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Dynamics and structural changes of an oak dominated Natural Forest Reserve in Austria

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Abstract Natural forest reserves provide a rare opportunity to study forest dynamics after the cessation of human management. Inventories were carried out in 1996 and 2006 in an oak (*Quercus* spp.) dominated forest reserve formerly managed as coppice forest using the Bitterlich sampling method, an inventory method with a fixed angle of sight to select trees based on their stem diameter. The total living stand volume increased from 245.2 to 276.5 m^3/ha (+12.8%) over the 10-year period. This net increase resulted from the growth of individual trees (+3.7%), the ingrowths of young trees (+17.7%) and tree mortality between 1996 and 2006 (−8.6%). Tree mortality included 14.8 m^3/ha of standing deadwood and 6.2 m^3/ha of fallen deadwood. Stand dynamics differed among tree species: the volume of oak (*Quercus* spp.) increased due to strong growth and low mortality, whereas hornbeam (*Carpinus betulus*) showed a decrease in stand volume due to high mortality and low growth. The findings suggest an increase in oak dominance at the expense of hornbeam although inventories repeated over longer time periods would be needed for confirmation. Our data indicate that the Bitterlich sampling method can be used for assessing tree species dynamics and structural changes in natural forest reserves, but some important processes (seedling recruitment, wood decomposition) would need to be investigated separately.

Zusammenfassung In einem von Eiche (*Quercus* spp.) dominierten Naturwaldreservat wurde in den Jahren 1996 und 2006 auf einer Fläche von 29 ha eine Inventur mittels der Winkelzählprobe nach Bitterlich durchgeführt. Der Gesamtvorrat erhöhte sich in der 10-jährigen Beobachtungsperiode von 245.2 m^3/ha auf 276.5 m^3/ha. Im Durchschnitt konnten 14.8 m^3/ha stehendes Totholz und 6.2 m^3/ha liegendes Totholz ermittelt werden. Die Mortalitätsrate lag zwischen 1996 und 2006 bei 8.6%. Hainbuche (*Carpinus betulus*) zeigte aufgrund der hohen Mortalität und dem geringen Einwuchs im Vergleich zur Eiche und den anderen Baumarten eine Abnahme im Gesamtvorrat. Die Ergebnisse erlauben einen Einblick in die dynamischen Prozesse unter nahezu natürlichen Bedingungen. Die Eignung der Winkelzählprobe für die Beurteilung der Dynamik und die Analyse von strukturellen Veränderungen wird kritisch diskutiert.

Keywords Mortality · Ingrowths · Deadwood · Stand volume · Bitterlich sampling method · Mortalität · Einwuchs · Totholz · Vorrat · Relaskop Messung nach Bitterlich

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Introduction

Undisturbed forests are valuable objects to study vegetation structure and dynamics (Mayer et al. 1987; Leibundgut 1982). The Austrian "Natural Forest Reserves Program" was launched in 1995 to support the in situ conservation of rare and endangered forest types and the study of natural dynamic processes, including the effect of natural disturbances and catastrophes (Frank and Müller 2003; MCPFE 2003). The natural forest reserves also serve as references for biodiversity assessments and ecological monitoring, as they are not subject to any human activities (Frank and Koch 1999; Frank and Müller 2003). The establishment of natural forest reserves in Austria is based on a voluntary approach where private forest owners receive an annual compensation from the government. The compensation is calculated on the basis of a fixed basic rate, site conditions and the average stocking level. The latter is determined on the basis of periodic inventories done with the angle count method or Bitterlich sampling method (Bitterlich 1947), a quick and cost effective method to measure stand basal area, number and volume of trees in forests (Bill 1993; Holck 2008).

The grid of Bitterlich sampling plots established in the forest reserves could potentially also serve to study natural forest dynamics by comparing successive inventories. The methods normally used to study recruitment, growth and mortality rates in protected forest areas (Meyer et al. 2001; Frank et al. 2007; Kint et al. 2004) involve a full sampling of living and dead biomass on larger study areas (Parviainen et al. 2000; Rentch et al. 2003). Such studies are time-consuming, and it would be more efficient if the same information could be obtained with the Bitterlich method, especially if this is already used to calculate compensation payments. However, the practicability of the Bitterlich sampling method for monitoring the dynamics in natural reserves has not been tested so far.

