontane forests mainly occupied sites up to 700m altitude, but a few were as high as 825m. They mainly comprised deciduous mixtures of beech, oak (Quercus petraea/robur), ash (Fraxinus excelsior), and/or maple (Acer pseudoplatanus, A. platanoides). The montane forests were mainly mixtures of beech, European silver fir (Abies alba) and Norway spruce (Picea abies) and occupied sites over 575 m and mainly up to 1200m altitude (Figure 3). Beech was generally more abundant in lowland/submontane versus montane sites, on average accounting for 83% versus 52% of the living volume respectively. Geographically, most of the major beech forest regions in Europe were represented, though only one reserve (Massane) from the Pyrenees (France/Spain) and none from Italy and Romania were available (Figure 1). A wide range of climatic conditions were covered, from the mild, oceanic climate~~s~~ of S England and Belgium (January average temperature around 2-4°C), to the cold, montane and continental climates of E Slovakia (January average temperature below -5°C). Precipitation ranged from < 600 mm/year in NE Germany and SE Denmark to > 2000 mm/year in the Swiss Alps and the mountains of Slovenia.

3.2 Dead wood volumes

Summary details of dead and living wood volumes in each reserve are given in Table 1. The variation in total dead wood volume was high, but followed a normal distribution. The average for all the reserves was 130 m^3/ha, ranging from almost nothing to 550 m^3/ha (Table 1). The total dead wood volume and the dead to live wood ratio was highest for long-established montane reserves (220 m^3/ha and 37%), followed by long-established lowland/ submontane reserves (131 m^3/ha and 30%), then recently-established montane (116 m^3/ha and 23%), and finally recently-established lowland/submontane reserves (100 m^3/ha and 13%) (Table 2). The differences were statistically significant ($p<0.001$ for total dead wood volume, $p<0.0001$ for dead/living wood ratio). In addition, the dead wood volume size-distribution differed between recently- and long-established reserves. Long-established reserves showed a bell-shaped distribution, with few forest reserves having a very high or low dead wood volume. In contrast, recently-established reserves had a left-skewed distribution with many reserves having a low dead wood volume (< 80 m^3/ha) (Figure 4).

A statistical analysis showed that the total dead wood volume depended significantly on the forest type ($p<0.001$), reserve age ($p<0.01$), and volume of live trees ($p<0.01$), with an interaction between the reserve age and volume of live trees ($p< 0.05$). However, this model only explained 36% of the total variation in dead wood volume. Thus, an increase in reserve age and volume of live trees contributed positively to the total dead wood volume.

3.3 Standing and fallen dead wood

Dead wood was present in all the reserves as logs (fallen) and snags (standing). However, logs contributed more to the total dead wood volume than snags, with the volume of snags ranging from 1 to 282 m^3/ha with an average of 39 m^3/ha, and the volume of logs ranging from 3 to 456 m^3/ha with an average of 94 m^3/ha (Table 1). Data for both was normally distributed.

The proportion of the total dead wood volume in snags formed a bell-shaped distribution for lowland/submontane reserves and montane reserves (Figure 5). This proportion was up to twice as high in montane forests than in lowland/submontane forest reserves, regardless of the age of the reserve (Table 2). Indeed, in some C and SE European reserves more than 70% of the total dead wood volume was found in snags (i.e. Hoxfeld, Germany; Rajhenavski Rog and Bukov vrh, Slovenia), whereas in some reserves in NW Europe as little as 3% of the volume was in snags (Ridge Hanger, UK; Lohn, Germany; Weversbergen, The Netherlands).

The statistical analysis comparing the log volume with the forest type (F), reserve age (R), and living wood volume (L) (Table 3), showed that this depended significantly on all three factors (F: $p< 0.05$, R: $p< 0.01$, L: $p< 0.01$); that there many interactions between these factors; and that they explained 46% of the total variation in log volume. Thus, an increase in reserve age and living wood volume both contributed positively to the log volume. In contrast, the analysis of snag volume showed this depended only on forest type ($p<0.0001$), and that the model explained only 35% of the total variation (Table 3).

3.4 Dead wood dynamics

Twenty time-series were used to show the trend in dead wood volume over time (Figure 6). Many sites showed a relative increase in volume over time, but for some the increase was small and others declined. There was a distinct difference between the two forest types: lowland reserves had a higher mean relative change (+0.41) and variation (standard deviation = +/-0.84) than montane reserves (mean = +0.10, standard deviation = +/-0.25). Although the difference between the means was non-significant ($p=0.07$), the variances differed significantly ($p<0.0001$).

4. Discussion

4.1 Total dead wood volumes

The total volume of dead wood varied greatly between the beech forest reserves studied. This was shown to be partly related to the type of forest, live standing tree volume and time since establishment of each reserve, with the interaction between reserve age and volume of live trees accounting for about a third of the total variation. Overall, dead wood volumes tended to be higher in montane reserves than in lowland/submontane reserves; in reserves with higher live tree volumes; and in long-established than recently-established reserves. The main exceptions were small and/or recently-established reserves in NW Europe, where several mature/old-growth stands in the UK had broken-up under the influence of severe drought and/or windstorms creating extraordinarily high volumes shortly or just a few decades after they were established as strict reserves (e.g. Toy's Hill 485 m^3/ha, Noar Hill Hanger 339 m^3/ha, Denny Inclosure 273 m^3/ha, Ridge Hanger 265 m^3/ha).

