Gap disturbance patterns of a *Fagus sylvatica* virgin forest remnant in the mountain vegetation belt of Slovenia

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Abstract
This study investigated disturbance patterns of a *Fagus sylvatica* virgin forest remnant based on an inventory of the horizontal canopy structure. Stand data were collected from the Krokar reserve in the Slovenian Dinaric Alps. The canopy layer was classified in gap and non-gap areas based on the terrestrial inventory, and compared with aerial photography interpretations. The study identified 49 canopy gaps, which covered 5.6 % of the reserve area. Gap size varied from 6 to 833 m^2, with a mean value of 137 m^2. Gap size frequency at 50 m^2-class intervals followed the log-normal distribution. Single-tree gaps were predominant and the directions of the main gap axes were randomly distributed. Considering the canopy dichotomously as gap and non-gap areas proved to be a suitable procedure to analyse gap dynamics in one-layered, beech-dominated virgin forests. Gap formation was influenced by a combination of both endogenous and exogenous environmental factors. Saprophytic fungi and wind were the main components of the disturbance regime. Gaps were relatively small and they occupied a small land area. These features may be attributed to interactions between climate, landform, rich soils, disturbance regime and the ability of beech to close gaps by lateral branch growth.

Keywords: *Fagus sylvatica,* European beech, canopy gap, disturbance regime, virgin forest, gap formation

1 Introduction

Ecological research in virgin and natural forests of the northern hemisphere has been carried out since the middle of the 20th century. In East and South-East Europe, analyses with special regard to stand and age structure were performed and developmental stages distinguished (e. g. LEIBUNDGUT 1959, 1982; KORPEL' 1995). In North America, methods for analysing canopy structure and regeneration in relation to tree fall gaps, which are an important environmental factor, have been developed in hardwood and coniferous forests (e.g. RUNKLE 1982; CANHAM 1988; SPIES *et al.* 1990; BUSING 1994). Little is known about the disturbance regime of European beech (*Fagus sylvatica* L.) forests in relation to tree fall gaps. In our study, a gap-based method was used to investigate the canopy structure of a mountainous European beech virgin forest remnant in Slovenia. The aim of this study was to obtain an overall view of its disturbance regime.

2 Material and methods

2.1 Study area

The 74 ha virgin forest remnant Krokar (45°33'N, 14°47'E) is located on a plateau in the Dinaric mountain range Borovska Gora, Southwest Slovenia, and ranges from 880 to 1192 m in elevation. The climate is temperate, with a mean annual temperature of 5° C and a mean precipitation of 2000 mm. In this region, wind and fog can be strong and snow may be present longer than at lower sites. Moreover, the micro-climate may vary substantially due to the heterogeneous topography, characterised by ridges, rocks and depressions. Parental substrate consists of limestone and dolomite from the Trias formation, and is mostly covered by carbonated Cambisols. In the study area, vegetation is part of the Illyric beech forest zone, and is dominated by European beech, with some Silver fir *(Abies alba)* scattered in the subcanopy. Mountain maple *(Acer pseudoplatanus),* common ash *(Fraxinus excelsior)* and mountain elm *(Ulmus glabra)* are also present, but rare. The basal area per ha is 44.4 m^2 (96 % beech), and the average canopy height is approx. 35 m.

2.2 Approach

A complete gap survey was conducted as a one-time-sampling in the southern part of the reserve on a 12 ha-plot where beech dominated stands were present. This study was carried out in August 2000. The canopy was classified dichotomously as gap and non-gap areas. A canopy opening was defined as a gap created by the fall of one or several canopy trees. Almost all gaps identified in the study area can be classified as developmental gaps (*sensu* LERTZMAN *et al.* 1996). For this study, gap closure occurred when regeneration in the gap was one-half of the average canopy height. For gap sampling, a 25 by 25 m grid was set up in the study site, and gap number, size, shape, direction, and position were recorded. The minimum size of gaps considered was 6 m^2. Gaps were measured using the canopy gap definition (RUNKLE 1982, 1992). Gap size was calculated using the ellipse formula:

$$A = \pi LW/4$$

L describes the longest and W the widest perpendicular distance within the gap. This estimation was appropriate for the majority of the gaps (RUNKLE 1982, 1992). If there was a major deviation from the elliptical form, the gap was divided into smaller elliptical compartments with each measured separately. Subsequently, the areas obtained were summed except for gap direction (section 3.3). The shape of each gap was drawn on paper in the field. The position of each gap was recorded as the distance and compass direction from the nearest point of intersection of the grid and the gap centre.