The oak-dominated forest of Lange Leitn in eastern Austria has been among the first natural forest reserves established in Austria. It is one of the rare examples where the natural dynamics of oak forests formerly managed as coppice forests can be studied. Indeed, quantitative information on the dynamics of oak-dominated European forests is scarce (Hochbichler 2008) because most studies of old growth stands and natural reserves in Europe were conducted in beech dominated high forests (Standovár and Kenderes 2003).

The objectives of the present study were therefore to study the mortality and growth rates of oak and hornbeam in a former coppice forest after a short period of natural conditions, and to critically discuss the appropriateness of the Bitterlich sampling method for assessing the dynamics and structural changes in natural forest reserves.

Study site and methods

The study site at the Lange Leitn Natural Forest Reserve consists of 29 ha of forested land near to Neckenmarkt (Burgenland), at the borderline to Hungary. The natural forest reserve is located in the colline and submontane vegetation zone with oak-dominated vegetation. The forests have been used for coppice production in the past, but there have been only minimum human interventions since 1942. From old management plans it is known that the whole area was clear-cut by several entries except for 20–30 so-called "seed trees" in the time between 1930 and 1935. Since 1942, no silvicultural treatments are documented. The sites are characterized by brown podzolic soils with an elevation ranging from 415 to 490 m. The soils of the lowest slopes are relatively humid, alkaline and 20–30 cm deep, those of the middle slopes are slightly acidic and 10–20 cm deep, and those of the top slopes are acidic and 5–10 cm deep. The mean average temperature is 9°C with an annual precipitation including snowfall of 850 mm. The duration of snow cover varies from 60 to 80 days with a maximum of 50 cm snow depth. That results in a total length of the growing season of around 250 days per year. The forests are dominated by oak (*Quercus petraea* (Mattuschka) Liebl., *Quercus cerris* L. and *Quercus* sp.), with a mixture of hornbeam (*Carpinus betulus* L.), birch (*Betula pendula* Roth) and European beech (*Fagus sylvatica* L.).

Tree measurements using the Bitterlich sampling method were done at 24 sampling points each on a regular grid with a distance of 100 m in 1996 and 2006. The Bitterlich sampling method uses a fixed angle of sight to select trees from the center of the sampling point by a Relascope (Bitterlich-Treemeter). Trees whose breast height diameters appear larger than the fixed angle (basal area factor—BAF) are sampled. The probability for trees to be sampled is proportional to their size; a tree can be sampled by being very large or, if small, very close to the sampling point (for details refer to Bitterlich 1947). Additionally, the diameter at breast height (DBH; >5 cm "Kluppschwelle") and the tree height of trees and trunks (living trees and standing deadwood) were measured. In addition to the Bitterlich sampling, the position of each measured and marked tree on each sample point was mapped in 1996 and 2006; therefore, it was possible to trace the life history of each individual in the samples from 1996 to 2006. Trees that were alive in 1996 and found as dead in 2006 were considered 'dead'. The living trees (L) of 2006 were classified as still alive (SL) if measured in both inventories (1996 and 2006), or as ingrowths (IL) if they had not yet been measured in the inventory of 1996 due to insufficient size of the breast height diameter. Deadwood was considered as standing deadwood (SD) or fallen deadwood (FD). Standing deadwood in 2006 was either an outcome of the mortality from 1996 to 2006 (LSD) or from the time before 1996 (SSD). The fallen deadwood mostly originated from standing deadwood (SFD) but occasionally also from living trees (LFD) (Fig. 1). It was not possible to include the fallen deadwood by the Bitterlich sampling method directly, but with the help of a sketch from 1996 it