In general, the dead wood volumes in the beech forest reserves included were comparable to those in reported from old-growth stands in NE America. The average for all reserves was 130 m^3/ha (Table 1), which compares to an average of 121 m^3/ha for 25 old-growth sites dominated by Eastern hemlock (Tsuga canadensis) in Wisconsin and Michigan (Tyrrell and Crow 1994), and to an average of 82-132 m^3/ha from old-growth oak-beech (Quercus-Fagus grandifolia) forests in Tennessee (Harmon et al. 1986). However, they were high in comparison to boreal parts of Europe and Fenno-Scandinavia, where pine and spruce forest reserves averaged 60-120 m^3/ha dead wood (Siitonen 2001), and well below the extreme volumes of to 1500 m^3/ha reported from Douglas-fir-Hemlock (Pseudotsuga-Tsuga) forests in NW America (Harmon et al. 1986, Stevens 1997).

4.2 Dead to live wood ratio

The ratio of dead to live wood varied greatly between the beech reserves studied. This contrasted with the ratios reported from several mixed beech forests in N America, which were more constant at 23-28% (Rubino and McCarthy 2003, Stewart et al. 2003). Also, a rather constant dead to live wood ratio has been observed in boreal forest reserves (Ferguson and Archibald 1992). The highest ratios found were in long-established (>50 years) as opposed to recently-established beech reserves, and for both the montane reserves had higher ratios than the lowland/submontane reserves. This pattern is probably related to several factors: (i) widespread dieback of silver fir in montane forests, for example in SE European beech-fir forests (Boncina et al. 2003); (ii) montane stands have a higher proportion of conifers (mainly silver fir and Norway spruce), which generally decay more slowly than beech and other deciduous trees (apart from oak) (Harmon et al. 1986); (iii) the majority of the lowland/submontane and recently-established reserves have a recent history of silvicultural management and timber extraction, with dead wood input so far being limited and of small, rapidly-decaying material (e.g. Buckholt Wood, UK; Mountford 2003); (iv) many of the long-established reserves have an old-growth structure (*sensu* Oliver and Larson 1996), in which dead wood input has probably been more substantial and moreover of slow-decaying, large trunks and branches; and (v) possibly because decomposition might be generally more rapid in lowland/submontane reserves due to higher average temperatures (Stokland 2001, Hahn and Christensen 2004a).

4.3 Standing and fallen dead wood

A higher incidence of windstorm-damage at sites in NW Europe (see below) appeared a major factor accounting for the difference in percentage of the total dead wood volume recorded as standing. At montane reserves this was 41-47%, whereas at lowland/submontane reserves it was only 23-29%. Beech, being shallow-rooted, is vulnerable to uprooting during windstorms (e.g. Pontailler et al. 1997, Mountford et al. 1999, Wolf et al. 2004). However, the volume of snags in E and SE Europe has probably been recently enhanced by the widespread dieback and death-standing of silver fir due to bark beetle outbreaks and air pollution (e.g. Boncina et al. 2003). In addition, more snags are likely to be longer-standing in these forests as conifers are more abundant and decay more slowly (Harmon et al. 1986).

4.4 Dead wood dynamics and disturbance regimes

Within the natural distribution range of beech in Europe, the disturbance regime is characterised by a combination of frequent small-scale disturbance events (gap-dynamics) and occasional large-scale disturbances, mainly caused by wind/ice/snow-storms and drought (e.g. Leibundgut 1982, Mayer 1984, Prusa 1985, Koop and Hilgren 1987, Korpel 1995, Mountford et al 1999, Tabaku 1999, Tabaku and Meyer 1999, Emborg et al. 2000, Meyer et al. 2003, Wolf et al. 2004). This tends to generate an irregular input of dead wood, with a wide range of sizes, shapes and decay states present at any one time (Hahn and Christensen 2004b). Fire is not an important disturbance agent in European beech forests and was not recorded in any of the sites reviewed in the study. Indeed, our analyses showed how the dead wood volume can fluctuate over time, with a general increase (positive values for mean rate of change) evident for both montane and low/submontane reserves. The mean rate of change was not significantly different for the two forest types, but the fluctuations in the rate of change were significantly higher for lowland/submontane -than montane reserves. This was related to the impact of several severe windstorms in sites in NW Europe (Koop and Hilgren 1987, De Keersmaeker et al. 2002, Mountford 2002), and combines with other observations of stand-destroying windstorms as detailed above and by Kirby et al (1998). In contrast, no such severe events were recorded for montane sites. This indicates that natural fluctuations in dead wood volume are more substantial in the windier climate of NW Europe. After such an event, there will be a gradual decline in the dead wood volume as the decay of large beech logs takes about 40-50 years (Christensen and Vesterdal 2003, Kraigher et al. 2002, Ódor and Standovár 2003, van Hees 2003). Thereafter there will be a prolonged period during which the volume will remain low (e.g. Koop and Hilgren 1987).

4.5 Implications for forest management

Over more than 1,000 years, various types of forest use have resulted in the removal of timber and a drastic reduction in the quantity of dead wood in most European forests. In managed forests dead wood occurs mainly as logging waste and stumps, and large logs and snags are rare. For example, surveys in Finland, Sweden, Germany, France, Belgium and Switzerland show that the average dead wood volume in present-day production forests is less than 10 m^3/ha (Erdmann and Wilke 1997, Tabaku 1999, Fridman and Walheim 2000, UNECE/FAO 2000, Vallauri et al. 2002).