Gaps were also analysed in connection with the cause of gap formation. The gap maker was defined as a former canopy tree that created the gap. The number of gap makers per gap were recorded and four different modes of mortality (e.g. LERTZMAN and KREBS 1991) were distinguished: died from uprooting, died from breakage, died standing and remnants (smaller or larger parts of gap makers in decomposition and without any intact crown compartments). Because of the one-time sampling methodology, the mode of mortality was understood as the type of gap maker that was present during the sampling. A tree that died from uprooting was characterised by a visible intact root plate and a crown with twigs and buds. If a certain tree was uprooted in the year of the sampling, green leaves would have normally been visible. But an uprooted tree may have also been dead standing for a few years before falling. A tree that died from breakage was characterised by a broken stem in an uncertain height and a more or less intact crown with or without leaves. A tree that died standing was characterised by the absence of leaves. The presence of one or several gap makers or their remnants led to considering a certain canopy opening as a gap.

In addition to the terrestrial study, aerial photography interpretation was used to identify canopy gaps which had already been sampled in the field (e.g. WHITE *et al.* 1985; BARDEN 1989). The purpose was to test whether this approach is suitable to completely or partly replace the terrestrial study. Black and white aerial photographs from 1998 with a scale of 1:17 500 were available. They were scanned and geo-referenced to a 1:10 000 topographic map using the geographic information system “Arc View” in order to identify the study area by field marks. In this way a digital orthophoto was produced. Different scales of the orthophoto were used to interpret the gaps. Identified canopy gaps were visually outlined in the Arc View/GIS environment. Additionally, traditional stereoscopy as an optical method was used to identify canopy gaps on the aerial view.

2.3 Statistics

The data were analysed using both descriptive and test statistics. Gap frequency distributions were created with 50 m^2 and 200 m^2 size classes. Curvilinear regression (JANSSEN and LAATZ 1999) and Maximum Likelihood approximation (FAHRMEIR *et al.* 1996) were then fitted to describe the trend of the distribution. Gap eccentricity was determined by calculating of the longest related to the widest extent within the gap.

Gap direction was defined by the position of the longest distance (L) within the gap, indicated as the main gap axis. Minimum criteria for the existence of a direction were a gap size ≥ 22 m^2 and an eccentricity ≥ 1.6. That was the case with 33 gaps, which were tested for randomness of the direction of the main gap axes. As the axes are undirected, the data had to be transformed twice to test for randomness of the direction of the main gap axes (Batschelet 1981, pp. 22). First, all angles α_i were reduced modulo 180°; that is, angles larger than 180º were reduced by 180º, so that $\alpha_i < 181$. Second, these transformed angles were doubled, so that $\alpha_i < 361$. “Reduced modulo” means the angles were related to a half circle or circle (180° or 360°) using one of the two angular values per axis. After this, the Rayleigh test was applied (see BATSCHELET 1981, p. 54), which takes the length of the mean vector as an indicator of one-sidedness.

According to BATSCHELET (1981) coordinates of the mean vector are computed with:

1) $$\bar{x}_2 = \frac{1}{n}\sum_{i=1}^{n} \cos 2\theta_i$$

2) $$\bar{y}_2 = \frac{1}{n}\sum_{i=1}^{n} \sin 2\theta_i$$

The length of the mean vector is:

$$3)\quad m = \sqrt{\bar{x}_2 + \bar{y}_2}$$

The mean angle is (for $\bar{\chi}_2 > 0$):

$$4)\quad \bar{\theta} = \left(\arctan \frac{\bar{y}_2}{\bar{x}_2} \right) / 2$$

α	angular value of the original data
m	length of the mean vector
n	number of gaps
$x; y$	coordinates of the mean vector
θ	angular value of the transformed data

The gap type was distinguished using the number of gap makers per gap as a criterion. The relation between average gap size distribution and type of gap was analysed. The cause of tree fall and subsequent gap formation was taken into consideration in defining the gap type. The trees that had died from uprooting were taken into consideration with the surface area within the gap.

