Gap disturbance regime in an old-growth *Fagus–Abies* forest in the Dinaric Mountains, Bosnia-Herzegovina

**Thomas A. Nagel and Miroslav Svoboda**

**Abstract:** Due to the scarcity of old-growth forests in much of Europe, there is little quantitative information on disturbance processes that influence forest dynamics. However, this information is crucial for forest management that tries to emulate patterns and processes in natural forests. We quantified the gap disturbance regime in an old-growth forest dominated by European beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Miller) in the Dinaric Mountains of Bosnia and Herzegovina. We sampled 87 gaps in four stands using line-intercept sampling. The percentages of forest area in canopy gaps and expanded gaps ranged from 12% to 17.2% and 35.5% to 39.7%, respectively. Although many of the gaps were small (<100 m²) and formed from a single gapmaker, large canopy openings >1000 m² with numerous gapmakers made up a disproportionate amount of the total gap area. More than half the gaps had more than one gapmaker and were often in separate decay classes, indicating gaps had expanded over time during separate disturbance events. Furthermore, 51% of all gapmakers were uprooted or wind-snapped, whereas only 22% died standing. These results suggest that wind disturbance plays an important role in creating intermediate to large canopy openings through both gap formation and gap expansion processes.

**Résumé :** En raison de la rareté des vieilles forêts dans une grande partie de l’Europe, il y a peu d’information quantitative sur les processus de perturbation qui influencent la dynamique forestière. Cependant, cette information est fondamentale pour un aménagement forestier qui tente de reproduire les patrons et les processus des forêts naturelles. Nous avons quantifié le régime de perturbation par trouées dans une vieille forêt dominée par l’hêtre commun (*Fagus sylvatica* L.) et le sapin argenté (*Abies alba* Miller) dans les montagnes Dinariques de Bosnie-Herzégovine. Nous avons échantillonné 87 trouées situées dans quatre peuplements en utilisant un échantillonnage par transects d’interception linéaire. Le pourcentage du territoire forestier occupé par des trouées et par des trouées étendues variait respectivement de 12 à 17,2 % et de 35,5 % à 39,7 %. Même si plusieurs trouées étaient petites (<100 m²) et causées par la mort d’un seul arbre, la portion de la superficie totale occupée par les trouées plus grandes que 1000 m², causées par la mort de plusieurs arbres, était disproportionnée. Plus de la moitié des trouées avaient été causées par la mort de plusieurs arbres qui faisaient souvent partie de classes de décomposition différentes, ce qui indique que les trouées s’étaient agrandies avec le temps à la suite d’épisodes distincts de perturbation. De plus, 51 % de tous les arbres morts à l’origine d’une trouée avaient été renversés ou cassés par le vent alors que seulement 22 % étaient morts sur pied. Ces résultats indiquent que les chablis jouent un rôle important dans la création d’ouvertures de taille moyenne à grande dans la canopée, que ce soit par des processus de formation ou d’expansion des trouées.

[Traduit par la Redaction]

**Introduction**

Historic land use practices in the mountains of central Europe have influenced forest ecosystems to such an extent that current forest structure and composition are largely the result of these human activities. During the 19th century, for example, vast areas were clear-cut and the natural tree species composition was replaced by Norway spruce monocul-
documented large gaps (>4000 m²) with multiple snapped canopy trees over many years release resources more gradually and may tend to favour advance regeneration of more shade-tolerant species (Lertzman and Krebs 1991; Battles and Fahey 2000). In contrast, episodic intermediate intensity windstorm events can cause the sudden formation of numerous canopy openings, ranging from single tree-falls to large gaps caused by multiple fallen trees (Webb 1989; Ogden et al. 1991; Canham et al. 2001; Woods 2004). Trees at the margin of existing gaps may also be more susceptible to certain mortality agents, such as wind or pathogens, causing gaps to expand over time (Foster and Reiners 1986; Rebertus and Veblen 1993; Worrall et al. 2005). Thus, large canopy openings can form suddenly during a more intense disturbance or gradually from the expansion and coalescence of smaller gaps. The resulting patterns of gap formation from these various mortality agents influence vegetation recovery in gaps (Runkle 1982; Whitmore 1989) and are thus important for understanding forest dynamics.

