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Gap-Phase Dynamics in the Old-Growth Forest of Lom, Bosnia and Herzegovina

Alessandra Bottero, Matteo Garbarino, Vojislav Dukić, Zoran Govedar, Emanuele Lingua, Thomas A. Nagel and Renzo Motta

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We investigated forest canopy gaps in the mixed beech (*Fagus sylvatica* L.), silver fir (*Abies alba* Miller), and Norway spruce (*Picea abies* (L.) Karst.) old-growth forest of Lom in the Dinaric Mountains of Bosnia and Herzegovina. Gap size, age, gap fraction, gapmaker characteristics and the structure and composition of gapfillers were documented to investigate gap dynamics. The percentages of forest area in canopy and expanded gaps were 19% and 41%, respectively. The median canopy gap size was 77 m^2, and ranged from 11 to 708 m^2. Although there were many single tree-fall gaps, the majority had multiple gapmakers that were often in different stages of decay, suggesting gap expansion is important at the study site. Of the gapmakers recorded, 14% were uprooted stems, 60% snapped stems, and 26% were standing dead trees. Dendroecological analysis suggests that gap formation varied in time. The density of gapfillers was not correlated to gap size, and the species composition of gapfillers varied between seedling, sapling, and tree life stages. The results suggest that gaps are mainly formed by endogenous senescence of single canopy trees. Exogenous disturbance agents, most likely related to wind and snow, act mainly as secondary agents in breaking weakened trees and in expanding previously established gaps. Although the findings are partially consistent with other studies of gap disturbance processes in similar old-growth forests in central Europe, the observed gap dynamic places the Lom core area at the end of a gradient that ranges from forests controlled by very small-scale processes to those where large, stand replacing disturbances predominate.

Keywords Lom, old-growth forest, canopy gaps, beech-spruce-fir, small-scale, disturbance regime
Addresses *Bottero*, *Garbarino* and *Motta*, University of Turin, Department Agroselviter, Via Leonardo da Vinci 44, 10095 Grugliasco (TO), Italy; *Dukić* and *Godevar*, University of Banja Luka, Faculty of Forestry, Banja Luka, Bosnia and Herzegovina; *Lingua*, University of Padua, Department of TeSAF, Legnaro (PD), Italy; *Nagel*, University of Ljubljana, Department of Forestry and Renewable Forest Resources, Ljubljana, Slovenia
E-mail alessandra.bottero@unito.it
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1 Introduction

The role of canopy gaps in controlling forest dynamics is well recognized and documented in forests worldwide (e.g. Runkle 1982, Brokaw 1985, Uhl et al. 1988, Rebertus and Veblen 1993, Kneeshaw and Bergeron 1998, Nagel and Svoboda 2008, Rentch et al. 2010). In such forests, the death of a single canopy tree or several neighboring trees introduces environmental heterogeneity to the forest ecosystem, such as changes in light levels, nutrient availability, litter depth, and regeneration microsites associated with snapped or uprooted trees. It has long been thought that this heterogeneity plays an important role in maintaining the structure and composition in gap dynamic forests (Grubb 1977, Denslow 1980, Whitmore 1989).

Although gap dynamics has been well studied in forests worldwide for decades, it has only recently received attention in central, eastern, and southeastern Europe. Indeed, the previous generation of forest ecologists working in the region recognized the importance of small-scale tree mortality processes in old-growth forest remnants (Leibundgut 1987, Korpel 1995), yet early studies primarily focused on describing forest development phases rather than quantifying characteristics of the gap disturbance regime and tree regeneration in gaps. More recently, however, there has been a revival of more process-based research within old-growth remnants in eastern and southeastern Europe. These old-growth stands are mainly located in remote regions of the Dinaric and Carpathian mountains ranges (Diaci 1999), and are typically dominated by mixtures of European beech (*Fagus sylvatica* L.), silver fir (*Abies alba* Miller), and Norway spruce (*Picea abies* (L.) Karst.), depending on the site characteristics and the elevation. Recent work in these old-growth remnants suggests that the gap disturbance regime is rather complex. Gaps range from small, single-tree openings formed from the slow death of canopy trees, intermediate sized openings formed from asynchronous mortality of multiple canopy trees involving various mortality agents, to larger (e.g. > 1000 m^2) windthrown gaps related to periodic storm events (Drösser and von Lüpke 2005, Splechtna and Gratzer 2005, Zeibig et al. 2005, Nagel and Diaci 2006, Nagel and Svoboda 2008, Kenderes et al. 2009, Kucbel et al. 2010).