3 Results

3.1 General statistics

In the 12 ha plot, 49 gaps were recorded (gaps/ha = 4.1), which amounted to 5.6 % of the total land area. Gap size ranged from 6 to 833 m^2, with a mean size of 137 m^2 and median size of 81 m^2. 90 % of gaps recorded were < 300 m^2, and 61 % of these gaps were < 100 m^2.

3.2 Gap frequency distribution

The gap frequency distribution indicates that most gaps ranged from 51 to 100 m^2 in the 50 m^2-size class, while gaps larger than 300 m^2 rarely occurred (Fig. 1). The gap size frequency may be explained as log normal distributed and decreasing negatively exponential with increasing gap size from the maximum. The mean and variance of the estimator of the curvilinear regression are □ = 4.57 and $\sigma = 0.53$, respectively. The function curve shows an appropriate goodness of fit up to the 400 m^2-size class, but the probability that larger gaps occur is predicted to be zero (Fig. 1). The estimator of Maximum Likelihood describes gap frequency distributed as a negative exponential, with a mean and variance of □ = 5.61 and $\sigma = 0.97$, respectively. Although the function curve underestimates the gap frequency in the 100 m^2-size class, it shows an appropriate goodness of fit by an asymptotic approach to the x-axes up to the largest size-class (Fig. 1).

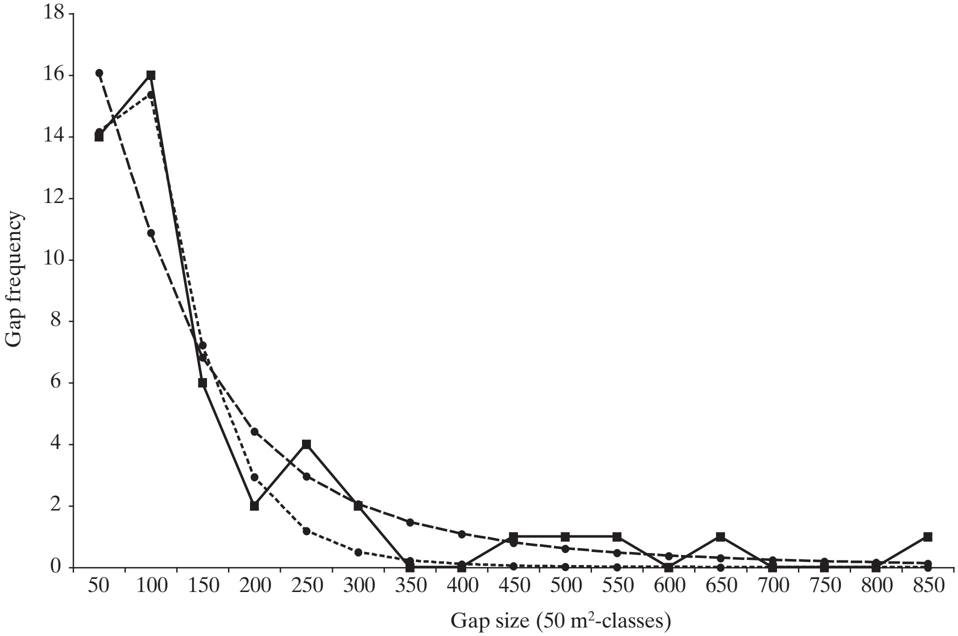

Fig. 1. Gap frequency distribution divided into 50 m^2-size classes (solid line with squares), estimated by curvilinear regression (fine broken line with points) and by Maximum Likelihood (large broken line with points). 50 = 6–50 m^2, 100 = 51–100 m^2, 150 = 101–150 m^2, and so on.

3.3 Land area in gaps (200 m^2-classes)

Most gaps identified in the study area were small (< 200 m^2), while larger gaps (< 1000 m^2) were much less frequent (Fig. 2). Gaps up to 200 m^2 made up more than one third (37%) of the total gap land area, while gaps between 200 and 600 m^2 made up 42 % and those between 600 and 1000 m^2 made up 21 % (Fig. 3).