The goal of this study is to gain a better understanding of natural gap disturbance processes in an old-growth *F. sylvatica* – A. alba forest in the Dinaric Mountains, Bosnia and Herzegovina. We address the following questions: (i) What do the characteristics of the gap disturbance regime (i.e., gap fraction, gap size distribution, and gap shape) reveal about disturbance processes? (ii) Are the mortality processes responsible for gap formation associated with endogenous disturbance, which results in standing dead mortality, or exogenous disturbance such as windthrow, which results in uprooted and snapped mortality? (iii) Are larger gaps formed from the expansion of smaller gaps or during single mortality events? We then discuss the results in the context of close-to-nature forest management of similar forests in central and southeastern Europe. We conducted this study in the Perucica forest reserve, which is one of the largest (1434 ha) remaining old-growth forests in Europe. Most old-growth remnants dominated by *F. sylvatica* in central and southeastern Europe rarely exceed a few hundred hectares (Diaci 1999), making them more vulnerable to edge effects. Furthermore, small reserves may not be large enough to capture the natural range of variability found in large tracts of old-growth forest (Rademacher et al. 2004). Therefore, Perucica offers a unique opportunity to study natural disturbance processes.

**Methods**

**Study area**

The Perucica forest reserve is located within Sutjeska National Park in the southern Dinaric Mountains, Bosnia and Herzegovina (Fig. 1). Topography in the park is mountainous and steep, with elevations ranging from 600 m a.s.l. in the Sutjeska river valley to 2386 m a.s.l. on Mount Maglic, the highest peak in Bosnia and Herzegovina. The climate is a mix of Mediterranean and continental, with a mean monthly temperature range from −3.1 °C in January to 18.0 °C in August and a mean annual precipitation >1400 mm, according to the closest meteorological station (Suha, 690 m a.s.l.) (Fukarek and Stefanovic 1958). Geology is dominated by limestone on the slopes and cliffs surrounding the reserve and acidic sandstone and shale in the central area. Consequently, soils are also diverse and may be derived from a mixture of parent materials, especially where calcareous soils have eroded down slopes (Fukarek and Stefanovic 1958).

Vegetation in Perucica varies depending on altitude, slope position, and soils. Most of the reserve comprises old-growth *F. sylvatica* – A. alba forests between 1000 and 1600 m a.s.l. (Fukarek and Stefanovic 1958). Within this zone, these two species represent approximately 98% of the canopy trees and occur in similar proportions, although the abundance of each species can vary substantially depending on local site conditions. Less frequent canopy species are also present, including sycamore maple (*Acer pseudoplatanus* L.), Scotch elm (*Ulmus glabra* Huds.), European ash (*Fraxinus excelsior* L.), and *P. abies*. Large canopy
trees >1 m diameter reaching heights >50 m are abundant, and basal area (trees >5 cm diameter) is generally between 40 and 80 m²·ha⁻¹ (T.A. Nagel and M. Svoboda, unpublished data, 2005). Most of the forest area in Perucica is old growth with no evidence of human disturbance, but people have influenced the vegetation in the park, mainly through forest clearing and animal grazing at higher elevations near the tree line. Also, a few small clearings are scattered where localized cutting and grazing occurred in the past, but the influence of these areas on the surrounding stands seems to be rather localized (T.A. Nagel, personal observation, 2005).

After extensive reconnaissance, we selected four stands in the mixed F. sylvatica – A. alba vegetation zone based on the following criteria: (i) presence of old-growth characteristics (i.e., large trees >200 years old, heterogeneous stand structure, and abundant coarse woody debris); (ii) located away from areas with past anthropogenic disturbance (e.g., forest clearings); and (iii) located within 2 hours walking distance from the nearest road access. All the stands were between 1000 and 1300 m a.s.l. The Tunjemir 1, 2, and 3 stands varied in aspect from north to northeast and were on slopes between 20° and 30°, whereas the Zanoglina stand was southwest in aspect on a more moderate slope (16°).

