Canopy gaps in two virgin beech forest reserves in Slovakia

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ABSTRACT: The formation, size distribution and percentage of gaps in two virgin deciduous forests are presented in two case studies. Gaps are defined as openings in the canopy above 2/3 of stand height. These gaps comprise 16% of the forest area in Havešová Reserve and 14.6% of the forest area in Kyjov Reserve. The estimated turnover time is 220 years. More than half the gaps were caused by the death of one tree, and 80% of the gaps were due to the death of up to 3 trees. The largest gap in Havešová Reserve was 0.40 ha, resulting from the death of 56 trees over the last 40 years. The area of the largest gap in Kyjov Reserve was 0.44 ha. It was caused by the death of 80 trees over the last 40 years. Such large gaps are scarce. 85% of the gaps are smaller than 250 m². A correction of the bias towards the over-abundance of large gaps by line-transect sampling was made by estimating the percentage area of gaps of different size from the percentage length along the transects. In Havešová an attempt was made to date the death of trees that were still visible in the gaps. 1/5 of the trees initiated gaps by their death, while 4/5 of the trees extended gaps. While uprooted trees dominate in Havešová, breakage is most common in Kyjov.

Keywords: natural disturbance; gap size distribution; gap formation; European beech

The creation of gaps in harvesting operations offers a good opportunity to form forests with structure resembling older, natural forests. If naturalness is a management aim, the percentage of gaps in the forest area, gap size distributions and gap formation rates should be known. Yet investigations of gap size in virgin European beech forests are scarce. Tabaku and Meyer (1999) described gap patterns in three Albanian forest stands, and Zeibig et al. (2004) described a forest in Slovenia. Additional research undertaken to enhance knowledge about the nature of gap patterns in relation to site conditions would make a useful contribution to the existing worldwide investigations of gaps in beech forests (e.g. Runkle 1982; Nakashizuka 1988; Yamamoto, Nishimura 1999). We present two case studies in which gap investigations were undertaken in virgin beech forests in Central Europe. We want to answer two questions: 1. What is the proportion of gaps in the forest? 2. Are small or large gaps the dominant canopy opening?

Study area

The research sites are located in eastern Slovakia (48°56´N, 22°11´E and 48°48´N, 21°59´E). The Havešová reserve is situated at a height of 500–650 m above sea level on a south facing slope in the Beskids Mountains and covers an area of 170 ha. The reserve is composed of the plant association *Dentario glandulosae-Fagetum* with a gradient to *Carici pilosae-Fagetum* on the upper slope. The annual rainfall ranges from 700 to 800 mm (450 mm in the growing season) and the average annual temperature is 7°C. The well-developed mesotrophic brown earth covers sedimentary sandstone, occasionally interspersed with shale. The moderately acidic soil has good water holding capacity and nitrogen availability. The stand height is approximately 45 m, but isolated trees grow higher than 50 m.

The Kyjov reserve is situated at 700–820 m a.s.l. on a north facing slope in the Vihorlat Mountains and covers an area of 53 ha. It is composed of the plant

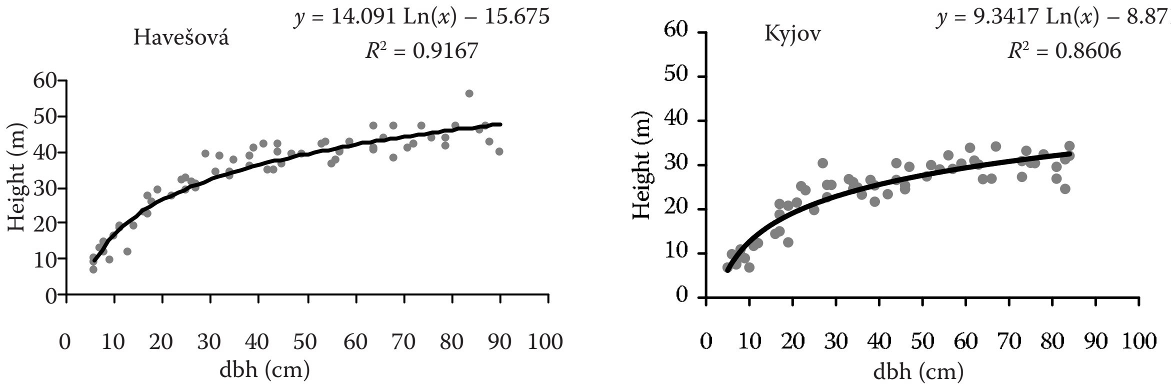

Fig. 1. Stand height curves for Havešová and Kyjov Reserves

association *Dentario glandulosae-Fagetum*. The annual rainfall ranges from 750 to 800 mm and the average annual temperature is 6°C. The mesotrophic brown earth over andesite is moderately acidic and has good water holding capacity and nutrient availability. Stand height is approximately 30 m, although the largest trees can reach 34 m. At Kyjov the tree height growth is limited by the occurrence of shallow soils, exposure of sites to strong winds and, sometimes, icy slopes due to the presence of an artificial lake nearby.

A continental climate prevails in both reserves, which are located 50 km apart. The admixture of other tree species (*Acer pseudoplatanus*, *A. platanoides*, *Fraxinus excelsior*, *Ulmus glabra*) is less than 1%. A more extensive description of the forest stand structure is given in Korpeľ (1995).

METHODS

Gap definition

In each reserve the dbh and height of 60 trees, regularly distributed in all size classes, were measured to obtain stand height curves. These curves facilitated the estimation of stand height and the division of stands into 3 height strata. Following Runkle's (1992) recommendations, a gap was recorded where a canopy opening occurred in the upper stratum above 2/3 of dominant tree height. The stand height at Havešová was 45 m, with the upper stand stratum beginning at 30 m height. The stand height in Kyjov was 30 m, with the upper stratum beginning at 20 m height (see Fig. 1).