The levels of dead wood reported here serves as a ‘natural benchmark’ for production and other beech forests around Europe, where there is an interest in developing more ‘natural’ levels of dead wood. Although the ‘naturalness’ of the dead wood levels recorded in our database of European beech forest reserves is open to debate, it nevertheless clearly indicates that the amount of dead wood is in the order of ten-twenty times higher in unmanaged than in intensively managed production forests. Admittedly, certain types of managed forests retain higher volumes of dead wood because larger quantities are left on the forest floor (Ódor and Standovár 2001, Green and Peterken 1997, Kirby et al. 1998), for example special thinning or coppice systems. Nature-based forest management as exemplified in the LÖWE-programme of Lower Saxony (Otto 1992), has attempted to mimic the natural dynamics of beech forests more closely than traditional, large-scale harvesting systems, but because most of the largest trees are still harvested and removed, the dead wood volume has not necessarily been increased. Indeed, it is widely appreciated that if this is to be achieved a substantial sacrifice of timber trees will be necessary. In the short term this can be achieved by leaving some harvestable material in the forest and by protecting a number of trees to develop into veteran trees to decay and collapse naturally (Butler et al. 2002).

4.6 Implications for biodiversity conservation

The amount, quality and continuity of dead wood are of importance for biodiversity conservation in forests. Dead wood is essential for many organisms and, as it is practically absent in most managed forests, many species dependent on dead wood are threatened or rare in European deciduous forests. These include various insects and lichens that have a strong preference for sun-exposed stumps, snags and standing decay columns, bird species that prefer veteran or standing dead trees for nesting and seeking food, and bats that preferentially roost in hollow trees. Often the number of snags available is directly limiting the population size for cavity breeding animals (Hunter 1990, Mikusinski and Angelstam 1997). Fungi and bryophytes have their highest diversity connected to fallen logs (Ódor and Standovár 2002, Heilmann-Clausen and Christensen 2003), but in contrast to fungi, which have the highest diversity in the intermediate decay stages, bryophytes have a preference for both medium and late decay stages and a special requirement for a constantly high level of air humidity (Andersson and Hytteborn 1991, Söderström 1988, Rambo and Muir 1998, Ódor and Standovár 2001). Whilst the size of individual dead wood pieces is important for bryophytes (Ódor and van Hees 2004), the total volume of dead wood in combination with dead wood continuity are particularly important for fungi (Christensen and Heilmann-Clausen 2002, Heilmann-Clausen and Christensen 2003, Nordén et al. 2004). Thus, it is desirable to not only increase the quantity of dead wood, but to develop a range of sizes, decay states and locations for both fallen and standing material (see Kirby 1992 for examples).

Moreover, a targeted approach directed at particular sites with a known or suspected faunal/floral 'deadwood' interest (with a long continuity of deadwood habitat or adjoining such a site), should have maximum conservation benefits (Hodge and Peterken 1998). Our studies indicate there are natural differences between montane and lowland/submontane European beech forests in terms of the overall level and fluctuation in dead wood over time, and the frequency of standing and fallen dead wood. Assuming organisms are locally adapted to these features this place an emphasis on retaining more dead wood, keeping the levels high and a high proportion of snags in montane beech forests. However through massive influence of human for centuries in all part of Europe these natural balances are not always present and key-species in the decay-chain can be missing. The preservation of dead wood in different beech forest types in Europe is therefore an important first step in saving wood-inhabiting organisms.

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Table 1

Summary details of the European beech forest reserves included in the study. The dead wood volumes have been standardised where the minimum diameter used to measure dead wood was >5cm diameter (see Figure 2 and text for details).