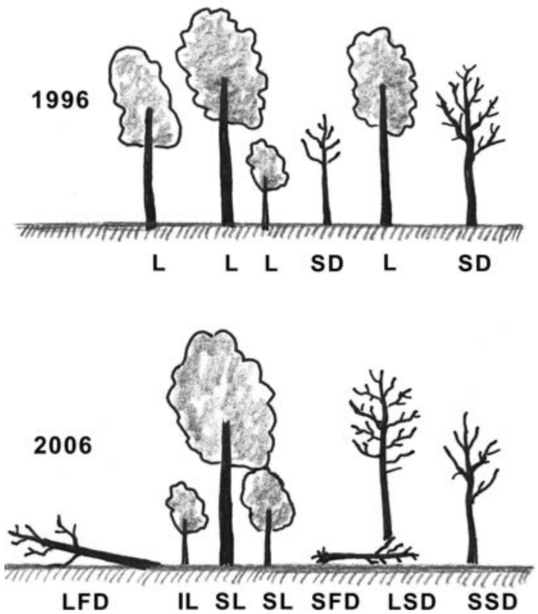

Fig. 1 Classification of trees according to their life cycle

was possible to identify the number and coordinates of each tree classified as fallen deadwood in 2006.

For the tree volume calculation, the form factor curves of the Austrian Forest Inventory were used (Pollanschütz 1974; Schieler 1988). Different forms were used according to tree species, the size of the DBH and the origin of the trees (vegetative, generative). For the calculation of the volume of the standing deadwood trunks it was necessary to use an approximation: The relation between the measured tree height of the broken trunks in the field and an estimated total tree height (assuming that the top of the trees is not broken) based on the height curves from Prodan (1965) was used to calculate a reduction factor RF1. This factor was used to reduce the stem volume of a deadwood trunk in relative terms to the stem volume of a living tree without a broken top. Additionally, it was assumed that the size of the fallen deadwood decreases from bark loss and fragmentation over one decade (Wilson and McComb 2005). On the basis of that assumption, the total amount of the volume of the fallen deadwood of 2006 was calculated by using reduction factor RF2 (−10% of the volume in 1996). Paired *t* tests were performed to compare the mean values between different compartments of the living volume between 1996 and 2006 using SPSS 15.0 software (SPSS 2006).

The absolute difference in diameter distributions between 1996 and 2006 was calculated using the following formula (Pommerening 2002):

$$\mathrm{AD} = {}^1\!/_2 \sum\nolimits_i |d_{1996} - d_{2006}|,$$

where d_{1996i} is the relative frequency of the ith diameter class of the population in 1996, d_{2006i} the relative frequency of the ith diameter class of the population in 2006 and n the number of diameter classes. Thus, AD represents the relative proportion, which must be exchanged between the classes if the empirical distribution of 1996 is transformed into the distribution of 2006. Correspondingly, $1 - \mathrm{AD}$ is the proportion common to both distributions. A value of $\mathrm{AD} = 1$ means that both distributions have no common class, whereas $\mathrm{AD} = 0$ signifies that the distributions are absolutely identical.

Results

Loss and gain

In the Natural Forest Reserve in Lange Leitn oak contributed 80.7% to the total volume in 1996 and 83.7% in 2006 (Table 1). Hornbeam contributed 15.6% of the total volume in 1996 and 11.9% in 2006. The other tree species (European beech, Birch, Sycamore) contributed only 3.7% of the total volume in 1996 and 4.4% in 2006.

The average stand volume increased from 245.2 to 276.5 m^3/ha, where the volume of oak increased from 199.7 to 232.8 m^3/ha and hornbeam showed a decrease of volume from 1996 to 2006. Considering the mean differences between the stand volume of all plots in 1996 and 2006, significant differences were found for the total volume and for oak, respectively (Table 1).

During one decade a total volume of 21.0 m^3/ha of trees died, this was equal to 8.6% mortality according to the stand volume of 1996. The mortality of hornbeam (17.8%) was higher than oak (7.4%). 43.3 m^3/ha was reported as ingrowths, which was 17.7% of the 1996 stand volume (Table 1). For oak and the other species, ingrowth (19.0 and 12.7%, respectively) exceeded mortality, whereas for hornbeam mortality exceeded ingrowth (Table 1). Due to individual growth, the volume of the living trees that were sampled both in 1996 and 2006 increased by 10.0 m^3/ha in 10 years, which was equal to 4.1% of the 1996 stand volume (Table 2). The increment of oak (4.6%) was higher than that of hornbeam (1.7%) and the other species (2.0%).