**Field methods**

In studies that characterize forest gaps, canopy openings are typically described by measuring both the actual and expanded gaps (after Runkle 1982). The actual canopy gap (hereinafter referred to as gap) is delineated by the vertical projection of the tree crowns surrounding the gap, whereas the expanded gap includes the gap plus the area delineated by the boles of these trees. We defined gaps as openings in the forest canopy >5 m² caused by the mortality of a tree (or in some cases a broken branch) >25 cm diameter at breast height (DBH), so that canopy openings were only considered gaps if the remains of a gapmaker were present. Mortality of trees <25 cm DBH was not considered large enough to create a canopy opening. Small interstitial spaces between crowns, which sometimes occurred between A. alba trees in our study site, were considered as closed canopy. Additionally, gaps resulting from various edaphic conditions (e.g., waterlogged soil or rock outcrops) were not encountered in the study. A gap was considered closed when regeneration within the gap reached a height of 20 m (equivalent to a DBH of approximately 25 cm), approximately half the height of the surrounding canopy.

In each stand we established three transects varying in length from 200 to 400 m parallel to slope contours for sampling gaps. The transects were separated by 50 m to ensure that large gaps were not sampled more than once. In a few cases, the transects encountered a stream bed or deep ravine and were either terminated or continued after these discontinuities. In such cases, the transects continued until the canopy opened or was affected in some other way as a result of these features. Each expanded gap (inclusive of the gap) intersected by a transect was sampled. We precisely mapped the shape and size of each gap and expanded gap by measuring radii (distance and direction) from the approximate gap center to the edge of each tree crown and corresponding bole that defined the gap, respectively. For example, if 10 canopy trees bordered a gap, we measured 10 radii for both the gap and expanded gap separately. These measurements
were digitized with computer aided drafting software, to calculate the size and perimeter of both gaps and expanded gaps.

In three of the study stands, we encountered areas with more extensive disturbance. These extensive disturbances (after Worrall et al. 2005) were defined as canopy openings >1500 m², often with scattered trees remaining in the gap interiors. The approximate boundary of each extensive disturbance area was usually easy to distinguish from the surrounding intact canopy. To estimate the size of these areas, we measured the longest length and the longest perpendicular width and fit these measurements to the formula for the area of an ellipse.

For each gap and extensive disturbance we identified the species of each gapmaker and recorded the DBH and mode of mortality (i.e., standing dead, uprooted, snapped, and broken branch). When possible, we noted whether snapped trees broke cleanly or splintered, which indicated if they snapped while dead or alive. Thus, snapped gapmakers were categorized into one of three classes (i.e., snapped alive, snapped dead, or snapped unknown). To estimate the time since death of each gapmaker, we assigned a decay class to each gapmaker based on morphological characteristics. The decay class system was based on a similar system to each gapmaker based on morphological characteristics that they should cover a broad time period to be representative of asynchrony gapmaker mortality. However, because *F. sylvatica* tends to decay faster than *A. alba* (Kraigher et al. 2002; Saniga and Schutz 2002), we made the following adjustment for calculating the minimum number of disturbances per gap: in cases in which both *F. sylvatica* and *A. alba* gapmakers were present in the same gap, and the *F. sylvatica* gapmaker was one decay class older than the *A. alba* gapmaker, we counted this as one disturbance. This particular situation occurred in only seven gaps.

**Table 1. Decay class system for gapmakers.**

<table>
<thead>
<tr>
<th>Decay class</th>
<th>Foliage</th>
<th>Small branches</th>
<th>Large branches</th>
<th>Bark</th>
<th>Wood decay</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fresh</td>
<td>Present</td>
<td>Present</td>
<td>Present</td>
<td>Intact</td>
<td>None</td>
</tr>
<tr>
<td>Young</td>
<td>Absent</td>
<td>Present</td>
<td>Present</td>
<td>Intact</td>
<td>None</td>
</tr>
<tr>
<td>Medium</td>
<td>Absent</td>
<td>Absent</td>
<td>Present</td>
<td>Sloughing</td>
<td>Moderate</td>
</tr>
<tr>
<td>Old</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Mostly absent</td>
<td>Advanced</td>
</tr>
<tr>
<td>Very old</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Nearly decomposed</td>
</tr>
</tbody>
</table>

**Note:** Logs associated with very old gapmakers were sometimes completely incorporated into the forest floor, but their stumps were still present. The cutoff for small and large branches was approximately 5 cm DBH.