Because of this emerging pattern of complexity in these studies, determining patterns of geographic variation in the gap disturbance regime and gap regeneration over the larger region of southeastern and eastern Europe remains an important task. This is especially important if we are to make generalizations about old-growth pattern and process that is used to guide ecologically based forest management in the region (Motta 2002, Bauhus et al. 2009). Such a geographic perspective can only be accomplished by piecing together data from many different old-growth remnants scattered across the larger region.

Thus, the objective of this study was to add to the growing body of research on gap dynamics of old-growth mixed beech-fir-spruce forests. This study was carried out in the Lom forest reserve in Bosnia and Herzegovina, which is one of the largest old-growth remnants in the Dinaric Mountain range. Our specific objectives were 1) to describe the characteristics of the gap disturbance regime (i.e. gap fraction, gap size distribution, mode of gapmaker mortality, and gap age) and 2) to examine the structure and composition of regeneration in gaps to better understand the role of gap formation on forest development.

2 Materials and Methods

2.1 Study Area

This study was conducted within the core area of the Lom forest reserve, located in the Klecovača mountainous region in the Northwestern part of Bosnia and Herzegovina. The reserve is situated in the Drinic municipality (between 44°27´ and 44°28´ N, and 16°27´ and 16°30´ E, DATUM WGS84) and covers a total area of about 300 ha. The elevation is between 1250 and 1522 m a.s.l. The underlying geology consists mainly of compact limestones (dolomite limestones are locally present) and the morphology has typical karst characteristics, such as limestone outcrops and deep sinkholes (Maunaga et al. 2001). The climate is influenced by continental and maritime airstreams, with an average annual precipitation of approximately 1600 mm (maximum in December and minimum in July). The mean annual temperature was 7.6 °C at the nearest meteorological station (Drinic, 730 m a.s.l.). The Lom forest reserve (297.8 ha) was established in 1956, in order to protect its old-growth character (Maunaga et al. 2001). It consists of a strict reserve area (the core area, 55.8 ha) and an outer buffer zone (242.0 ha). The main difference between the two areas is that some anthropogenic disturbances took place in the past in the buffer zone. The reserve is accessible only for research purposes. Most of the reserve (75% of the area, between 1250 and 1420 m a.s.l.) is comprised of the *Piceo-Abieti-Fagetum illyricum* forest type, followed by the *Aceri-Fagetum subalpinum* type at higher elevations, and by the *Abieti–Piceetum* on the south-western slope, from 1350 m a.s.l. to 1470 m a.s.l. (Bucalo et al. 2007). The main tree species (live trees per ha, diameter at 1.30 m height > 7.5 cm) in the core area are silver fir (24.9%), Norway spruce (14.1%), and European beech (60.5%), but beech is mainly in the subcanopy layer (Motta et al. 2011). Less frequent species include sycamore maple (*Acer pseudoplatanus* L.) and Scots elm (*Ulmus glabra* Hudson) (Bucalo et al. 2007). In the whole reserve browsing of the terminal shoots, fraying, and bark stripping by red deer (*Cervus elaphus* L.) and roe deer (*Capreolus capreolus* L.) are rare. The reserve has typical old-growth characteristics, including very large and old trees, heterogeneous vertical and horizontal structure at small spatial scales, and abundant coarse woody debris (Maunaga et al. 2001, Motta et al. 2011, Garbarino et al. in press).

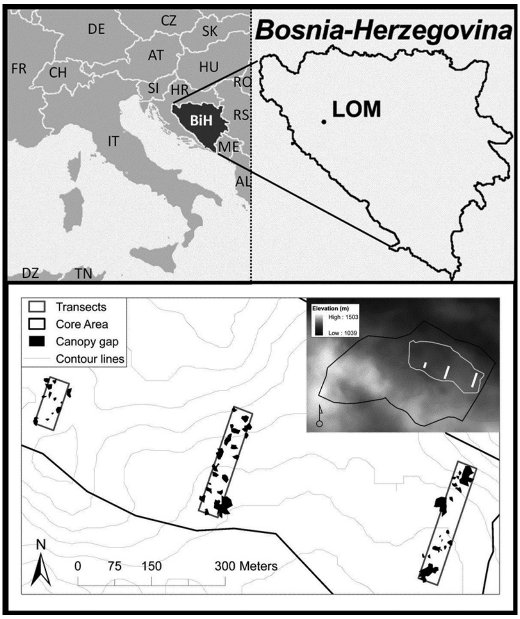

Fig. 1. Location of the study area of Lom, Bosnia and Herzegovina, and detail of the Lom forest reserve (in the right upper part of the lower picture) showing the core area (white contour) and the buffer zone (black contour). The lower enlargement shows the sampling scheme used in the study: three parallel belt transects and 56 gaps measured.