Structural changes

The smallest DBH class (5–10 cm) consisted largely of hornbeam in 1996 and 2006, while oak did not occur in the smallest DBH class (Fig. 2). Hornbeam, the co-dominant species showed a decrease of the relative percentage within the middle DBH class (10–20 cm) and an increase in both the smallest (5–10 cm) and the largest (20–30 cm) DBH class from 1996 to 2006. Hornbeam and the other tree species had no individuals in larger DBH classes (>30 cm), while oak had 32% of its total volume in larger DBH

Table 1 Average stand volume, ingrowths, increment and mortality for oak (*Quercus* spp.), hornbeam (*Carpinus betulus*) and other tree species in 1996 and 2006 ($N = 24$ plots; mean ± standard deviation)

Species	Stand volume 1996		Stand volume 2006		Mean difference		Ingrowths 1996–2006		Mortality 1996–2006	
	m^3/ha	Relative volume (%)	m^3/ha	Relative volume (%)	m^3/ha	% of 1996 volume	m^3/ha	% of 1996 volume	m^3/ha	% of 1996 volume
Oak	199.7 ± 91.5	80.7 ± 24.6	232.8 ± 85.2	83.7 ± 19.7	33.1**	16.6	37.9 ± 38.0	19.0	13.7 ± 20.9	7.4
Hornbeam	35.3 ± 43.0	15.6 ± 20.7	32 ± 35.5	11.9 ± 13.9	3.3 (ns)	−9.3	4.1 ± 9.6	11.6	7.4 ± 13.7	17.8
Others	10.2 ± 31.4	3.7 ± 11.2	11.7 ± 32.2	4.4 ± 13.9	1.5 (ns)	15.3	1.3 ± 6.4	12.7	0.0 ± 0.0	0.0
All	245.2 ± 78.2	100.0	276.5 ± 77.5	100.0	31.3**	12.8	43.3 ± 42.2	17.7	21.0 ± 20.4	8.6

Differences between 1996 and 2006 were tested with paired *t* tests

ns not significant

** $p = <0.01$

Table 2 Average stand volume and increment for oak (*Quercus* spp.), hornbeam (*Carpinus betulus*) and other tree species based on the individual growth of trees considered as living in 1996 and 2006 only ($N = 184$ trees; mean ± standard deviation)

Species	1996 (m^3/ha)	2006 (m^3/ha)	Mean difference (increment)	
			Volume (m^3/ha)	% of 1996 volume
Oak	185.7 ± 81.8	194.9 ± 85.1	9.2***	4.6
Hornbeam	27.3 ± 33.3	27.9 ± 33.8	0.6*	1.7
Others	10.2 ± 31.4	10.4 ± 32.0	0.2 (ns)	2.0
All	223.2 ± 73.6	233.2 ± 76.0	10.0***	4.1