We sampled 87 gaps over a total transect distance of 3200 m in the four stands. The mean gap fraction was 14% and ranged from 12% at Zanoglina to 17.2% at Tunjemir 3.
The expanded gap fraction was similar among the four stands, ranging from 35.5% to 39.7%, with a mean of 37.8% (Table 2). If the five extensive disturbance areas are excluded from the gap fraction calculation, the mean gap and expanded gap fraction change to 11.4% and 37.6%, respectively.

Gaps were highly variable in size, ranging from 5 to 774 m² excluding the extensive disturbance areas, and had a median area of 68 m² over all four stands (Table 2). The bias-corrected frequency distribution of gap size showed a negative exponential form, with 70% of gaps <100 m², 28% between 100 and 500 m², and the remaining 2% >500 m² (Fig. 2). Expanded gap size varied from 47 to 1575 m², with a median of 290 m² (Table 2). The corrected size distribution of expanded gaps was approximately log normal, with 79% of expanded gaps being between 100 and 500 m² (Fig. 2). The five extensive disturbance areas encountered in three of the stands ranged in size from 1698 to 5922 m² (Fig. 2). The median gap and expanded gap sizes increase to 82 and 313 m², respectively, when these gaps are included.

Even after the gap size distribution was corrected for the tendency to oversample large gaps, the extensive disturbances along with the largest gaps encountered in the study made up a disproportionate amount of the total area in gaps (i.e., the bias-corrected sum of all the gap sizes in the study). For example, the five extensive disturbances and the five largest gaps comprised 40% of the total gap area. In comparison, gaps <100 m² (n = 48) contained only 20% of the total gap area. Many of the gaps encountered in this study had complex shapes. To quantify this complexity, we examined the relationship between gap perimeter and gap area compared with the area–perimeter relationship for a circle (Lertzman and Krebs 1991). As gap size increased, the gap area–perimeter relationship differed markedly from circular gaps, indicating that gap geometry became more complex with gap size (Fig. 3).

Gapmaker mortality

More than half of the gaps (64%) were formed by the death of more than one tree and 20% involved five or more gapmakers (Fig. 4). The maximum number of gapmakers recorded in a gap was 10, whereas the five extensive disturbance areas had between 13 and 40 gapmakers (Fig. 4). In many of the gaps with multiple gapmakers, mortality of gapmakers was asynchronous, as indicated by their different decay classes. When the different decay rates of A. alba and F. sylvatica were taken into consideration, 45% of all gaps showed evidence of expansion after initial gap formation (Fig. 5). The remaining 55% of gaps either involved single gapmakers or had multiple gapmakers in the same decay class, suggesting that they formed from a single disturbance event. Gap expansion processes are well illustrated by the extensive disturbance areas. For example, in the largest extensive disturbance (5922 m²), the 40 gapmakers present were found in each of the five decay classes: 6 very old gapmakers initiated the area, 7 old gapmakers began to expand the opening, followed by 10 medium-aged gapmakers, most of which were uprooted, 15 young wind-snapped and uprooted gapmakers, and 2 fresh wind-snapped gapmakers that led to further expansion.

Of the total 322 gapmakers, 40% were F. sylvatica and 57% were A. alba. Less abundant species, including A. pseudoplatanus, P. abies, and U. glabra, made up the remaining 3% (Table 3). If we use the gap border trees (N = 676) as an estimate of canopy composition, the proportion of F. sylvatica gapmakers was lower than its share in the canopy (53%), whereas the proportion of A. alba gapmakers was higher than its share in the canopy (45%).
be a result of several factors, including a long-term change in canopy composition from *A. alba* to *F. sylvatica* and slower decay rates of *A. alba* logs, leading to a longer residence time on the forest floor. The mean diameter of *F. sylvatica* gapmakers (64.2 cm, *N* = 124) was similar to *A. alba* gapmakers (64.6, *N* = 183) (*t*-test, *p* = 0.45).