2.2 Field Sampling

Three parallel belt transects (Nakashizuka 1989) 40 m wide and 100 (transect 3) or 200 (transects 1, 2) m long were established perpendicular to the long access of the core area of the Lom forest reserve (Fig. 1). The starting points of the three transects were established at restricted (by 300 m) random distances along the long access of the core area. All canopy gaps that intersected with the belts were sampled. This sampling approach is a modified form of line intersect sampling (Van Vagner 1968), but helps to account for the inherent bias of oversampling large gaps with line transects. Physical site characteristics, including slope, aspect, and elevation were recorded for each gap.

Following Runkle (1982), both canopy gaps and expanded gaps were measured. The canopy gap was measured as the hole in the canopy defined by the tree crowns bordering the gap, and the expanded gap was the area delineated by the trunks of these adjacent trees. Gaps were defined as openings in the forest canopy larger than 10 m^2 caused by the mortality of a tree with a diameter at 1.30 m height (DBH) > 25 cm. Therefore, canopy openings were only considered gaps if at least a remnant of a gapmaker was present. Dead trees less than 25 cm DBH were not considered large enough to create a canopy gap. When gapfillers reached a height of 20 m, the gap was considered closed. For purposes of comparison, the definition used here was similar to that used by Nagel and

Svoboda (2008) in a similar old-growth beech-fir forest in Bosnia and Herzegovina. Due to the high variability and complexity of gap shapes recorded in the old-growth forest of Lom, it was not appropriate to approximate gap size with an ellipse, which is typical in many gap studies. Therefore, the shape and size of each canopy and expanded gap were mapped by measuring radii (distance and direction) from the centroid of the gap to each vertical crown projection and the corresponding bole of the trees bordering the gap, respectively. With these measurements, we used the triangles method to calculate gap size, which does not require the gap centre for measurement, and gives a small standard error and a high accuracy (Ferreira de Lima, 2005).

For each gap we identified the species and the mode of mortality (uprooted or partially uprooted, standing dead, and snapped) of each gapmaker and measured its DBH, the height or the length, and the eventual direction of fall (base to top). We assigned a decay class (Nagel et al. 2006) based on morphological characteristics to estimate the relative age of each gapmaker.

Gap filling was assessed by measuring all trees (DBH > 7.5 cm and < 20 m tall) growing inside the expanded gap. For these individuals, we recorded the species, DBH, and height. We also counted seedlings (10–100 cm height) and saplings (height > 100 cm and DBH < 7.5 cm) of each species in a 6 m radius circular plot located in the centroid of the gap.

In each gap, one increment core from 3–5 of the largest and tallest gapfilling trees within the gap (Schliemann and Bockheim 2011), and one core from three adjacent trees (i.e. bordering the gap), were collected at 50 cm from the ground. To determine the gap age, we screened the cores for synchronous growth releases among the trees bordering a gap and the gapfilling trees (Lorimer 1985, Hart and Grissino-Mayer 2009). We assumed that growth responses were mostly caused by gap formation, and that other causes had a negligible effect (de Römer et al. 2007). The increment cores were air-dried, glued to wooden mounts, and sanded. Ring widths were measured using the LINTAB™ measuring system, with a measurement precision of 0.01 mm, and analyzed by the Time Series Analysis Program TSAP-Win™ (Rinntech, Heidelberg, Germany, 2003). For cores missing the pith by less than approximately 15 mm, the missing years in the innermost part of the core were estimated using a geometric procedure (Motta and Nola 2001). Incomplete cores (i.e. rotten centre or that did not pass near the pith) were considered for growth releases, but not for the tree age estimation (Fraver et al. 2009). Ages are for 50 cm height (no correction for the coring height was made) (Motta and Lingua 2005).

2.3 Data Analysis

The results are reported with summary statistics, and the relationships between the different variables were examined with Spearman's ρ correlation using the SPSS 16.0 statistical package (SPSS Inc., Chicago IL). The dendroecological analysis of the tree cores is based on the premise that gap formation results in a growth release of both advance regeneration in the gap and canopy trees bordering the gap (Frelich 2002). The program JOLTS (Holmes 1999, unpublished, University of Arizona) was used to detect growth releases for each tree by computing a ratio of the forward and backward 10-ring widths for each year (running mean). When the ratio exceeded 2.0 (i.e. a 100% increase in ring width), it scored a release for that given year. Running mean release identification methods are the most commonly used and produce suitable results for canopy disturbances (Rubino and McCarthy 2004, Axelson et al. 2009), and the 10-year window is useful to detect short duration releases that follow low-intensity disturbance events (Berg et al. 2006). The ratio of 2.0 has been used in several studies to document major growth releases for shade-tolerant species (Frelich 2002). In our analysis of gap age, we only used release events indicative of canopy accession. For example, if a core had a series of several suppression and release events, we used the last (youngest) release that was not followed by a suppression to date the gap. Older releases may be the result of increased light due to gap formation near the released tree rather than directly above.