Differences between 1996 and 2006 were tested with paired *t* tests

ns not significant

* $p = <0.05$, *** $p = 0.001$

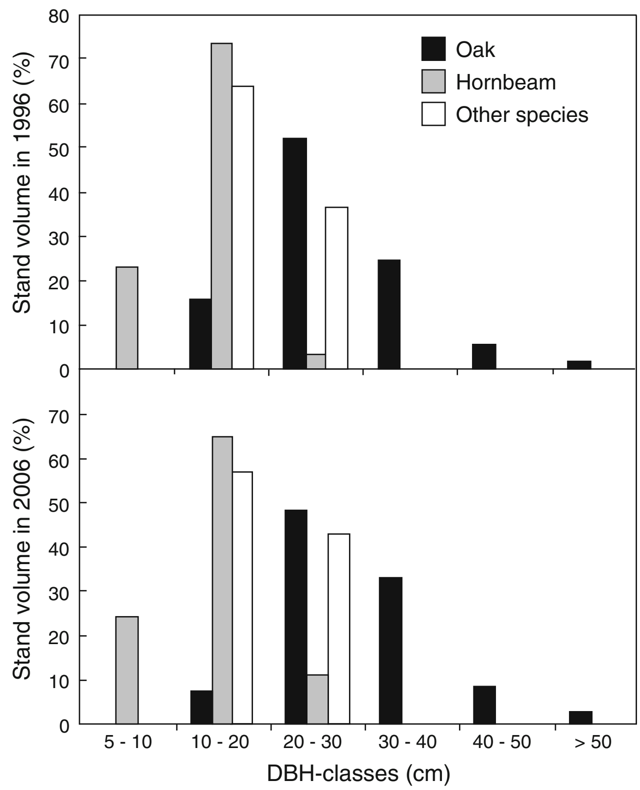

Fig. 2 Diameter distributions (diameter at breast height, DBH) of living trees in 1996 and 2006 according to stand volume and tree species per DBH class (% of total stand volume)

classes in 1996 and 45% in 2006. The relative percentage of the volume of oak decreased in smaller classes (10–20 and 20–30 cm) and increased in higher classes (30–40, 40–50 and >50 cm) from 1996 to 2006 (Fig. 2). The absolute differences in diameter distributions between 1996 and 2006 for oak, hornbeam and the other tree species were 0.12, 0.09 and 0.07, respectively, where the overall absolute difference was 0.11.

Due to the growth of individual trees between 1996 and 2006 the percentage of living trees decreased from 1996 to 2006 in the DBH classes 5–10 and 10–20 cm while increasing in the other classes. Most ingrowths occurred in the 20–30 cm DBH class, and a relatively high proportion of trees shifted from the DBH classes 10–20, 20–30 and 30–40 cm to the next higher class, respectively (Fig. 3).

Tree mortality and deadwood

Of the stand volume of living trees found in 1996 (245.2 m^3/ha), 233.2 m^3/ha (91.7%) were still living in 2006, while 14.8 m^3/ha (5.8%) had become standing deadwood, and 6.2 m^3/ha (2.5%) had become fallen deadwood. The proportion of surviving trees was 93.4% for oak, 79.3% for hornbeam trees and 100% for the other species. The proportion of deadwood from hornbeam (20.7%) was higher than that from oak (6.6%).

Changes in the distribution of standing deadwood according to DBH class between 1996 and 2006 are shown in Fig. 3. The highest increase of standing deadwood was found in DBH class 10–20 and 20–30 cm. Of the standing deadwood measured in 1996, 49.8% remained standing deadwood and 50.2% became fallen until 2006. The fall rates of standing deadwood for oak, hornbeam and other

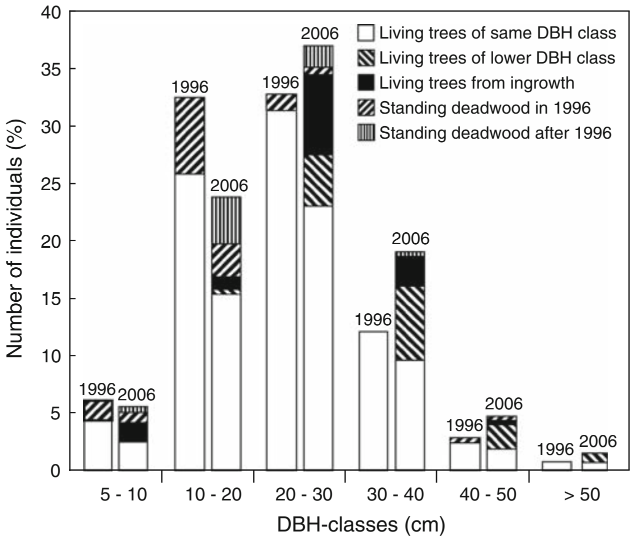

Fig. 3 Diameter distributions (diameter at breast height, DBH) of living trees and standing deadwood from 1996 and 2006 according to number of individuals per DBH class (% of total number of trees)

species were 48.6, 43.4 and 100%, respectively (Table 3). Most of the fallen deadwood (17.0 m^3/ha) was in the 10–20 cm DBH class, followed by the 5–10 and 20–30 cm classes.