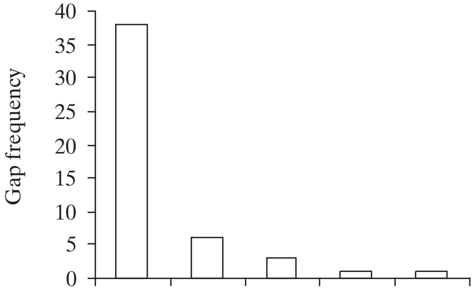

Fig. 2. Gap frequency distribution divided into 200 m^2-size classes. 200 = 6–200 m^2, 400 = 201–400 m^2, and so on.

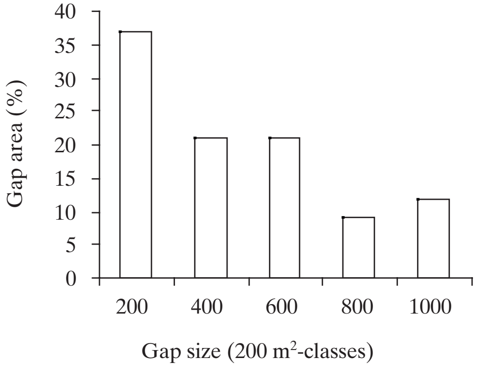

Fig. 3. Proportion of land area in gaps divided into 200 m^2-size classes. 200 = 6–200 m^2, 400 = 201–400 m^2, and so on.

3.4 Testing for randomness of the direction of the main gap axes

The length of the mean vector is m = 0.233 and the angle of the (undirected) mean axis of the sample is 26.2° (this is congruent with 206.2°). In connection with the sample size of 33 gaps we obtained a significance level (from table H in BATSCHELET 1981) $\alpha > 0.15$. That is, the null hypothesis of randomness cannot be rejected.

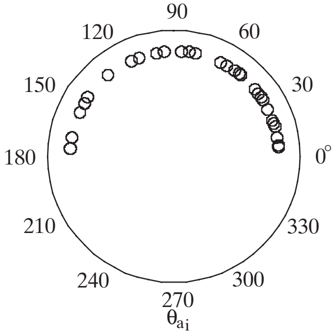

Fig. 4. Circular scatter diagram for the data of 3.4. The scatter describes the position of the angle θa_i (degree) of the main gap axes (n = 33) modified modulo 180°.

3.5 Gap type and cause of tree fall

Most gaps were created by the mortality of one canopy tree (57 %) (Fig. 5). Gaps with several gap makers were less frequent, and were mostly formed by two canopy trees. The mean gap area ranged from 62 m^2 for gaps created by one tree to 472 m^2 for gaps created by three or more canopy trees.

Gap makers died in a variety of ways in the study area (Fig. 6), and almost all gaps were a result of their mortality. Stem breakage was the dominant mode of mortality of the gap makers (66 %). Damaged wood tissue caused by saprophytic fungi was common, and is an important endogenous process affecting tree mortality. Exogenous influences, such as windthrow within the exposed sites, lead to uprooting as a minor cause of death (22 %). This mode of mortality was commonly found where gaps were located on ridges and on upper steep slopes with shallow, rocky soil (12 gap makers). Four uprooted gap makers were found on lower slopes and three uprooted gap makers were found on the plateau and in depressions. Remnants of former gap makers could be found in a progressed state of decay. If remnants were found in single tree gaps, the gap size was usually small and the mode of mortality of the remnants could not be identified. Likewise, stem breakage forms multiple gaps, and combinations with uprooted trees and remnants are frequent. As a result, as gap size increased, the number of gap makers and their variation in type of death increased.

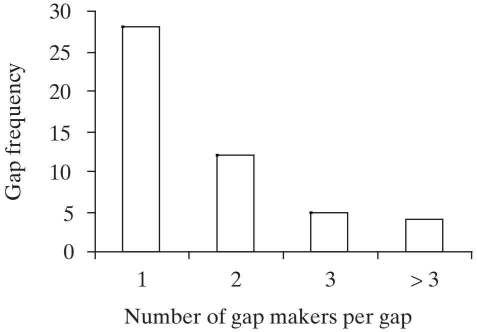

Fig. 5. Gap frequency distribution regarding gap type. 1 = single tree gaps, 2 = gaps with two gap makers, and so on.