3 Results

3.1 Canopy Gap Characteristics

Fifty-six gaps (i.e. 24 per hectare) were found inside the three parallel belt transects. The mean canopy gap fraction among the transects (defined as proportion of openings in an area, and is expressed as a percentage) was 19.3% and ranged from 11.2% (transect 3) to 21.5% (transect 2), while the percentage of forest area in expanded gaps averaged 41.4%, and ranged from 29.0% to 44.6%. The median canopy gap size was 76.9 m^2, but gap size was variable, ranging from 11.1 m^2 to 708.0 m^2. Consistently, a similar pattern was observed for the expanded gap size, which had a median of 192.9 m^2, and ranged from 41.7 m^2 to 1085.2 m^2 (Table 1).

The frequency distribution of canopy gap size showed a negative exponential form. Most gaps were less than 100 m^2 (62.5%), whereas only 3.6% of gaps were larger than 500 m^2. Expanded gaps between 100 and 300 m^2 were the most frequent (64.3%), reaching a maximum (33.9%) in the 200 m^2 size class (Fig. 2). Finally, it is important to note that although canopy gaps smaller than 100 m^2 were the most frequent, they occupied only 26.5% of the total canopy gap area, while canopy gaps larger than 500 m^2 occupied 22.5% of the total canopy area (Fig. 3).

Table 1. Summary of canopy and expanded gap characteristics in the old-growth forest of Lom (Bosnia and Herzegovina).

Gap characteristics	Canopy gaps	Expanded gaps
Mean gap fraction (%)	19.3	41.4
Range	11.2–21.5	29.0–44.6
Median gap size (m^2)	76.89	192.89
Range	11.12–708.03	41.66–1085.16
Median expanded gap/ canopy gap size ratio	2.5	\
Range	1.5–9.7	\

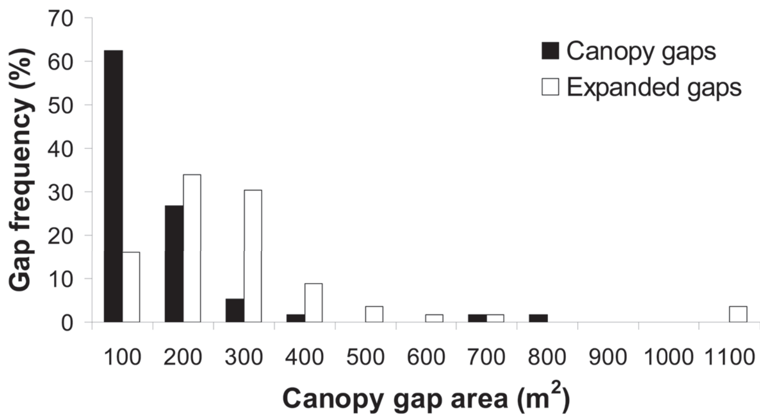

Fig. 2. Frequency distribution of canopy and expanded gaps according to size classes. Gaps were defined as openings in the forest canopy larger than 10 m^2 caused by the mortality of a tree with a diameter at 1.30 m height (DBH) > 25 cm. A canopy gap was measured as the hole in the canopy defined by the tree crowns bordering the gap, and the expanded gap was the area delineated by the trunks of these adjacent trees.

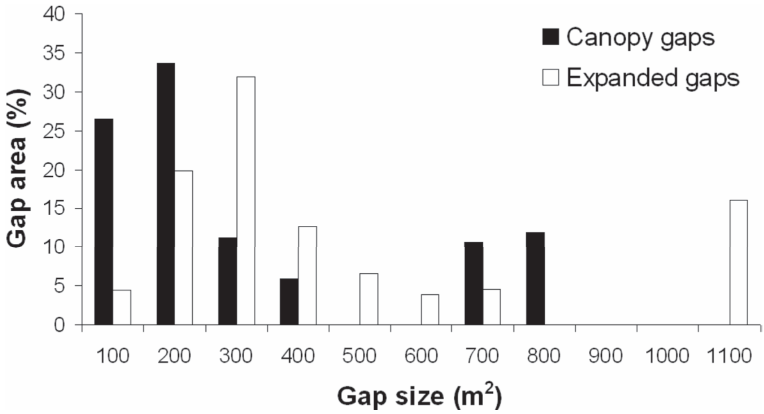

Fig. 3. Proportion of gap area (total gap areas on transect area) divided in gap size classes of canopy and expanded gaps.