Discussion

Forest structure and dynamics

Our study of the Lange Leitn Natural Forest Reserve focused on an estimation of both increment rate and mortality rate in a 10-year interval. The Lange Leitn can be characterised as an oak-dominated forest reserve where hornbeam is the substantially co-occurring species. The relative proportion of the volume of oak increased, while the proportion of hornbeam decreased during the last 10 years under natural conditions. The age of the forest since the last coppicing is estimated at 70 years. Considering this age, Lange Leitn seems to be at an early stage of development, considering that the life cycle of a mixed oak hornbeam forest is several hundred years long. Due to the scarcity of similar types of natural reserves, the present life cycle stage cannot be compared with others. Presently, small changes in the proportions of the tree species are happening, in which the share of hornbeam (a species with pioneer characteristics and fast growth during youth) decreases and the share of oak (a climax tree species with a flatter growth curve) increases. Both the increment and the mortality rate of oak showed a tendency towards a more oak-dominated development phase of the stand, even if it must be considered still a 'young development phase' in the life cycle of a forest. Although the stages of development and observed changes in species composition were quite different between the 24 sample plots (illustrated by the high standard deviations for all growth parameters), the trend towards an increasing dominance of oak and a decrease of hornbeam was evident. However, a 10-year period is too short to draw conclusions about the general natural dynamics in the forest, and other directions in natural development might be possible as well. For instance, studies from the Białowieża National Park in Poland show the opposite result that the major tree species in oak-dominated forest communities can be gradually replaced by lime and hornbeam (Brzeziecki and Bernadzki 2008). Therefore, further monitoring will be needed in the Lange Leitn natural reserve.

A comparison of the results with other published data was hampered by the fact that most studies have worked on beech dominated natural reserves in Europe (Schnitzler and Borlea 1998). In that context only results from forest stands located in Poland and dominated by beech like the Gorce Mts. (Łopuszna reserve), Walusiőwka stand (Pieniny National Park) and Jawornik 1 stand (Bieszczady National Park) could be obtained. These studies found changes in species composition according to the stand volume of 0–3.2% (Jaworski and Karczmarski 1994), 0.4–2.6% (Jaworski and Podlaski 2007) and 1.9% (Jaworski and Kolodziej 2002a, b). The small changes among the different species in our forest reserve occurred within one decade, which was too short to draw a conclusion about

Table 3 Structural changes of living trees from 1996 (L), living trees from 2006 (SL), standing (SD) and fallen (FD) deadwood from 2006 (mean volume ± standard deviation)

Species	Living trees (L) in 1996						Standing deadwood (SD) in 1996			
	SL_{2006}		SD_{2006}		FD_{2006}		SD_{2006}		FD_{2006}	
	Volume (m^3/ha)	%	Volume (m^3/ha)	%	Volume (m^3/ha)	%	Volume (m^3/ha)	%	Volume (m^3/ha)	%
Oak	194.9 ± 85.1	93.4	12.5 ± 20.7	6.0	1.2 ± 5.9	0.6	9.0 ± 16.2	51.4	8.5 ± 16.5	48.6
Hornbeam	27.9 ± 33.8	79.3	2.3 ± 6.3	6.5	5.0 ± 17.8	14.2	1.7 ± 6.8	56.6	1.3 ± 4.4	43.4
Others	10.4 ± 32.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0 ± 5.1	100.0
All	233.2 ± 76.0	91.7	14.8 ± 20.2	5.8	6.2 ± 13.4	2.5	10.7 ± 15.9	49.8	10.8 ± 17.5	50.2

the causes of these changes (Jaworski and Kolodziej 2002a, b).

The decrease of hornbeam in the stand volume between 1996 and 2006 in the Lange Leitn natural reserve occurred due to a high mortality and low ingrowths compared to oak. As mortality of hornbeam took place in the lower diameter classes mostly it is supposed that inter- and intraspecific competition were the main reason for this development. If this trend continues, it can be assumed that approximately after five decades hornbeam might get lost from this reserve. However, the absolute differences in diameter distributions between 1996 and 2006 indicated that the distributions changed less for hornbeam than for oak. The greater growth increment of oak compared to hornbeam justified this discrepancy. The mean increment of 1 m^3 ha^{-1} $year^{-1}$ is low, but comparable to other studies in managed oak-dominated forests (Hochbichler 2008).