Forest reserve	Country	Area of study (ha)	Sampling method	Forest type	Reserve establishment (year)	Living wood volume (m3/ha)	Minimum diameter (cm)	Year recorded	Snag volume (m3/ha)	Log volume (m3/ha)	Total CWD volume (m3/ha)	CWD/living wood ratio (%)	Snag/CWD ratio (%)	References/recorders
Dobra	Austria	6	.	F5a	1910	582	8	1970	.	.	45	8	.	Mayer & Reimoser 1978
Rothwald	Austria	300	PP	F5b	1900	547	1	1977	92	164	256	54	36	Mayer & Neumann 1981 ao
Zoinenwoud*	Belgium	11	CS	F5a	1993	794	30	2000	19	123	142	17	14	De Keersmaeker et al. 2002
Boubín*	Czech Rep.	47	CS	F5b	1858	772	10	1996	74	185	258	30	29	Vrska et al. 2001c
Milesice*	Czech Rep.	10	CS	F5b	1948	567	10	1996	52	101	153	24	34	Vrska et al. 2001b
Mionsí	Czech Rep.	171	CS	F5a	1933	590	10	1994	63	108	172	26	37	Vrska et al. 2000b
Polom*	Czech Rep.	19	CS	F5b	1955	593	10	1995	49	104	152	23	32	Vrska et al. 2000a
Razula*	Czech Rep.	24	CS	F5b	1933	592	20	1995	89	199	287	35	31	Vrska et al. 2001a
Salajka*	Czech Rep.	22	CS	F5b	1956	473	10	1994	89	159	248	47	36	Vrska 1998
Stozec	Czech Rep.	53	CS	F5b	1989	663	10	1974	.	.	63	9	.	Prusa 1982, 1985
V Klucí*	Czech Rep.	25	PP	F5a	1953	681	10	2000	54	169	223	30	24	Odehnalova 2001
Zákova hora*	Czech Rep.	38	CS	F5b	1933	580	10	1995	33	114	147	23	23	Vrska et al. 1999
Zofin	Czech Rep.	98	CS	F5b	1838	666	10	1975	54	87	141	19	38	Prusa 1982, 1985
Knagerne	Denmark	6	LT	F5a	1990	449	5	2003	31	56	87	20	35	Christensen & Hahn, unpubl.
Møns Klinteskov	Denmark	25	LT	F5a	1935	201	0	2001	24	48	73	37	33	Christensen & Hahn, unpubl.
Strødam Reservatet	Denmark	25	LT	F5a	1949	490	0	1983	38	101	139	29	27	Christensen & Hahn, unpubl.
Suserup Skov	Denmark	11	LT	F5a	1927	674	3	2002	9	154	163	25	5	Christensen & Hahn, unpubl.
Velling	Denmark	24	LT	F5a	1990	489	0	2001	31	68	99	21	31	Christensen & Hahn, unpubl.
La Massane	France	336	PP	F5a	1920	.	1	1998	8	25	33	.	25	Garrigue & Magdalou 2000
La Tillaie*	France	36	PP	F5a	1853	260	5	2000	55	165	220	85	25	Wijdeven 2003
Bw Birkenkopf	Germany	15	SP	F5a	1992	333	7	1994	2	8	10	3	20	Labudda 1999b
Bw Feldseewald	Germany	102	SP	F5b	1973	423	7	1992	39	23	62	14	63	Labudda 2000
Bw Grubenhau	Germany	16	SP	F5a	1970	604	7	1997	22	47	69	11	31	Labudda 1999a
Bw Napf	Germany	140	SP	F5b	1970	483	7	1996	82	32	114	23	72	Hanke 1998
Bw Pfannenberg	Germany	15	SP	F5a	1986	469	7	1994	17	51	69	14	25	Seiler 2001
Bw Sommerberg	Germany	43	SP	F5a	1994	333	7	1995	5	16	22	6	24	Wotke & Bücking 1999
Bw Zweribach	Germany	77	SP	F5b	1970	538	7	1999	22	43	65	12	33	Keller & Riedel 2000
Eisgraben	Germany	28	PP	F5a	1978	774	.	.	39	142	181	23	21	Kölbel 1999
Fauler Ort	Germany	21	SP	F5a	1938	481	7	2000	104	156	260	47	40	Winter, unpubl.
Franzhorn	Germany	43	PP	F5a	1972	584	7	1997	4	15	19	3	23	Meyer, unpubl.
Gitschger	Germany	75	PP	F5a	1978	640	.	.	42	96	138	21	30	Kölbel 1999
Grosser Stauenburg	Germany	50	PP	F5a	1972	545	7	1999	4	24	28	5	15	Meyer, unpubl.
Hainich	Germany	28	SP	F5a	1990	567	.	.	22	42	64	11	35	Beneke & Manning 2003
Heiligen Hallen*	Germany	25	SP	F5a	1938	506	7	1999	74	211	284	48	26	Winter, unpubl.
Hoher Knuck	Germany	109	PP	F5a	1978	576	.	1991	16	81	97	16	17	Kölbel 1999
Hoxfels*	Germany	55	SP	F5a	1972	360	.	2000	46	10	56	15	82	Heupel 2002