3.2 Gap Formation

Regarding the number of trees involved in the formation of a gap, the most frequent class was one gapmaker per gap (25%), and in more than 41% of gaps there were one or two gapmakers. In more than 29% of gaps, there were five or more gapmakers, up to a maximum of 25 gapmakers recorded in the largest gap (Fig. 4). Gapmakers were often in different decay classes within individual gaps; 31% of the gaps had trees of the same decay class, 47% were characterized by the presence of two different decay classes, and the remaining 22% contained gapmakers of three or four different decay classes (Fig. 5). A significant positive correlation ($\rho = 0.49$; $P < 0.01$) was found between gap size and number of decay classes recorded in each gap. Similarly, gap size and number of gapmakers per gap showed a significant positive correlation ($\rho = 0.67$; $P < 0.01$) between canopy gaps and number of gapmakers, and between expanded gap and number of gapmakers ($\rho = 0.67$; $P < 0.01$). The dominant tree fall direction (45.9%; χ^2 test; $P < 0.001$) of snapped and uprooted trees was between northwest and northeast (Table 2). Of the total 229 gapmakers, 27% were Norway spruce, 19% were silver fir, and 13% were beech; the remaining 41% were considered unknown species because of their advanced decay state (Table 3). The mode of mortality of gapmakers varied: 60% were snapped and had a mean DBH of 45.8 cm; 26% were

Table 2. Proportion of gapmakers (snapped and uprooted trees) divided by tree fall direction, expressed by azimuth intervals (°).

Tree fall direction	Gapmakers (%)
North–northeast (1–45°)	22.9
Northeast–east (46–90°)	15.6
East–southeast (91–135°)	6.4
Southeast–south (136–180°)	5.5
South–southwest (181–225°)	6.4
Southwest–west (226–270°)	12.8
West–northwest (271–315°)	7.3
Northwest–north (316–360°)	22.9

Table 3. Summary of gapmakers characteristics (species, decay class and mode of mortality).

	Standing dead	Uprooted	Snapped
Species (%)			
Abies alba	36	14	23
Fagus sylvatica	6	32	9
Picea abies	58	41	16
Unknown species	0	13	52
Decay classes (%)			
Fresh	27	15	11
Young	21	15	8
Medium	31	17	20
Old	10	27	25
Very old	11	26	36

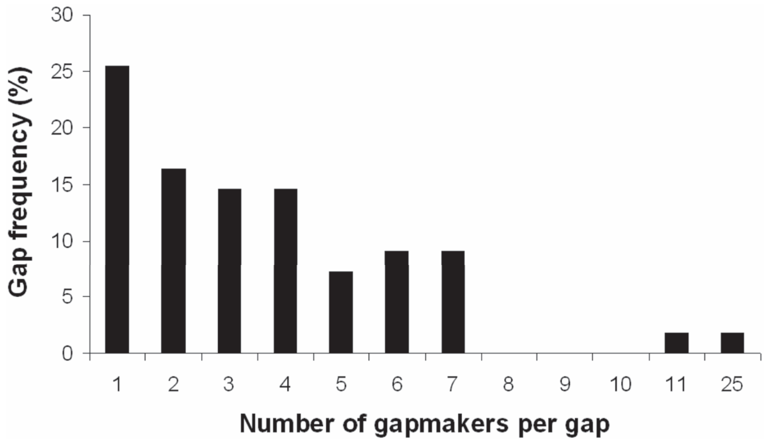

Fig. 4. Gap frequency as a function of number of gapmakers per gap (i.e. number of gaps with a certain number of gapmakers out of the total number of gaps in the study, expressed as a percentage).

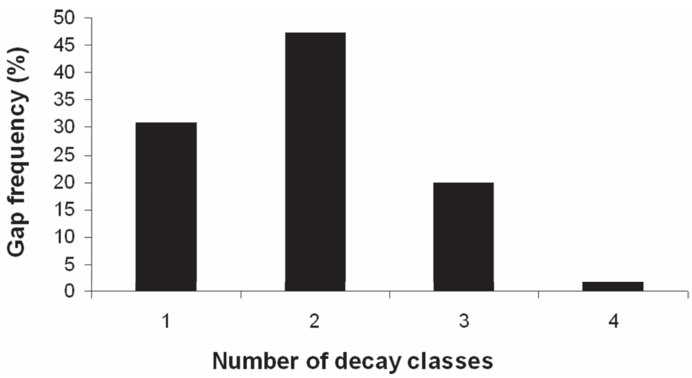

Fig. 5. Gap frequency according to the number of different decay classes (following Nagel et al. 2006) recorded for gapmakers present in each gap.

standing dead and had a mean DBH of 39.5 cm; and 14% were uprooted with a mean DBH of 29.4 cm. The mean DBH of the three main species of dead wood were 56.1 cm for Norway spruce, 69.2 cm for silver fir, and 41.8 cm for beech. The high incidence of unknown species (41%) made it difficult to analyze the effective incidence of each single species among the gapmakers. As expected, dead standing trees were mainly characterized by younger decay classes (48% of the individuals), and snapped trees were much more represented (61%) in the old and very old decay classes.