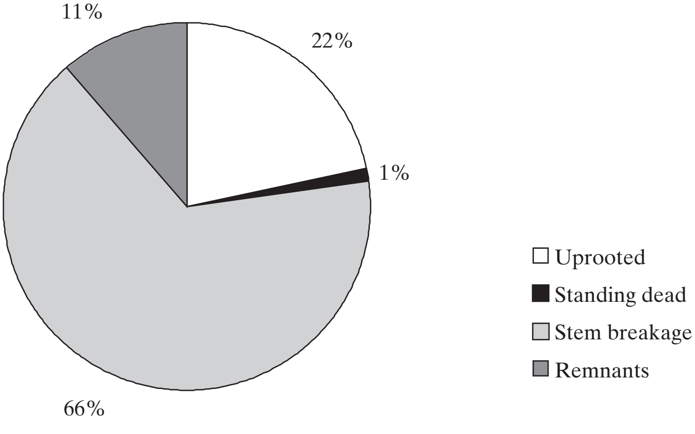

Fig. 6. Mode and proportion of mortality of the gap makers.

3.6 Aerial photography

The gap analysis by aerial photography interpretation identified 13 of the 49 terrestrial sampled gaps (Fig. 7). The gap size spectrum ranged from 103 to 833 m^2. Moreover, all 13 gaps were identified by traditional stereoscopy, while with the orthophoto in the Arc View/ GIS environment only 8 of the 13 gaps were identified.

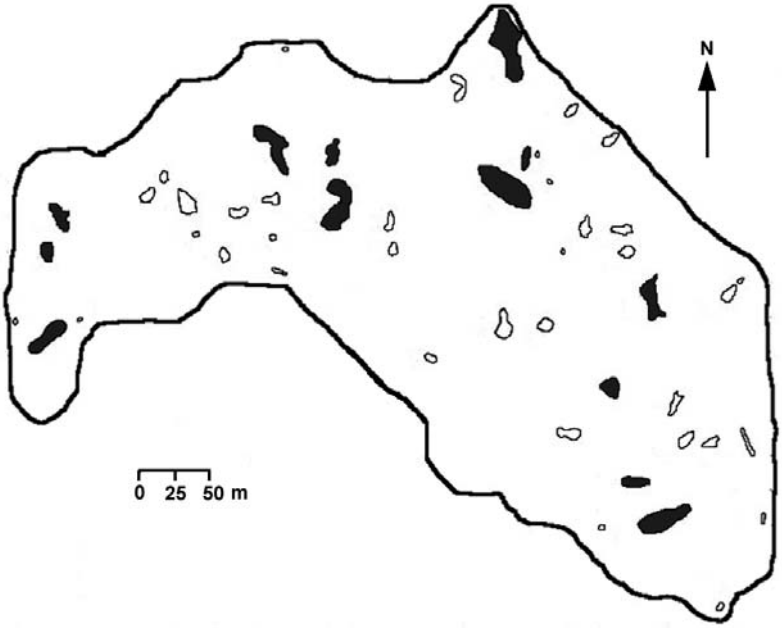

Fig. 7. Map with dichotomously classified gap positions. Terrestrial sampled gaps in comparison with gaps identified by aerial photography interpretation. The black patches describe terrestrial sampled gaps identified by aerial photography interpretation. The patches with just solid lines describe terrestrial sampled gaps not identified by aerial photography interpretation.

4 Discussion

Most gaps identified in the study were small, suggesting that they occur more frequently than larger gaps. Furthermore, small gaps made up a significant part of the gap-covered land area, suggesting that low intensity, small tree fall gaps are an important disturbance in these mountainous beech forests. However, larger gaps were also present. Although they occurred less frequently, they comprised a significant amount of the total gap-covered land area and should also be considered an important disturbance process in these stands. These larger gaps are probably the result of less frequent exogenous events, such as strong wind storms. Gaps with two or more gap makers may not necessarily be created in this way. Temporal and spatial distribution of disturbances, e. g. sun exposure or fungi can cause gradual widening of gaps over time. In *Fagus grandifolia* old growth forests, KRANSY and WHITMORE (1992) mainly observed standing dead trees and branch loss due to beech bark disease. They emphasised the importance of gradual gap widening in North American hardwood forests. WORRALL *et al.* (2005) found that wind was a major cause of expansion of smaller canopy gaps in *Picea-Abies* forests in the White Mountains, New Hampshire, USA. In this region, margin trees showed extensive damage from wind. In contrast, TABAKU and MEYER (1999) assume gradual gap widening in Albanian *Fagus sylvatica* virgin forest remnants is rare. However, gap widening can be confirmed in some cases in the present study. Thus, the structure and dynamics of these stands are a result of disturbance processes that create a range of canopy gap sizes.