According to the height curves, a tree growing into the upper stratum has a dbh of approximately 30 cm at Havešová and 20 cm at Kyjov. These dbh values were used to distinguish between gaps in regeneration and closed forest.

In addition, gaps along the transects were delineated using a common gap definition (trees ≥ 7 cm dbh) to facilitate comparisons with other gap investigations.

In accordance with Runkle (1992) gaps were not confined to the area directly below the canopy opening. The extended gap, i.e. the area between the bases of the trees forming the gap boundary (Fig. 2), was also recorded and is similar to Runkle's expanded gap.

Gap sampling

A grid of line transects, similarly apportioned parallelly and perpendicularly to the slope, was used to determine the percentage area of gaps in the forests. The segments along the transects were measured where canopy openings, extended gaps and closed canopy cover occurred. The percentage length of these forest characteristics along the transects served to estimate their percentage area in the forest.

Atypical sites, such as deeply eroded streambeds or sites with slopes > 30°, were excluded from further measurements. Eight gaps in Havešová were thus excluded. For the remaining gaps the areas of the canopy gap and extended gap were measured.

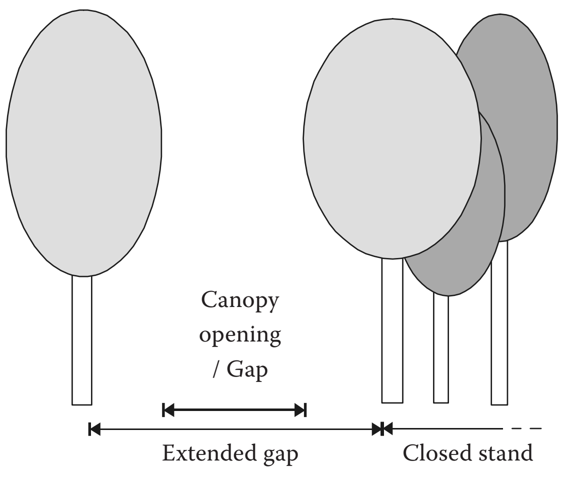

Fig. 2. Gap definitions for canopy opening and extended gap

Adopting Runkle's (1992) recommendation the formula for the area of an ellipse was used to estimate the area of individual gaps, where the maximum width of the gap and the width at right angles to this length constituted the length and width of the ellipse, respectively. Where more than 10 dead canopy trees occurred in a gap, or in other cases where gap shapes were non-elliptical, the gap area was derived as a polygon.

Dead canopy trees with dbh ≥ 30 cm in Havešová and dbh ≥ 20 cm in Kyjov were recorded in the extended gap and regarded as gap creating trees. The mode of death (uprooting, partial uprooting, breakage with stump height, standing death and partial death) was recorded according to Runkle (1992).

Gap size distribution

When sampling with line transects, large gaps are over-represented. Since the relative probability that a gap is crossed by the transect line is approximately equal to the gap diameter, Runkle (1982) takes the square root of the area of every gap, which is proportional to the diameter of a circular gap. However, one may also correct the bias by estimating the percentage gap area from the percentage gap length along the transects. This error of estimation needs to be calculated for each gap. The first step is to calculate the percentage gap length from the total transect length. Percentage of length in gaps serves as an estimate of the percentage of forest area in gaps. The second step is to calculate the percentage area of each gap from the total area of all gaps. The percentage length of a gap would correspond to the percentage area if the gap were sampled representatively. Differences may be corrected by the quotient derived from the percentage length of a gap along the transect length and the percentage area of this gap. This quotient represents one gap. The theoretical number of gaps is then obtained from the sum of the quotients of all gaps. The representative percentage of each gap is derived from the theoretical number of gaps.

For example, assume there is a gap of the length 8.2 m along the transects, comprising an area of 42 m^2. All gaps have a total length of 815.1 m along the transect with a total area 28,288 m^2. Thus the percentage length of the gap along the entire transect is 1.006%, and yet the percentage of the total gap area is only 0.148%. The ratio of these factors provides a correction factor: 1.006/0.148 = 6.797. By adding up the correction factors of each gap we calculate the theoretical number of gaps to be 318.6. Consequently the representative percentage of the gap is 2.13% (= 6.797/318.6).

To obtain representative percentages of dead trees (Figs. 6 and 8, Tables 2 and 3), every dead tree was given the representative value of its gap. Theoretical absolute frequencies were then converted to relative frequencies.

Estimating time since death of trees

In Havešová an attempt was made to estimate the year of death of trees creating gaps. Initial estimates were based on the observed state of decay. However, sometimes the actual year in which trees estimated to be in a similar state of decay died differed by 10 years. In most cases trees in the understorey or regeneration demonstrated rapid acceleration of shoot growth or damage as a result of release. Such events could be dated by counting the annual bud scars of understorey trees and provided accurate estimates of the year of death for trees that died in the last 20 years. For trees that had died earlier, a core was extracted from trees released as a result of tree death to identify sudden increases in annual ring width. The error in the dating is subjectively estimated to be ± 5 years for periods longer than 20 years and ± 10 years for periods longer than 30 years.

In Kyjov the estimation of the year of death was limited to trees that died in the last 10 years. Estimates were difficult as vigorous ground vegetation had impeded regeneration growth in the intervening years. In Havešová the seedlings were not impeded

Table 1a. Percentage area of canopy gaps in the forest area: gap closure by regrowth reaching 2/3 of the stand height (see gap definition)

	Total transect length	Canopy gaps (%)	Extended gaps (%)	Closed stand (%)
Havešová	5.753 m	16	50	50
Kyjov	3.051 m	15	55	45

Table 1b. Percentage area of gaps with gap closure defined by trees of 7 cm dbh

	Total transect length	Canopy gaps (%)	Extended gaps (%)	Closed stand (%)
Havešová	5.753 m	7	21	79
Kyjov	3.051 m	8	28	72