3.3 Gap Age

The distribution of estimated gap ages obtained from the analysis of cores ranged from 20 to 140 years, but most gaps were between 50 and 100 years old (Fig. 6). Also, if gapfiller trees established after gap formation, we were not able to identify the age of gap formation with our release method. Nevertheless, the more reliable time period (50–100 years) shows that gap formation varied nearly twofold at a decadal scale. These results were based on the analysis of growth releases in gapfiller trees; adjacent trees did not contain growth

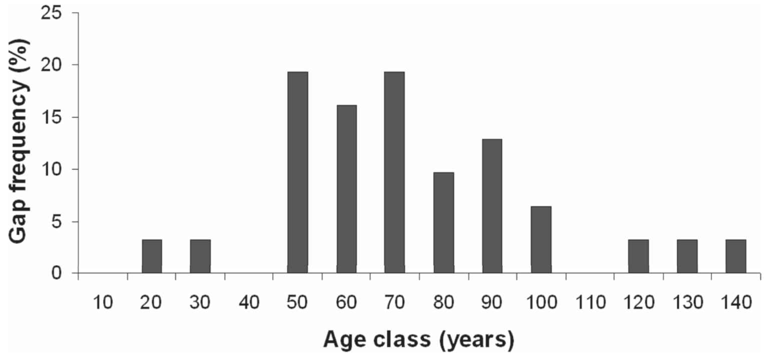

Fig. 6. Gap frequency according to gap age (10 years classes).

releases (because of the small size of the gaps and the height of the adjacent trees) and were thus not useful for dating gaps. No significant correlation was found between gap age and gap size. Small and large gaps had both young and old ages. A significant positive ($\rho = 0.61$; $P < 0.01$) correlation was found between the number of common releases shown and the number of different decay classes present in each gap, which provides further support for gap expansion.

3.4 Gap Fillers

The average density of gapfillers in gaps (i.e. seedlings, saplings and gapfilling trees with DBH > 7.5 cm up to 20 m height) was 2407 ha^{-1}, and ranged from 164 to 12 973 individuals ha^{-1}. The seedling layer was much more dominant (1638 ha^{-1}) than saplings (297 ha^{-1}), while the average density of gapfilling trees was 472 ha^{-1}. No significant correlation was found between gap size and density within any of the three gapfiller height classes.

Silver fir was the dominant species in the seedling layer, accounting for 67% of all seedlings, followed by beech (17%) and Norway spruce (10%). The remaining 6% was comprised of more light demanding species, including sycamore maple (4%) and rowan (*Sorbus aucuparia* L.) (2%). Saplings showed a different pattern: the most represented was beech (74%), followed by silver fir (18%) and Norway spruce (8%). Tree

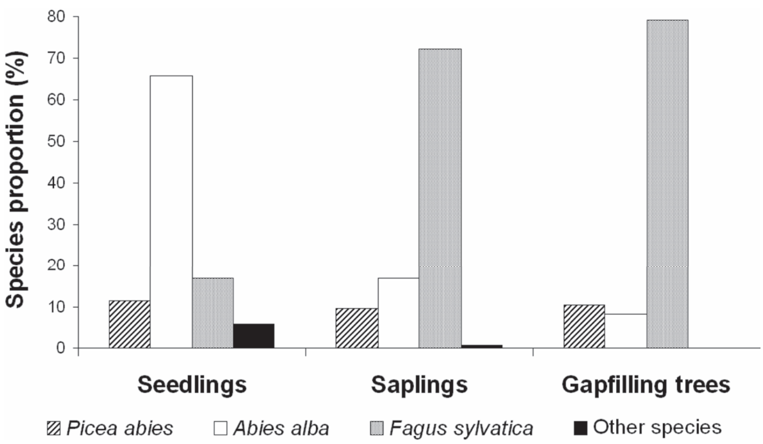

Fig. 7. Species proportion of the three regeneration classes for the three main canopy species. Gapfilling trees are <20 m tall and have DBH >7.5 cm.