The gap density (gaps/ha = 4.1) and total gap-covered land area (5.6 %) suggests that canopy gaps occur scattered over the study area and are created only occasionally in these beech forests. TABAKU and MEYER (1999) found a higher density of small gaps (land area in gaps = 3.3–6.6; mean gap size = 60–74 m^2; gaps/ha = 4.76–8.96) in multi-layered Albanian *Fagus sylvatica* virgin forest remnants with a similar gap-covered land area. This may be due to the study area as well as the sampling methodology which differed from those of the present study. While the Slovenian *Fagus sylvatica* forest is one-layered, the Albanian *Fagus sylvatica* forests are multi-layered. The gap measurement of the present study was carried out in the field, whereas TABAKU and MEYER (1999) estimated gaps on the basis of crown maps. These were obtained from a crown model based on 8 crown radii per tree. Furthermore, trees with a DBH >7 cm were included. In that case, gaps estimated using this crown model might be smaller than directly measured gaps because small trees might be considered as margin trees although they probably do not reach the canopy.

The predicted frequency distribution of gap sizes showed different patterns when modelled with the Curvilinear regression and Maximum Likelihood method. The non linear regression fits the model in the part of the frequency of small gaps better than the estimator of Maximum Likelihood. The second model might, however, be more exact because it predicts the probability that, in the case of an exogenous event, large gaps occur, is more than zero. Log normal gap distributions seem to be typical of virgin hardwood forests of the cool-temperate climate zone (e.g. SPIES *et al.* 1990; YAMAMOTO 2000). In contrast, subalpine coniferous forests show negative exponential gap distributions (e.g. FOSTER and REINERS 1986, LERTZMAN and KREBS 1991). Similar results were found in planted coniferous forests in Great Britain (QUINE 2001).

The gaps identified in the study area were probably caused by the interaction of several different endogenous and exogenous factors. More than 50 % of the single-tree gaps were formed by stem breakage of one canopy tree associated with saprophytic fungi. The occurrence of *Fomes fomentarius* on the stems of beech trees leads to damage to wood tissue. It is assumed that gap makers which died from breakage were mostly infected by fungi before they were broken. Fruit-bodies of *Fomes fomentarius* were observed on logs caused by stem breakage. They showed a change in direction of annual growth with the change of the stem position after breakage. Once a tree is infected and weakened by fungi, it is likely that wind plays a major role in stem breakage. Moreover, falling canopy trees may injure or cause surrounding trees to fall, resulting in larger gaps with two or more gap makers. Tree injury might promote fungi infections. In a *Picea-Abies* forest in Northern America, WORRALL *et al.* (2005) found that *Armillaria* root disease was more common in gaps than extensive disturbance plots (patches > 0.1 ha). In an old-growth *Fagus grandifolia* forest in Northern America branch loss, standing dead and breakage were observed by KRANSY and WHITMORE (1992). They explain this as due to proneness to beech bark disease. Mortality of hardwood species generally affected a smaller proportion of the live canopy than in coniferous forests (WORRALL *et al.* 2005). Thus, endogenous disturbances, e.g. fungi, may create more small canopy gaps in a range of forest types.

Larger gaps may also be created by strong windthrow events on exposed sites, which probably played a role in the uprooting of exposed trees growing in the shallow ridge-top soil in our study site. The majority of trees that died from uprooting were found on sites which were characterised by steep slopes and shallow rocky soils. Uprooting can create pits and mounds on the surface. The surface coverage of windthrow disturbances increased with increasing slope in *Fagus sylvatica* primary forests in the Carpathian Mountains (ULANOVA 2000). This agrees with the finding in our study area that with increasing slope the soil depth decreases and trees might be more predisposed to uprooting on such sites. In contrast, uprooted trees play a minor role on wind protected sites characterised by deep soils, e.g. depressions.