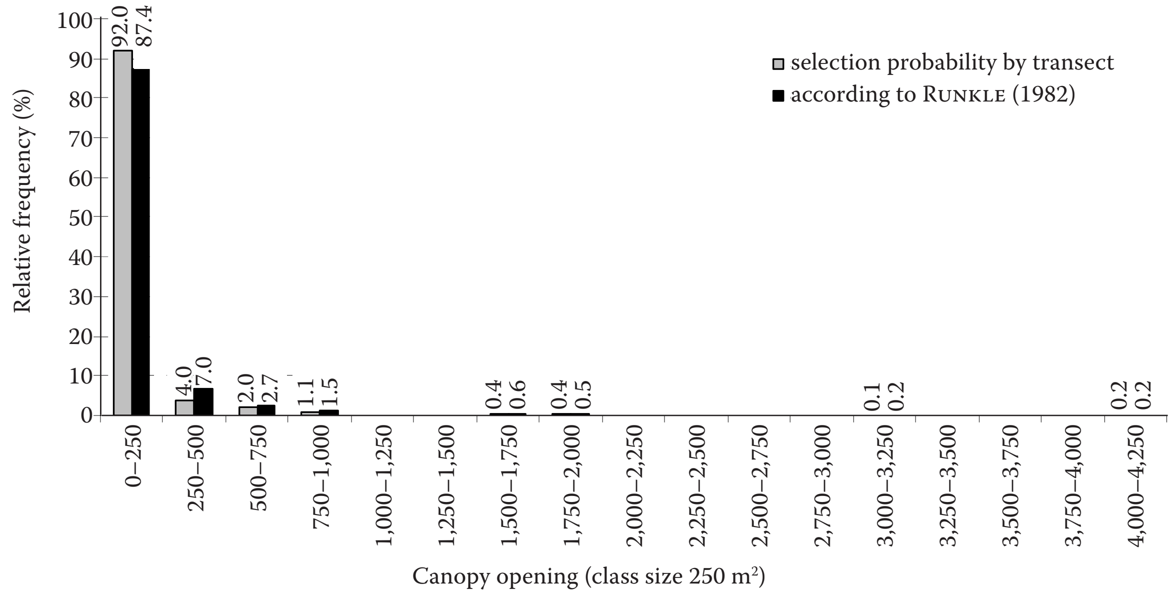

Fig. 3a. Frequency of canopy openings of different size in Havešová, corrected as described in Gap size distribution and by RUNKLE (1982). The gap is defined as an opening in the canopy where regrowth is less than 2/3 of the stand height

by such vigorous undergrowth following the gap creation and were already partly visible.

Gap formation rate

RUNKLE (1992) calculated the gap formation rate as the percentage of total gap area ≤ n years old divided by n. In this study the time since death of trees was recorded because trees in any given gap did not die in the same year. Thus the calculation of gap formation rate is not based on the proportion of gaps formed during a certain time period, but on the proportion of trees that died in that period. The proportion of dead trees < n years was multiplied by gap percentages. This reduced value was divided by n to obtain an annual gap formation rate.

For example, if the area in gaps at a site is 15% and 31% of the trees in that site died in the last 10 years, the annual rate of gap formation is 0.465% (15% × 0.31 = 4.65%). The reciprocal value of the gap formation rate provides turnover time (RUNKLE 1992) which, in this example, is 215 years.

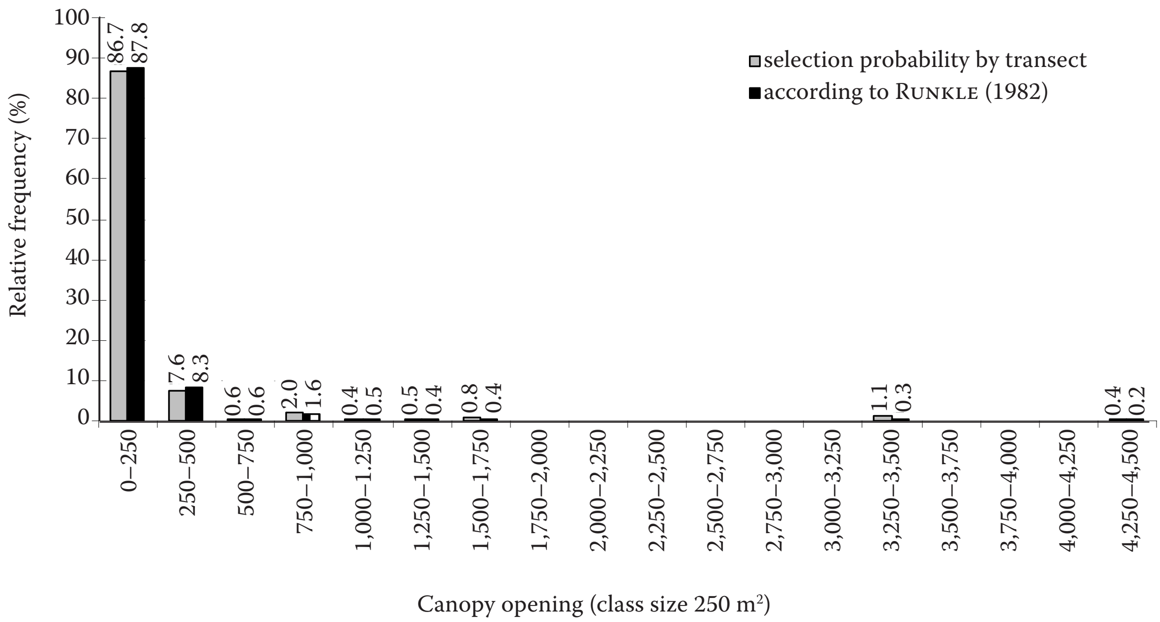

Fig. 3b. Frequency of canopy openings of different size in Kyjov, corrected as described in Gap size distribution and by RUNKLE (1982). The gap defined as in Fig. 3