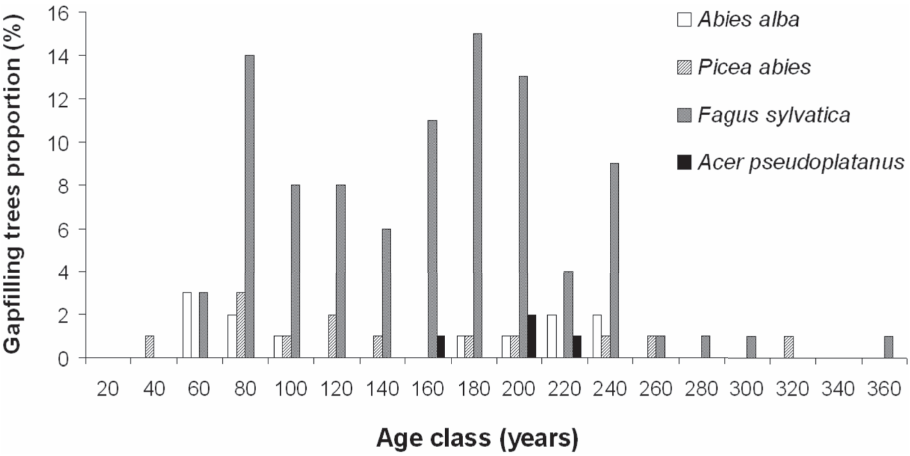

Fig. 8. Age structure of gapfilling trees divided by age class (20 years) and species.

gapfillers showed a similar pattern: the most represented species was beech (80%), followed by Norway spruce (11%) and silver fir (9%) (Fig. 7). The mean DBH of the three main species of gapfiller trees was 16.7 cm for silver fir, 15.9 cm for beech, and 15.5 cm for Norway spruce. The diameter distribution of these species followed a negative exponential distribution.

The age structure of gapfilling trees differed among the main tree species (Fig. 8). Spruce showed rather continuous, low levels of establishment for the past several centuries, while fir had equally low levels of establishment between 60–100 and 180–240 years ago. In contrast, beech had an abrupt and sustained increase in establishment beginning around 240 years ago, with peaks around 180 and 80 years ago. The low number of trees less than 70 years old is likely a sampling artifact, as this figure only shows ages for trees >7.5 cm and <20 m tall. The maximum age of a gapfilling tree was a beech of 360 years. Due to the high variability of tree age recorded in gaps, no significant correlation was found between the age of tree gapfillers within gaps and gap size.

4 Discussion

There have been a small number of studies on gap disturbance processes in temperate, old-growth forests in central, eastern, and southeastern Europe in the past decade. These studies have been carried out in both beech dominated forests (Drösser and von Lüpke 2005, Zeibig et al. 2005, Kenderes et al. 2008) and fir-beech-spruce forests similar to the Lom forest reserve (Splechtna and Gratzer 2005, Nagel and Diaci 2006, Nagel and Svoboda 2008, Kenderes et al. 2009, Kucbel et al. 2010). In general, these studies show similar patterns and processes regarding the gap disturbance regime that can be summarized as follows: 1) gap size distribution follows a negative exponential form (i.e. most gaps are small); 2) although intermediate to large sized gaps (e.g. >500 m^2) are rare, they make up a disproportionate amount of the total land area in gaps; 3) many gaps form from the death of multiple gapmakers; 4) gaps often expand after their initial formation; 5) a large proportion of gapmakers are snapped or uprooted indicating the influence of wind related mortality (snow, ice, or pathogens may also be important); and 6) in several of these studies, periodic, intermediate intensity windstorm events seem to be an important part of the disturbance regime, especially for creating large openings (i.e. >1000 m^2).

Our description of the gap disturbance regime in Lom is partially consistent with the patterns described above, but there are some differences that are worth noting. These differences are expanded upon in the following sections.

4.1 Gap Formation

The gap fraction found in Lom (19.3%) is rather high compared to the studies mentioned above, which report gap fractions from 3 to 16 %. The upper canopy layer in Lom is dominated by fir and spruce, whereas beech is considerably less abundant in the upper layer (Motta et al. 2011). Since conifers have less capacity for lateral crown growth, we may expect a higher gap fraction than in stands with more beech in the canopy layer. Indeed, the gap fraction is also dependent on the particular disturbance history of a site, and is likely to vary in time. Unfortunately, few studies examine the temporal dynamics of gap formation, as this requires rather time consuming dendroecological analyses. Our gap age data suggest that the rate of gap formation varies from decade to decade. Whether or not this variation is due to increased exogenous disturbances in particular decades or variation in rates of background, endogenous mortality is difficult to ascertain.

Other gap studies in similar forests in Austria and Slovakia describe variation in the rate of gap formation due to disturbance events (Splechtna and Gratzer 2005, Kucbel et al. 2010). In support of this, dendroecological reconstructions of disturbance history in old-growth fir–beech forests in Slovenia and Austria found peaks in the disturbance chronology that likely related to past storm events that cause intermediate levels of mortality (Splechtna et al. 2005, Nagel et al. 2007), and direct observations of such storms have been made in the same old-growth stand in Slovenia mentioned above (Nagel and Diaci 2006). Rather than blowing down large areas, these storms create intermediate levels of canopy damage, ranging from creation of scattered, small gaps to intermediate sized, multiple tree fall openings (Nagel and Diaci 2006).