The overall mortality rate for the period of 10 years was 0.9% per year. Oak had a mortality rate 0.7%, while the mortality rate of hornbeam was 1.8%. Our results are comparable to studies from beech and oak-dominated forests, where rates of 0.8–1.0% in France (Lemée 1978), 0.8–1.2% in Poland (Jaworski and Kolodziej 2002a, b; Jaworski and Podlaski 2007), 1.0% in northern temperate regions (Peterken 1996) or 0.9% in North America (Wilson and McComb 2005) were found. Among the standing deadwood of 1996, 49.8% remained standing and 50.2% became fallen deadwood until 2006. Wilson and McComb (2005) found 63% fall rate within 10 years in a North American Forest. The diameter of the fallen deadwood did not exceed 30 cm, but there was still some standing deadwood with diameters of 30–50 cm (Fig. 3). So it can be concluded that in larger diameter classes the fall rate is lower and the period of time that snags remain standing is positively correlated to their diameter (Everett et al. 1999; Morrison and Raphael 1993).

Sampling method

One of the main objectives of establishing natural forest reserves is to monitor natural vegetation processes, which will be used as a reference value in near-to-nature management of the same forest types. The Austrian Federal Forest Research Institute adopted the Bitterlich sampling method in their inventories because they considered this method a quick and inexpensive technique to determine the annual compensation for landowners (Frank and Müller 2003). As the probability for trees to be sampled with the Bitterlich method is proportional to the size of the sampled trees, the use of this technique for assessing forest dynamics in natural reserves is limited.

Our results demonstrate that the Bitterlich sampling allows the description of changes in the proportions of tree species and diameter classes as well as an estimation of the mortality rate. However, a limitation of the technique is that losses and recruitments, which occur simultaneously in forests with natural dynamics (Dziewolski and Rutkowski 1987; Jaworski and Kolodziej 2002a), are not fully covered. Usually, recruitment occurs within the smallest diameter class, while deadwood can be expected in all diameter classes. For this reason, the volume of recruited trees usually remains lower than that of deadwood (Jaworski and Kolodziej 2002a; Jaworski and Podlaski 2007). In contrast, we estimated a total amount of 43.3 m^3/ha as "recruitment" (considered as ingrowths in this study) but only 21.0 m^3/ha as deadwood during 1996–2006. The highest proportion of ingrowths occurred in the 20–30 and 30–40 cm DBH classes, rather than in the smallest ones (Fig. 3). The reason for these contra-intuitive results is the systematic favouring of trees with larger diameters by the sampling method.

The reliability of estimates based on the Bitterlich sampling method can be checked by also considering the growth of individual trees. In our study, the growth of living trees sampled both in 1996 and 2006 indicated a large difference in mean growth between oak (+4.6%) and hornbeam (+1.7%), which corroborated the estimated changes in total volume for these two species.

Another limitation of the Bitterlich sampling technique is that fallen deadwood cannot be measured directly. As we identified fallen deadwood by observing the individual life history of each tree only, we missed the information regarding the fallen deadwood before 1996 and the changes regarding the decay stages, which is important for biodiversity aspects (Heilmann-Clausen and Christensen 2003). In that context it can be assumed that we missed an important part of the overall forest dynamics. Another limitation of the study was the small plots size (1 plot representing 1.21 ha) resulting in high standard deviations of the measured parameters among the 24 plots.

There is a scarcity of data for analyzing forest dynamics in most of the established 200 natural reserves in Austria. Since the initiation of the natural reserves, the Bitterlich method has been used to calculate the compensations for forest owners. We conclude from our study that the Bitterlich sampling can be used effectively for this purpose, but that a minimum core area in the reserve should additionally be established for an intensive monitoring of the forest dynamics under natural conditions (Parviainen et al. 2000). These core areas should be used for detailed measurements according to site and stand characteristics (e.g. shrub and ground vegetation layer, natural regeneration, deadwood). The combined analysis of detailed data from such core areas and the stand inventory data will then allow drawing a holistic picture of the natural stand development.

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