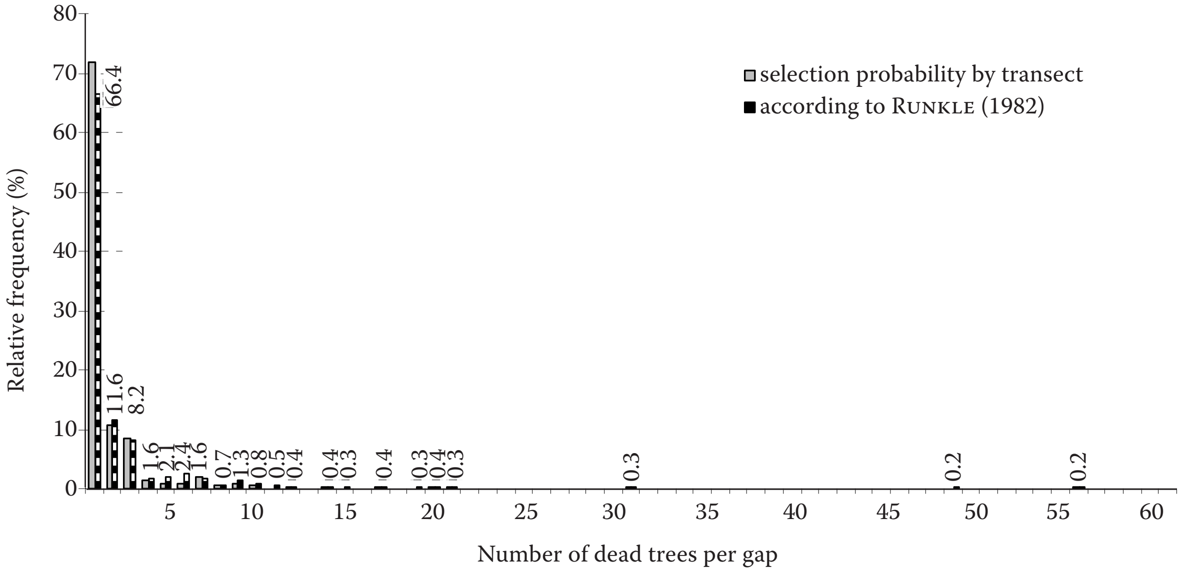

Fig. 4a. Frequency of gaps in Havešová in relation to the number of dead trees per gap (both correction methods are presented here and described in Gap size distribution and by RUNKLE 1982; values according to RUNKLE are given)

RESULTS

Gap fraction

Canopy gaps in the upper canopy comprise approximately 15% of the forest area (Table 1a), with extended gaps comprising 50% to 55%. Only about half the forest area constituted closed stands. However the gap area decreases when the gap closure is defined by trees with dbh 7 cm (Table 1b), indicating that the percentage gap area is largely dependent on how the threshold is defined.

Gap size distributions

In Havešová and Kyjov Reserves 66 gaps and 43 gaps were recorded along the transects respectively. This corresponded to 445 dead trees in Havešová, and 366 dead trees in Kyjov. In Figs. 3a and 3b more than 85% of the canopy gaps are smaller than 250 m². Around 10% of gaps are openings between 250 and 1,000 m², and 1–3% of the gaps are larger than 1,000 m². If one divides the first gap class into 4, about 75% of all gaps are smaller than 62.5 m². The area of 7% of gaps ranges from 62.5 to 125 m².

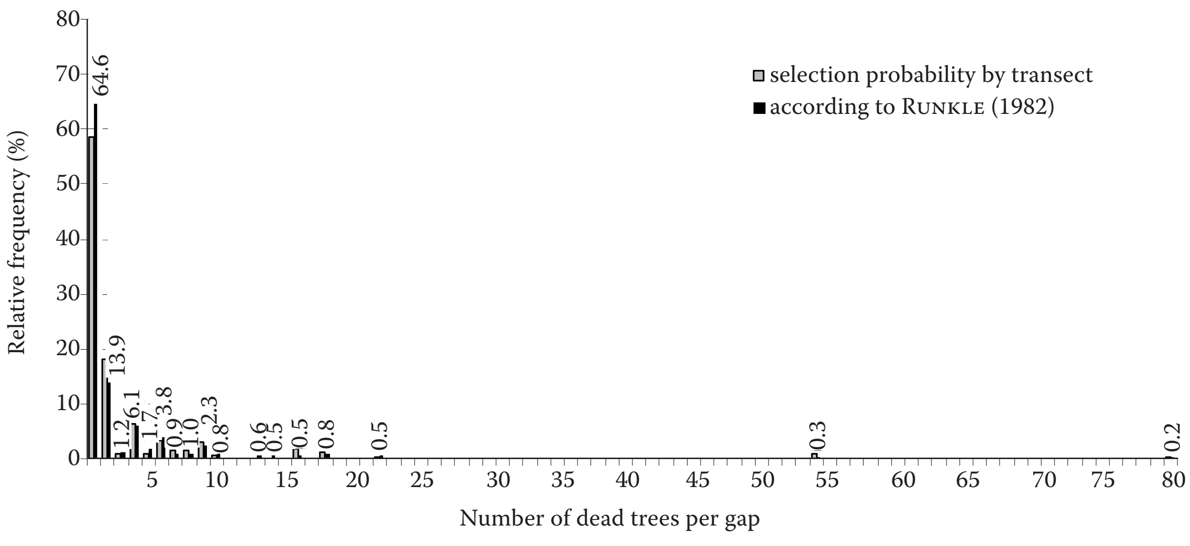

Fig. 4b. Frequencies of gaps in Kyjov in relation to the number of dead trees per gap (both correction methods are presented here and described in Gap size distribution and by RUNKLE 1982; values according to RUNKLE are given)