In the Lom reserve there is no evidence of past storms that blew down significant parts of the canopy layer, and the vertical and the horizontal structure are quite regular both at the local and at the core area scale (Motta et al. 2011). Taking into account that

1) the average size of the gaps is very small and in the whole reserve large canopy gaps (> 1000 m^2) are very rare (Garbarino et al. in press);
2) there is a positive correlation between gap size and number of decay classes recorded in each gap;
3) there is more than one release date in the gap fillers of 69% gaps formed by more than three gapmakers;
4) among the gapmakers there is an high incidence of standing dead trees,

we can speculate that in most cases the gap formation proceeds from a one or two tree fall gap (42% of the gaps observed) to relatively larger gaps through the expansion of already established gaps (Worrall et al. 2005). The largest gaps are probably shaped through the joining of two or more gaps. At the same time, the snapped and uprooted gapmakers suggest that wind and/or snow are important disturbance agents, but in this site these disturbance agents seem to play a secondary role breaking already weakened trees, as supported by the high incidence of standing dead trees (26%) among the gapmakers.

Fungi and pathogens may have played an important role in increasing the susceptibility of many of the snapped trees we attribute to wind or snow related mortality. Approximately 20% of trees in Lom were reported to be affected by root-rotting fungi, especially *Heterobasidion annosum* (Fr.) Bref., which attacks the wood of conifers (Maunaga et al. 2001). Even if it is difficult to estimate the real proportion of endogenous versus exogenous mortality the incidence of endogenous disturbances in Lom is higher than in other central European old-growth forests.

4.2 Gap Filling

In the structure and composition of gapfillers in Lom we did not find a positive relationship between gapfiller densities and gap size in any of the three life stages. This is not surprising given that fir, beech, and Norway spruce are shade tolerant, and typically establish as advance regeneration under the canopy. In fact, in the whole core area the average density of regeneration was quite high being 4837 individuals ha^{-1} of which beech comprised 43.9%, silver fir 37.0%, Norway spruce 16.2% and other species made up 2.9% of the regeneration layer (Motta et al. 2011). All of the three species showed a high incidence of individuals with very narrow rings near the pith as evidence that most of the trees established under the canopy (Motta et al. 2011).

The higher density of seedlings compared to saplings in gaps is also a normal demographic pattern for tree regeneration, yet the high density of small trees (>7.5 cm and <20 m tall) was unexpected. The species composition of the different life stages (seedlings, saplings, and gapfillers) was also puzzling; beech was much more abundant than both fir and spruce in the small tree and sapling life stages, while fir dominated the seedling stage. Compared to fir, beech may be more competitive in a higher light environment due to faster height growth (Burschel et al. 1985, Rozenbergar et al. 2007, Nagel et al. 2010). At the same time, beech may lose the ability to produce an upright stem after being exposed to shade over a long period (Diaci and Kozjek 2005); if too much time is spent in shade, beech growth becomes plagiotropic, or flat (Rozenbergar et al. 2007). Therefore, it is much more difficult for the established beeches to compete with silver fir and Norway spruce in the further canopy accession. The few sycamore maple that occur in the gapfiller tree layer established between 160–220 years b.p., and maple recruitment is indicative of higher light levels due to its intermediate shade tolerance (Petritan et al. 2007, Nagel et al. 2010). However, the gap age data do not show evidence of a disturbance so far back in time, but this could be because we did not include rapid initial growth rates on the tree cores as evidence of gap origin. The larger gaps of the core area are characterized by the presence of some sycamore maple seedlings that could be an indicator that this gap size is sufficient for sycamore maple establishment. At the same time it is difficult to explain the quite regular incidence of the Norway spruce in the three life stages observed in the gaps and in the canopy cover of the whole reserve. However, it should be noted that the demographics of seedlings and saplings have been shown to be highly dynamic in fir-beech forests (Szewczyk and Szwagrzyk 2010), and that inter-specific competition plays an important role in further steps of the stand development (Szwagrzyk and Szewczyk 2001, Motta et al. 2011).

4.3 Gap Disturbance Regime

The gap fraction found in Lom is rather high compared to the other studies in central European mixed old-growth forests. The gaps in Lom are mainly formed by endogenous senescence of single canopy trees as a more traditional, steady state view may suggest. Exogenous disturbance agents, most likely related to wind and snow, act mainly as secondary agents in breaking weakened trees and in expanding previously established gaps. Even if our observation only captures a relatively small window in time (if compared with the length of the forest dynamics), the actual small scale replacement dynamic places the Lom reserve at the end of a gradient from forests controlled by large, stand replacing disturbances to those where very small-scale processes predominate.

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