Hünstollen	Germany	56	PP	F5a	1970	576	7	1996	5	16	21	4	26	Meyer 1999
Kalkberg	Germany	24	SP	F5a	1978	681	.	1991	10	28	38	5	27	Kölbel 1999
Königsbuche	Germany	27	PP	F5a	1972	611	7	1996	18	62	79	13	22	Meyer 1999
Limker Strang	Germany	20	PP	F5a	1972	496	7	1999	7	18	25	5	29	Meyer 1999
Lohn	Germany	37	PP	F5a	1972	458	7	1996	1	41	42	9	3	Meyer 1999
Lüssberg	Germany	29	PP	F5a	1972	335	7	1997	2	8	9	3	17	Meyer 1999
Niddahänge_1	Germany	20	SP	F5a	1954	542	7	1988	5	44	49	7	10	Hocke 1996
Niddahänge_2	Germany	21	SP	F5a	1954	599	7	1988	6	35	41	5	14	Hocke 1996
Platzer Kuppe	Germany	24	SP	F5a	1978	595	.	1991	24	35	58	10	40	Kölbel 1999
Serrahn	Germany	43	SP	F5a	1977	458	7	1999	45	113	158	29	29	Winter, unpubl.
Stöberhai	Germany	15	PP	F5a	1970	622	7	2000	21	36	57	9	36	Meyer, unpubl.
Swarzwihrberg	Germany	24	PP	F5a	1978	876	.	1991	13	61	75	8	18	Kölbel 1999
Vilm	Germany	20	SP	F5a	1936	561	7	1997	44	109	153	27	29	Schmaltz & Lange 1999
Vogelherd_1	Germany	11	PP	F5a	1972	439	7	1996	3	24	27	6	12	Meyer 1999
Vogelherd_2	Germany	11	PP	F5a	1972	478	7	1999	3	41	44	9	6	Meyer, unpubl.
Waldhaus	Germany	11	SP	F5a	1978	780	.	1991	6	118	124	16	5	Kölbel 1999
Alsohegy	Hungary	113	LT	F5a	1978	284	2	2001	17	23	40	14	43	Ódor & Standovár, unpubl.
Öserdö	Hungary	59	LT	F5a	1976	765	2	2001	23	152	175	21	13	Ódor & Standovár, unpubl.
Kekes	Hungary	55	LT	F5a	1986	454	2	2001	14	92	106	22	13	Ódor & Standovár, unpubl.
Dassenberg	Netherlands	12	LT	F5a	1990	402	5	2000	18	43	61	16	30	Van Hees et al. 2004
Gortel	Netherlands	15	LT	F5a	1990	507	5	2000	8	56	65	13	13	Van Hees et al. 2004
Pijpebrandje	Netherlands	27	LT	F5a	1975	457	5	2000	11	32	43	10	26	Van Hees et al. 2004
Weversbergen	Netherlands	12	LT	F5a	1991	469	5	2000	1	46	48	11	3	Van Hees et al. 2004
Barbia Gora NP*	Poland	2	PP	F5b	1954	537	6	1996	99	168	267	50	37	Jaworski & Paluch 2001
Bieszczady*	Poland	1	PP	F5a	1973	596	6	1998	34	148	182	31	19	Jaworski et al. 2002
Gorce NP	Poland	2	PP	F5b	1981	683	6	1991	71	99	169	24	42	Jaworski & Skrzyszewski 1995
Swietokrzyski NP	Poland	451	PP	F5b	1924	362	8	1992	144	152	296	78	49	Jaworski et al. 1999
Badin*	Slovakia	31	PP	F5b	1913	627	7	1997	42	228	271	46	16	Saniga 1999, Saniga & Schütz 2001b
Dobroc*	Slovakia	102	PP	F5b	1913	741	7	1998	66	190	256	41	26	Saniga & Schütz 2001b
Havesova*	Slovakia	171	PP	F5a	1964	736	7	1999	32	70	103	17	32	Saniga & Schütz 2001a
Kyjov*	Slovakia	53	PP	F5a	1974	465	6	1993	47	115	162	42	29	Korpel 1995, Saniga & Schütz 2001a
Rastun	Slovakia	18	PP	F5a	.	527	7	1983	28	31	58	13	47	Korpel 1992, 1997
Rozok*	Slovakia	67	PP	F5a	1964	816	6	1999	28	96	124	18	22	Saniga & Schütz 2001a
Sitno	Slovakia	45	PP	F5a	1951	594	7	.	24	62	86	17	28	Korpel 1997
Stuzica_4	Slovakia	218	PP	F5a	1965	569	7	1991	51	40	91	19	56	Korpel 1997
Stuzica_5	Slovakia	442	PP	F5a	1965	647	7	1991	50	40	90	17	55	Korpel 1997
Bukov vrh	Slovenia	9	CS	F5b	1983	525	5	1998	65	.	92	18	71	Kovac 1999
Krokar	Slovenia	73	.	F5b	1894	634	.	.	.	.	69	11	.	Papez 1997
Pecka*	Slovenia	60	PP	F5b	1953	687	5	1999	283	269	552	83	51	Debeljak 1999
Rajhenavski Rog*	Slovenia	51	PP	F5b	1894	813	5	1985	119	16	134	17	88	Hartman 1987
Strmec	Slovenia	16	CS	F5b	1913	660	10	2001	.	.	166	25	.	Rozenbergar et al. 2003
Neunkirch	Switzerland	2	LT	F5a	1950	470	5	1999	6	51	58	13	11	M. Dobbertin, pers. comm.
Buckholt Wood	UK	2	LT/PP	F5a	1976	.	.	2000	3	3	6	.	51	Mountford 2003
Dendles Wood	UK	8	LT/PP	F5a	1965	.	.	1998	61	109	170	.	36	Mountford et al. 2001
Denny Inclosure	UK	2	LT/PP	F5a	1955	.	.	1996	78	195	274	.	29	Mountford et al. 1999
Lady Park Wood	UK	35	PP/LT	F5a	1944	.	.	1995	28	53	81	.	35	Green & Peterken 1997
Noar Hill Hanger	UK	7	PP/LT	F5a	1987	.	.	2000	40	300	340	.	12	Mountford 2004
Ridge Hanger	UK	5	PP/LT	F5a	1987	.	.	2001	1	264	265	.	0	Mountford & Ball 2004
The Mens	UK	17	PP/LT	F5a	1970	.	.	2001	28	85	113	.	25	Mountford & Peterken 2001/Mountford, unpubl.
Toy's Hill	UK	20	PP	F5a	1987	.	.	1999	30	456	486	.	6	Mountford & Peterken 2000

Notes: Bw = Bannwald, NP=National Park.

Sampling methods: CS= Complete Survey, LT= Line Transect sampling, PP= Permanent Plot sampling, SP=Systematic Grid Plot sampling

Forest types: F5a=Lowland/submontane beech forests, F5b=Montane beech/mixed beech-fir-spruce forests (Bohn and Katenina 1996, Larsson 2001).

Data from forest reserves marked with an asterisk were used in the time series analyses

Table 2

Summary of the total dead wood volume, volume of live trees, ratio of dead wood to live tree volume, and percentage of dead wood in snags in the beech reserves studied. Values are given for the mean, +/- standard error, and (in brackets) number of sites. The table shows the values for long-established versus recently-established and montane versus lowland/submontane reserves separately. Mean, standard error (SE) and (in brackets) sample size (N). Corrected values with minimum diameter for dead wood >5 cm.