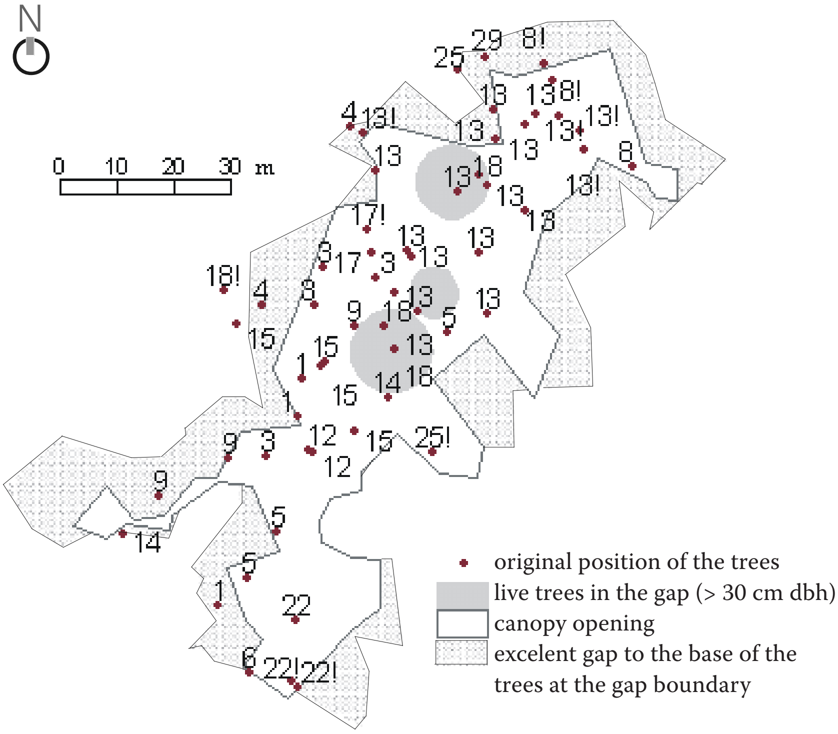

Fig. 5. Map of the largest gap along the transects in Havešová. The number adjacent to the original position of the trees is an estimation of the number of years the tree was dead. Cases where the timing of death is uncertain are identified with an exclamation mark

4% of gaps have an area ranging from 125 to 187.5 m^2, and 2% from 187.5–250 m^2. The number of gaps decreases exponentially with increasing gap size. The two correction factors used in this study produced very similar results.

Two thirds of gaps are single-tree gaps and 20% are caused by the death of 2, 3 or 4 trees (Figs. 4a and 4b). As the trees creating gaps were identified using woody debris analysis, a two-tree gap might be identified in which the first tree died 40 years ago and the second tree one year ago. About 3–5% of gaps have more than 10 trees. Figs. 4a and 4b depict clear exponential relationships between the number of dead trees per gap and relative frequency of gaps. More than 50 dead trees per canopy opening are very scarce, but they do occur.

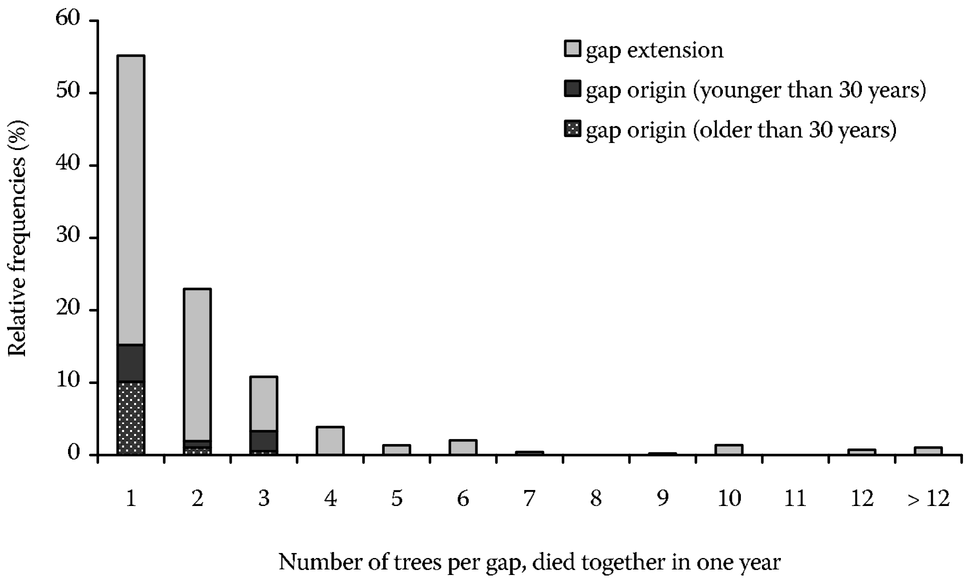

Fig. 6. Frequency of single dead trees or groups of dead trees in each gap. (Dating the origin of gaps more than 30 years old is fairly unreliable due to increasing probability of completely decomposed trees; correction for representativeness of trees in gaps of different size is described in Gap size distribution)

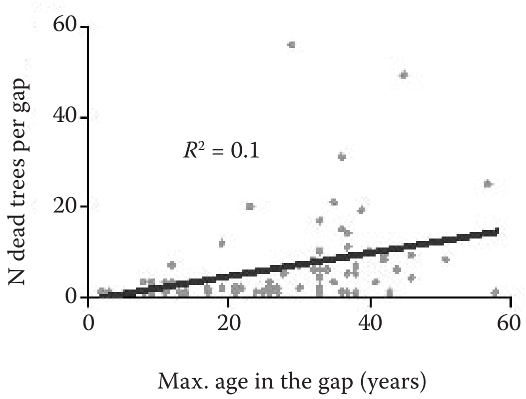

Fig. 7. Number of dead trees per gap in relation to the age of the oldest dead tree in the gap (without correction for the under-represented smaller gaps and over-represented larger ones)

The reconstruction of complete gap history is not possible. Former canopy trees that were completely decomposed were no longer visible and consequently neglected in the investigation. Time estimations of total decay of a canopy tree are presented in sections 4.4 and 5.3.