Powerful wind gusts with changing wind directions that occur during thunderstorms in summer are probably an important exogenous factor that leads to the fall or break down of mature and predisposed canopy trees in these stands. This may explain why the main gap axes were randomly distributed in our study site. Thunderstorms may create small gaps. That corresponds with a study in *Picea-Abies* forests where mortality agents such as windthrow and windsnap were identified as important factors in causing gap initiation as well as gap expansion rather than in producing larger patches of disturbance (WORRALL *et al.* 2005). The lack of trees that remained standing after dying might be an indicator for the frequent influence of wind that probably related to the climate conditions in the study area. We observed that for most gaps the direction of fall of the gap makers was not identical with the direction of the main gap axis. The direction of fall caused by breakage might be random especially for gap makers with badly damaged wood tissue. Gaps may also develop without any influence of storms, e.g. if they gradualy enlarge over time. However, a main wind direction could not be identified using the one time sampling methodology. In contrast, WOLF *et al.* (2004) found a prevailing wind direction in a long-term study in mixed deciduous forests in Denmark. They suggest that more than 60 % of *Fagus sylvatica* was broken or uprooted by wind. In planted spruce forests in Great Britain, QUINE and BELL (1998) confirm that windthrow events occur more frequently than in wind-prone forests elsewhere and cause a large proportion of small gaps. Both results can be explained as due to the strong impact of Atlantic climate conditions which differ from those in the present study, e.g. in wind intensity and duration. Therefore, we suggest that the occurrence of fungi and of multiple summer thunderstorms were most likely the causes of the smaller gaps that are undirected. A combination of all these causes might be important for gap formation in the study area.

Occasionally, we found remnants of gap makers, as a sign of a former gap formation, in small gaps. Therefore, it is assumed that such gaps might have been larger when they were initially formed. There are many ways small canopy gaps can be created (RUNKLE 1992). For instance, they may form from the death of a small canopy tree or strong branch, or they may represent remnants of larger gaps, which become smaller due to lateral branch growth of surrounding trees. Both of these processes may have been important in the study area because both beech trees with narrow crowns and large proportioned remnants of gap makers were observed. Although larger gaps were found in the study site, the rare occurrence of mixed tree species, e.g. *Acer pseudoplatanus* can be explained as due to significant lateral crown closures in connection with the special climate conditions. These species are likely to be favoured by the occurrence of large canopy openings, caused by infrequent, severe wind events, where the importance of lateral canopy closure decreases.

The use of aerial photography to identify canopy gaps was not as effective as the field sampling. The best results were obtained using a traditional approach with a stereoscope, though gaps smaller than 100 m^2 could not be reliably identified. The Orthophoto interpretation in the Arc View/GIS environment yielded even poorer results. The reason was the low resolution due to the original scale and tree shading. The research indicates that the interpretation of standard aerial photos on a scale 1:17500 from cyclic inventories in Slovenia can not be used for reliable analysis of prevalent small-scale gap dynamics in beech forests. The identification of small canopy openings may be more successful using aerial views on a larger scale, such as of 1:5000 (MÜNCH 1995).

5 Conclusions

The study area is characterised by small-scale disturbance patterns and widely scattered gaps, suggesting that infrequent, low-intensity canopy disturbance is the dominant process responsible for the dynamics of these stands. These small-scale canopy openings free resources for the recruitment of seedlings or advanced regeneration of established trees, resulting in small patches of regeneration. Research on European virgin forests has confirmed that regeneration typically establishes in small patches in the forest and saplings may exist for years under the canopy (MLINŠEK 1986). Therefore, the stand structure of the study area is primarily a one-layered *Fagus sylvatica* stand with a spatial pattern of small patches of released young trees. Remarkably, small gaps were often found with several gap makers, suggesting that lateral crown closure in beech forests is significant. In summary, small gap disturbance processes can help the long-term persistence of the *Fagus sylvatica* forest. The strong vitality and competitiveness of beech, combined with favourable soil conditions in the study area, can explain why that tree species is dominant in this mountainous region in Slovenia.

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