	Long-established, Montane	Long-established, Lowland/Submontane	Recently established, Montane	Recently established, Lowland/Submontane	Total
Dead wood (m^3/ha)	220±115 (16)	132±70 (20)	117±74 (6)	99±98 (43)	130±103 (86)
Living volume (m^3/ha)	625±110 (16)	538±148 (18)	529±88 (6)	545±143 (36)	559±136 (77)
Dead to live wood volume ratio (%)	36±21 (16)	29±18 (18)	21±14 (6)	12±7 (36)	22±17 (77)
Snag to total dead wood volume ratio (%)	41±19 (14)	29±13 (19)	47±19 (5)	23±15 (43)	29±17 (82)

Table 3

Summary of general linear models to predict corrected values of total dead wood volume, snag volume, and log volume according to three explanatory variables: forest type (F), reserve age (R), living wood volume (L), and their interactions.

Response variable	Source	DF	SS	F	P
Total dead wood volume	F	1	69256.23	12.00	0.0009
r^2=0.37	R	1	59253.33	10.26	0.0020
	L	1	46882.01	8.12	0.0057
	R x L	1	34811.13	6.03	0.0165
	Residual	71	409923.63		
Log volume	F	1	9813.49	4.21	0.0444
r^2=0.46	R	1	20106.96	8.62	0.0046
	L	1	18640.46	7.99	0.0063
	F x R	1	13202.77	5.66	0.0204
	F x L	1	13238.81	5.68	0.0202
	F x R x L	2	11808.73	5.06	0.0091
	Residual	63	146959.07		
Snag volume	F	1	46918.63	42.21	<0.0001
r^2=0.35	Residual	80	88917.54		

Figure 1. The position of all beech forest reserves included in the study.

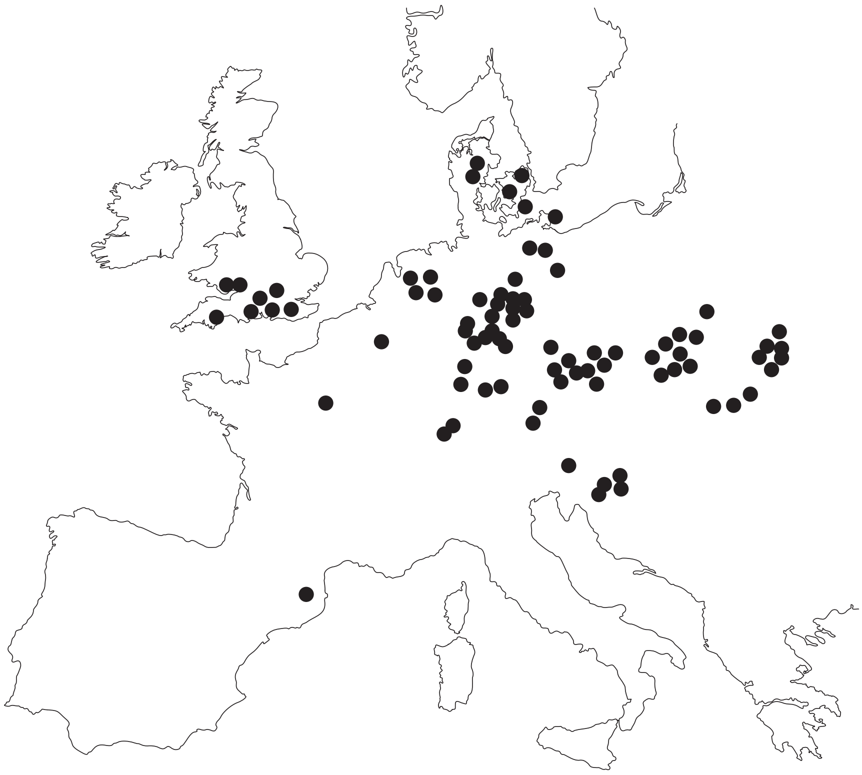
Figure 2. Correction used to standardise the dead wood volume at each site where the minimum diameter used to measure dead wood volume was >5cm diameter. The relationship was based on measurements in 13 forest reserves in Denmark (crosses), England (triangles), France (triangles) and Hungary (squares) (see Table 1 for sites).

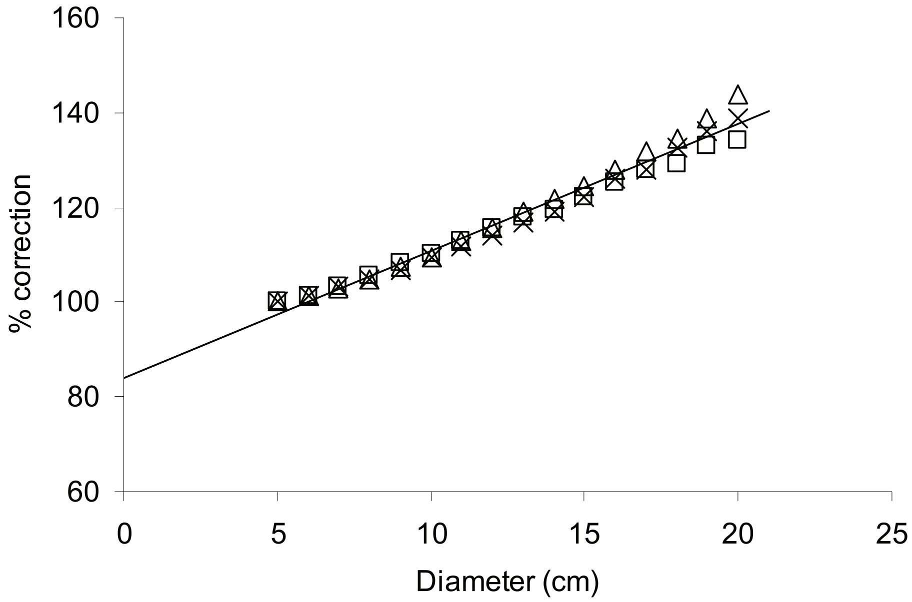
Figure 3. Total dead wood volume at each reserve shown in relation to altitude and for lowland/submontane (circles) and montane (triangles) separately. The two forest type groups showed overlap in altitude at 575-875 m.