Tree mortality and gap formation

Fig. 6 shows the proportion of trees that died in groups or singly in all gaps at Havešová. More than half of the trees creating gaps died singly. Groups with more than 12 trees occurred only once: 18 trees fell together in the largest gap (Fig. 5). Allowing for the uncertainties in dating, a gap was created suddenly (gap origin) by the death of 1/5 of the trees and the gap was extended by 4/5 of dying trees. However, the mean age of single-tree gaps (22 years) and of the oldest trees creating gaps in larger gaps (26 years) did not differ greatly, indicating a continuous extension of most small gaps. The number of dead trees increases proportionally with the age of the oldest trees in the gap on average. This relationship is very weak, however (Fig. 7).

An example of gap formation is provided in Fig. 5, showing the history of the largest gap at Havešová. The gap consisted of small spot gaps eighteen years ago. Around thirteen years ago most trees in the northeast section were windthrown. In the southwest corner isolated small gaps joined gradually.

In Havešová half the trees found in gaps died by uprooting (Table 2). The trees often had broken boles. In Kyjov Reserve most trees died after breakage and 1/5 by uprooting.

The maximum dbh for dead trees was 140 cm in Havešová and 116 cm in Kyjov.

Turnover time

The time of death of trees in a gap varied, sometimes considerably. Thus the calculation of turnover time is based on estimated ages of dead trees as described in 3.5.

The turnover time varies in relation to the chosen time period (Table 3). In our calculations we assumed a monitoring period of 35 years, based on the estimated average period of decomposition of the trees. The method used to derive this estimate is explained in detail below. The turnover time in Havešová and in Kyjov was 218 years and 239 years, respectively. One might also assume a period of 30 (or 40) years on average before trees decompose

Table 2. Percentages of mortality causes of canopy trees (values calculated representatively as described in Gap size distribution)

	Uprooting**	Partial uprooting	Breakage	Standing dead	Partial dead	No. of dead trees
Havešová	49.1	3.9	44.9	0.1	2.0	445
Kyjov	20.8	1.6	72.9	1.5	3.2	366

Table 3. Gap formation rate and turnover, calculated by gap percentages and proportion of trees that died less than 10, and 20 years ago

	Havešová			Kyjov	
Gap percentages (GP)	16.02	16.02	16.02	14.63	14.63
Time period (years), counted back	10	20	35**	10	35**
Percentage of trees that died in this period (TP)	24.18	66.04	100	31.21	100
GP × TP/100*	3.87	10.58	16.02	4.56	14.63
Gap formation rate (% per year)	0.387	0.529	0.458	0.456	0.418
Turnover time (years)	258	189	218	219	239

*Example of calculation in Gap formation rate, ** assumed monitoring period completely (e.g. Müller-Using, Bartsch 2003; Saniga, Schütz 2002). This assumption results in a turnover time of 187 (250) years at Havešová and 205 (273) years at Kyjov. Differences of 60–70 years exist because the average time of decomposition is not known exactly. Furthermore the turnover time was calculated for the last 10 years because dating the death of trees was most reliable in this period. In Havešová the turnover time in the last 10 years differs considerably from the turnover time in the last 20 years, because fewer trees died during the last decade than in the previous decade (Fig. 8).

A linear regression of trees dead for more than 20 years shows that a decreasing number of trees died between 20 and 50 years ago. It should be noted that the time required for complete decomposition of a tree or the course of decomposition are unavailable. 20 years was adopted as the beginning of the regression since the complete decomposition of a canopy trees after 20 years is not possible. That may also be the case in later years. Here a linear decomposition is assumed to determine the average duration of decomposition of trees. For Havešová we estimate a mean period of 35 years for total decay of canopy trees, ranging from 23 to 58 years. The maximum duration of decomposition was estimated for a large tree, probably stored dry at 1.5 m height, although backdating has an associated error of ±10 years.

DISCUSSION

Peters (1997) indicated that, in relation to growth rate increases in the stem diameter, greater dynamic changes occurred in the canopy of beech forests in North America than in Europe. He believed that high wind speeds in the south-eastern USA and in eastern Asia, in addition to the very high frequency of tornadoes in the USA, were the cause. The disturbance rate in North American forests, comprising mixed forests with American beech, amounts to 0.5–2.0% per year (Runkle 1982). Turkish and Asian forests appear to be less dynamic (Peters 1997). Yet even here Sagheb-Talebi and Delfan Abazari (2003) found a 1,680 m² canopy opening. They stressed the similarities between beech forests in the Orient and Eastern Europe. In Japanese beech forests gap percentages range from 6.2 to 37.5% (Nakashizuka 1988; Yamamoto, Nishimura 1999). This may be due to the small study areas (1–6 ha) or it may support a distinction between species. Although Runkle (1985) assumed that different mixed broadleaved forests did not probably exhibit large differences in their average rates of disturbance, here we restrict the discussion to *Fagus sylvatica*.

Methodological aspects

The spatial and temporal limitations in this investigation meant that large-scale disturbances in the landscape could not be detected. Thus conclusions about the naturalness of the silvicultural systems in this study, such as Seymour et al. (2002) proposed, are strictly limited to disturbances causing the removal of single trees or groups of trees. Shelterwood harvesting methods were not adequately considered where information about gap density was unavailable. Large beech forests that were not managed for timber extraction in the past still exist in Ukraine and Romania. These forests, covering an area of about 10,000 ha, provide an opportunity to investigate large disturbances. In such investigations aerial surveys and digital surface models of the vegetation layer are useful for computing gap percentage, size distribution and gap density (Tanaka, Nakashizuka 1997; Nuske, Nieschulze 2004).

In this terrestrial survey we opened a "time window" of 30–40 years, covering the period from death of trees to gap closure or the almost complete decomposition of trees. Although uneven-aged virgin forests should facilitate studies that are largely time independent, storm incidents are discrete and randomly distributed events in time (Bielec-Bakowska 2003; Dobrovolný, Brázdil 2003). A theoretical model of the dynamics of spatial structures in European beech forests by Neuert (1999) illustrates that the upper canopy cover depends mainly on heavy storm events. Furthermore, ice damage may affect the number of large gaps considerably (Standovar, Aszalos 2001).

Gap definitions, coverages and sizes

As young trees of different dimensions may occur in gaps, an arbitrary boundary must be drawn between regeneration in the gap and the closed stand. The definition of a gap as an opening in the canopy in the upper height stratum is justified by the traditional division of stand into 3 height strata (Leibundgut 1956) and our interest in the recruitment of the overstorey. We observed that 30 cm dbh in Havešová and 20 cm dbh in Kyjov were generally the smallest sizes at which trees were capable of creating overstorey gaps. These sizes are in accordance with Runkle (1982), who declared gaps to be closed when young trees prevented a ground observer from readily observing the canopy opening. Additionally, the definition of gaps as > ½ of stand height is more appropriate for comparisons with aerial surveys. While the distinction between regeneration in the gap and closed stand using dbh instead of tree height was adequate in Havešová, in Kyjov more tree crowns were damaged making the distinction by height measurements necessary.

The distinction between gap and non-gap represents a simplification of forest structure (Lieberman et al. 1989). However it was adhered to in this study for practical reasons. If a single branch touched a neighbouring tree, the gap boundary was delineated.

The percentage of gaps defined by 7 cm dbh (Table 2) is provided for comparisons with Tabaku and Meyer (1999) and studies in even-aged forests (e.g. Schmidt 1996). Zeibig et al. (2004) defined gaps by trees that had not reached half the stand height. The greater the dbh/height adopted to define the threshold, the larger the gap. Further research into percentage representation of development stages should involve the investigation of gaps defined by 10, 20, 30, ... cm dbh along the same transect.

The percentage of gaps found by Tabaku and Meyer (1999) in three stands, and by Zeibig et al. (2004) was 3.3–6.6% and 5.6%, respectively. The values in this study exceed the range reported by Tabaku and Meyer. When applying the above-mentioned gap definition, the gap percentage in the Slovenian forest (Zeibig et al. 2004) was found to be slightly lower than in the Albanian or Slovakian forests. In this study, by determining the differences between gap percentages using the different definitions (Tables 1a and 1b), half the gap area defined by 2/3 of stand height was covered by trees with a diameter of at least 7 cm.

In addition to assessing the percentage area of gaps the line transect sampling also allows to derive a representative frequency distribution for gaps of different sizes (Runkle 1992). Despite the non-representative collection of data along the transects, a representative distribution can be obtained. In this study the two independent correction methods were found to be consistent (Figs. 3 and 4).

Tabaku and Meyer (1999) identified an average gap size of 61–74 m^2 with the range of gap size from 20 to 270 m^2, based on 3.6, 5 and 6 ha plots. The average was strongly influenced by a few large gaps. Zeibig et al. (2004) reported 3/4 of gaps smaller than 200 m^2 and 9% gaps between 200 and 600 m^2. This size distribution (with 6m^2 minimum gap area), comprising 49 gaps on a 12ha study plot, is very similar to Figs. 3a and 3b. Our sample included all gaps along the transects. Consequently the recording limit could be defined after sampling.

It is interesting to note that Zeibig et al. (2004) indicated that gaps between 200 and 600 m^2 took up more land area than gaps < 200 m^2. In Havešová gaps greater than 535 m^2 comprise half the total gap area. In Kyjov gaps greater than 875 m^2 comprise half the total gap area.

In this study there was a higher proportion of large gaps in the total gap area but a higher number of smaller gaps. Thus in Havešová 80% of all gaps are smaller than 130 m^2, corresponding to the mean crown cover of a canopy tree with 60 cm dbh. A tree with 80 cm diameter has a projected crown cover of about 200 m^2.

By comparison, the Heilige Hallen forest reserve in Germany has been unmanaged for 150 years and is composed of 250-year-old beech trees. For this old even-aged stand Tabaku and Meyer (1999) demonstrated a scale of decay processes in the canopy openings similar to those in natural forests: 13.3% gaps. The boundary between closed stand and gap was defined by trees of 35 cm dbh. Even gap size distributions in 120–160 years old beech stands that were not managed for 11–18 years (Richter 1990) are similar to those in Figs. 3a and 3b. But Richter assumed a gap creation rate of about 0.2% per year in these natural forest reserves. Manning and Smaltschinski (2001) calculated a gap percentage of only 1.9% in an uneven-aged beech stand that was unmanaged for 50 years. The lack of disturbance may be explained by the younger tree age compared to the oldest trees in virgin forests.

Age estimation, gap formation and turnover time

The time since death of trees was estimated from decomposition rather than measured. Yet this estimate is more useful for silvicultural purposes than assessing decay stages, described by qualitative features only. In view of Figs. 6, 7 and 8 estimations over 30 years old should be interpreted carefully. In extreme cases gaps that were created up to 58 years ago were found.

In Fig. 8 we can estimate the mean decomposition time of dead trees. If one assumes a constant number of dead trees in virgin forests over time and a more or less constant removal of these trees through decomposition, then the duration of this time period is estimated to be 35 years on average. Saniga and Schütz (2002) reported a decomposition period of 30–35 years in virgin beech forests. Müller-Using and Bartsch (2003) estimated 38 years for the mean decomposition period.