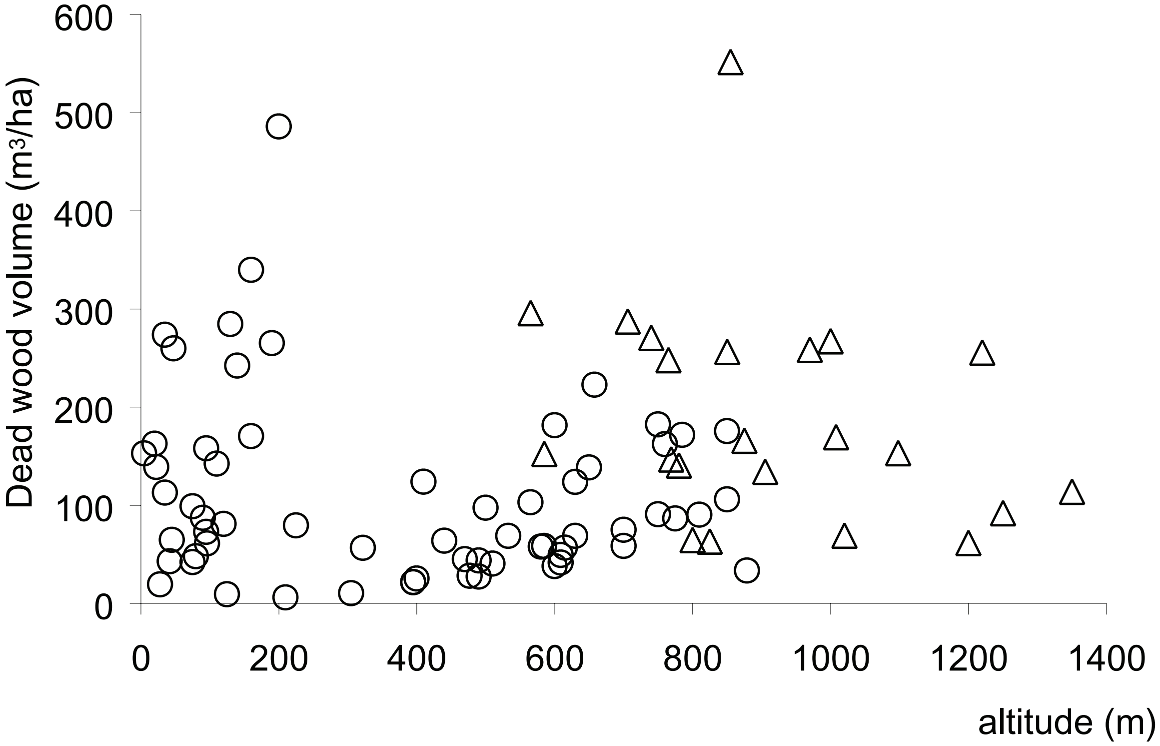
Figure 4. Total volume of dead wood (m^3/ha) in long-established (left) versus recently-established (right) beech forest reserves. Lowland/submontane (grey) and montane (white) forest types are distinguished.

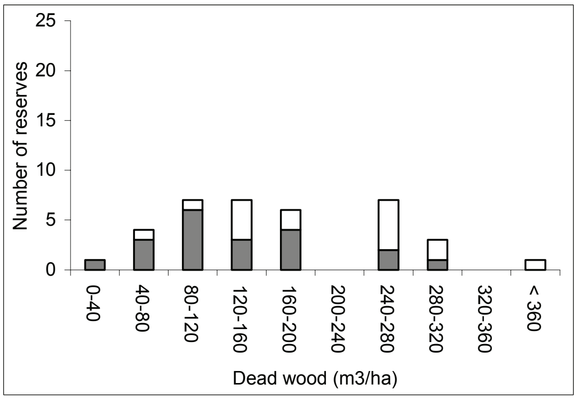
Figure 5. Percentage of total dead wood volume found in snags in lowland/submontane (left) versus montane (right) beech forest reserves. Recently-established (white) and long-established (grey) reserves are distinguished.

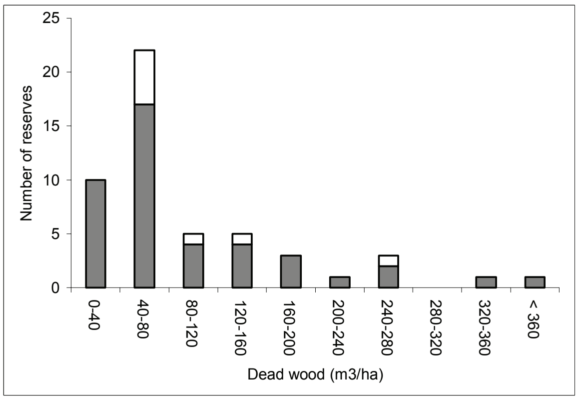
Figure 6. Change in dead wood volume over time for selected lowland/submontane (bold line) and montane (thin line) reserves. The diagram shows the proportional change in relation to previous measurement. The reserves included are marked in Table 1.

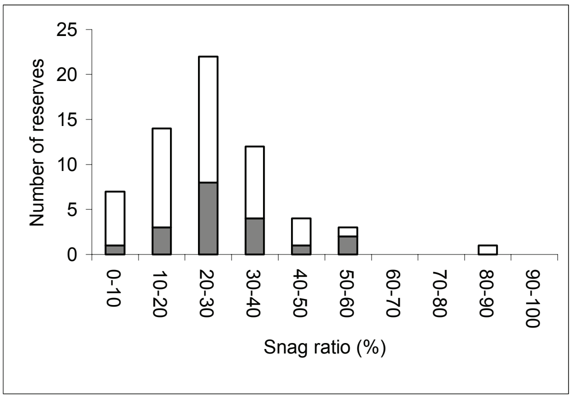


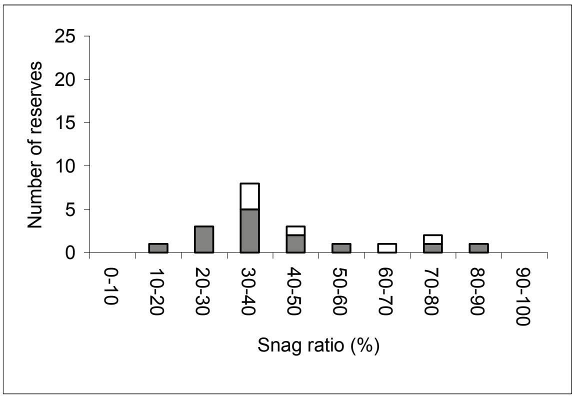

% correction
Diameter (cm)
160
140
120
100
80
60
0
5
10
15
20
25

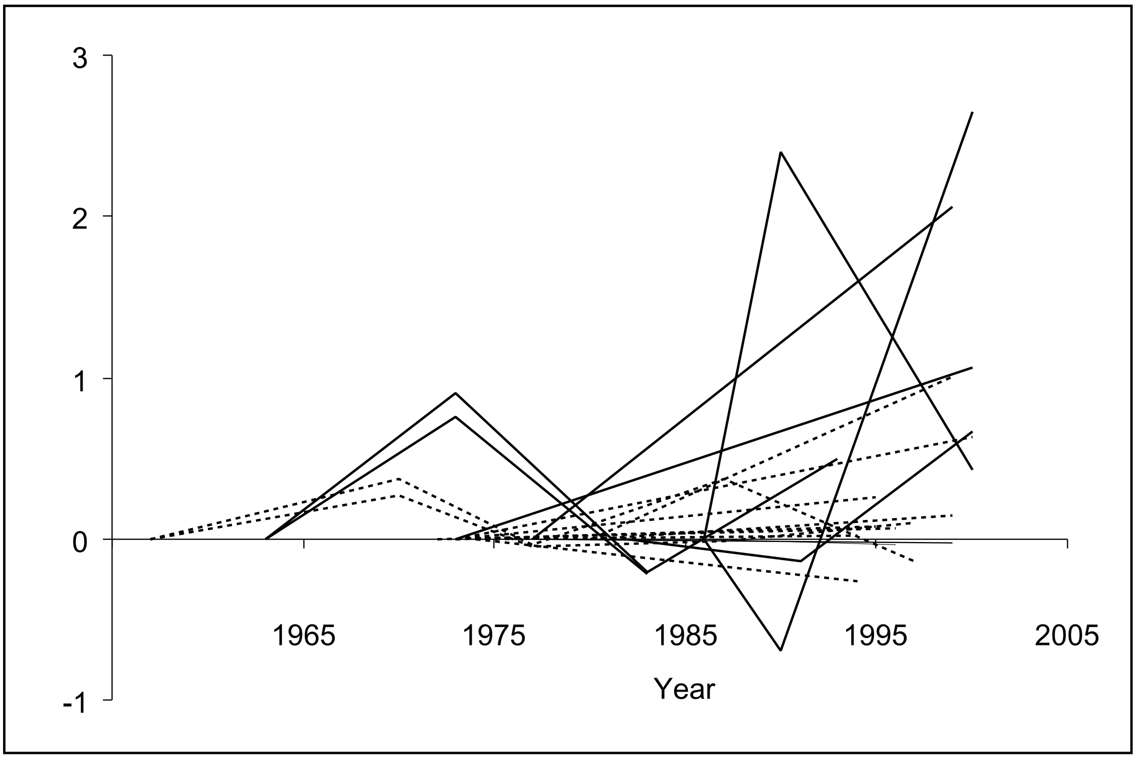

Dead wood volume (m3/ha)
0
100
200
300
400
500
600
0
200
400
600
800
1000
1200
1400
altitude (m)


Number of reserves
25
20
15
10
5
0
0-40
40-80
80-120
120-160
160-200
200-240
240-280
280-320
320-360
< 360
Dead wood (m3/ha)


Number of reserves
25
20
15
10
5
0
0-40
40-80
80-120
120-160
160-200
200-240
240-280
280-320
320-360
< 360
Dead wood (m3/ha)


Number of reserves
25
20
15
10
5
0
0-10
10-20
20-30
30-40
40-50
50-60
60-70
70-80
80-90
90-100
Snag ratio (%)


Number of reserves
25
20
15
10
5
0
0-10
10-20
20-30
30-40
40-50
50-60
60-70
70-80
80-90
90-100
Snag ratio (%)


3
2
1
0
-1
1965
1975
1985
1995
2005
Year