The calculated turnover time corresponds to the maximum life expectancy of 220 years (sometimes 250 years) of beech trees in Kyjov Reserve (Korpeľ

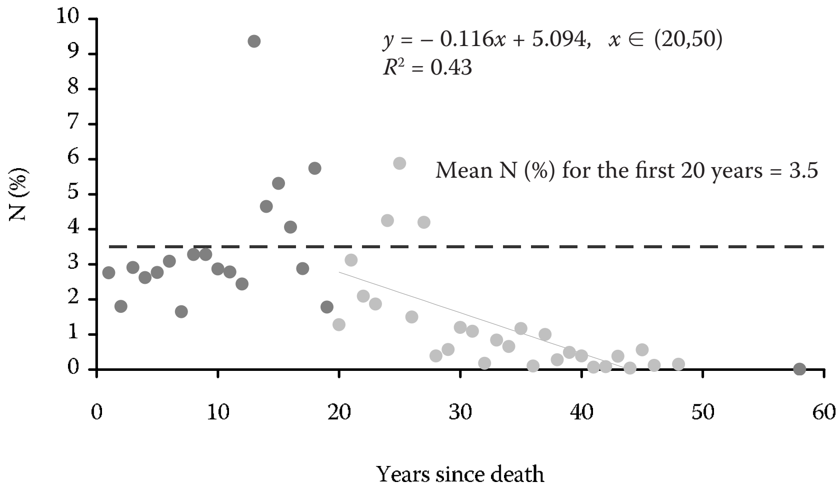

Fig. 8. Percentages of dead trees in relation to estimated time each tree was dead. Values up to 20 years are most reliable (see Estimating time since death of trees). Note that regression was performed for 20–50 years only

1967). Upon consideration of the different turnover times obtained for the monitoring periods of 10 or 20 years in this study, the turnover time for Havešová and Kyjov was estimated to be 220 ± 30 years (Table 3). Our canopy turnover rates are somewhat lower than observed in temperate deciduous forests in North America. Barden (1989) pointed to the effect of different sampling methods and gap definitions: he used 50 cm as minimum diameter of the trunk of a tree that could form a gap. That is why his turnover rate amounted to < 0.4%/yr in an old-growth hardwood forest of the Southern Appalachians while Runkle (1982) calculated 1%/yr. Our gap definition is in between, but in the upper range of Runkle's recommendations (1992): stand height 45 m (30 m) and gap closure > 30 m (20 m). Runkle (1982) commits in the forest with 32 m average stand height on gap closure in 10–20 m height and Barden (1989) on 18–30 m height. In this forest type Busing (2005) found a gap frequency ranging from 0.5% to 1.1% per year, estimated from canopy gap closure rates and the gap area. His estimations from the mortality of trees > 30 cm dbh gave frequencies ranging from 0.8% to 1.9% per year. Our modification of the gap definition might affect the estimates in comparison with Runkle (1982). But the canopy turnover rate is lower than 1%/yr as found in North American forests.

In Denmark Emborg et al. (2000) found that the complete forest cycle of a near-natural beech stand was a few decades longer, with a turnover time of 284 years. This may be due to the stand history. Individual trees released in managed stands may also exceed 300 years.

In addition Korpeľ (1967) identified the mean age of trees in closed stands 39 and 95 years in the lower and middle height stratum, respectively. Although trees grow faster in gaps, it is unrealistic to expect a 30 cm dbh tree after 35 years. In almost every gap at least one tree in the middle height stratum survived the canopy tree fall, explaining accelerated gap closure.

Adjacent canopy trees also contribute to gap closure (e.g. Schmidt 1996; Pedersen, Howard 2004).

Upon further consideration of the development stages in forests the presence of a large number of dead trees, which have expanded gaps further, supports the theory of shifting mosaics (Watt 1947) (Fig. 6). Fig. 7 also shows that a large portion of the single-tree gaps did not increase in size. Gaps can also been regarded as initial stages of development. Korpeľ (1967) identified isolated stages in Havešová und Kyjov on areas 0.5 ha in size. Differences certainly occur in the size distribution between gaps and later development stages although an exponential distribution is also probable. Isolated patches with an area of 0.5 ha are probably the less frequently occurring stages. If one adopts the theory of shifting mosaics, then the probability that these patches meet the more frequent smaller patches increases over time. For this reason we regard the documentation of the tree coordinates to be a useful addition to the valuable long-term studies in Slovakia, to assist the implementation of further research on development stages in the future.

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Porastové medzery v dvoch bukových pralesoch na Slovensku

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ABSTRAKT: Predmetom výskumu sú otázky vzniku a rozdelenia porastových medzier podľa veľkostí a plošné percentuálne podiely porastových medzier v dvoch listnatých (bukových) prírodných lesoch Slovenska. Porastová medzera je definovaná ako medzera v zápoji porastu, v ktorej existujúci porast je nižší ako 2/3 porastovej výšky. Tieto porastové medzery predstavujú 16 % porastovej plochy v Národnej prírodnej rezervácii Havešová a 14,6 % v Národnej prírodnej rezervácii Kyjov. Odhadovaná doba výmeny generácií je 220 rokov. Viac ako polovica porastových medzier bola vytvorená odumretím jedného stromu a 80 % medzier vzniklo ako dôsledok odumretia najviac troch stromov. Najväčšia porastová medzera v rezervácii Havešová mala výmeru 0,40 ha a bola spôsobená odumretím 56 stromov v posledných 40 rokoch. Rozloha najväčšej porastovej medzery v rezervácii Kyjov bola 0,44 ha. Bola vytvorená odumretím 80 stromov v priebehu posledných 40 rokov. Takéto veľké medzery sú zriedkavé. 85 % medzier je menších ako 250 m^2. Korektúra výchylky smerom k nadmernému zastúpeniu veľkých medzier v dôsledku výberu na líniovom tranzekte bola vykonaná pomocou odhadu percentuálneho podielu porastových medzier rozličných veľkostí a ich percentuálneho podielu na dĺžkovom zastúpení na tranzekte. V Havešovej bol vykonaný pokus o určenie času odumretia tých stromov v porastových medzerách, ktoré boli ešte stále viditeľné. Jedna pätina stromov bola východiskom pre vznik medzier, zatiaľ čo zvyšné 4/5 rozširovali medzery. Zatiaľ čo v Havešovej dominujú vývraty, je v Kyjove najbežnejšou formou odumretia zlomenie stromu.

Kľúčové slová: prirodzené narušenie; rozdelenie medzier podľa veľkosti; vznik medzier; buk lesný

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