The dominant mode of gapmaker mortality was uprooting (30%), followed by snapped unknown (25%), snapped alive (22%), snapped dead (12%), standing dead (9%), and broken branch (2%) (Table 3). Of the 81 gapmakers in the snapped unknown category, 86% were in the two oldest decay classes, and determining whether these stumps snapped while alive or dead was not possible. These results suggest that 52% of gapmaker mortality was at least partly associated with exogenous disturbance processes, most likely wind-related uprooting and snapping. However, this is probably an underestimate, as some of the snapped unknown gapmakers likely snapped while they were alive. Of the trees that died standing, most were large *A. alba* (71%). Correspondingly, the mean diameters of gapmakers in different mode of mortality categories were significantly different (ANOVA; *p* = 0.028), but only between standing dead trees (standing dead + snapped dead) and uprooted trees, which had mean diameters of 71.0 and 59.7 cm, respectively.

**Discussion**

The mean gap fraction (14%) we observed in Perucica is similar to old-growth *F. sylvatica* dominated forests in central Europe (Drösser and von Lüanke 2005; Splechtna and Gratzer 2005), but higher than similar old-growth stands in Slovenia (Ziebig et al. 2005) and Albania (Meyer et al. 2003), which reported gap fractions of 5.6% and 3.3%–6.6%, respectively. This could result from different sampling methods, including the criteria used to define gaps in these studies. The higher gap fractions observed in Perucica could also reflect a higher disturbance rate or the occurrence of periodic intermediate intensity disturbances, consistent with the larger gaps and multiple windthrown gapmakers observed in this study. Furthermore, the presence of *A. alba* in our stands may have contributed to a higher gap fraction, as conifers have less capacity for lateral crown expansion compared with *F. sylvatica*. In other old-growth temperate forests, the fraction of land area in gaps was within the range we observed in Perucica, including broad-leaved and coniferous forests in the eastern United States (Runkle 1982; Battles et al. 1995), *Nothofagus* spp. forests in the southern hemisphere (Ogden et al. 1991; Stewart et al. 1991; Rebertus and Veblen 1993), and Japanese beech (*Fagus crenata* Blume) forests in Japan (Nakashizuka 1984).

Gap sizes were also within the range reported in these studies, with a predominance of small gaps. Remarkably, gaps <100 m² (*N* = 48) made up only 20% of the total gap area, whereas intermediate to large sized gaps, as well as the extensive disturbance areas, made up a disproportionate amount of the total gap area. This suggests that while less frequent, larger openings may have a greater overall influence on forest dynamics than small gaps, given that small gaps are more likely to be closed by lateral crown growth from trees bordering the gap. A high mean expanded gap/canopy gap ratio (7.9) of gaps <100 m² in this study verifies the importance of lateral crown closure for small gaps. The increased light and temperature levels in large gaps may also be important for maintenance of shade-intolerant species in the forest, such as *A. pseudoplatanus, U. glabra*, and *F. excelsior*. 

© 2008 NRC Canada
To some extent, the larger gaps and the extensive disturbance areas observed in Perucica indicate that periodic intermediate intensity disturbance events play an important role in forest dynamics. Other studies in similar old-growth *F. sylvatica*-dominated stands in central Europe have also documented larger canopy openings (Drösser and von Lüpke 2005; Splechtna and Gratzer 2005; Nagel and Diaci 2006). For example, in two forest reserves in Slovakia, Drösser and von Lüpke (2005) recorded several gaps >0.4 ha with >50 gapmakers. In the larger gaps and extensive disturbance areas in Perucica, synchronous mortality of many uprooted and snapped gapmakers confirms the importance of wind disturbance in the study area. In fact, over all the gaps, uprooting and snapping (while the tree was alive) were the dominant gap forming processes and together represented over half of all gapmaker mortality. This suggests that exogenous disturbance, most likely wind-related mortality (possibly in combination with snow), was a more important gap-forming process than standing mortality associated with endogenous processes. However, it is possible that various pathogens could have made gapmakers more susceptible to wind- or snow-related mortality. The predominance of snapped and uprooted gapmakers is similar to observations in old-growth *F. sylvatica* forests in Slovakia, where >90% of gapmakers were uprooted and snapped (Drösser and von Lüpke 2005). However, it is rare to encounter large, standing dead *F. sylvatica* trees, as the pathogens old trees accumulate usually cause the bole to snap before they die standing. Most of the standing dead trees in our study were *A. alba*, although standing dead, uprooted, and snapped gapmakers of *A. alba* occurred in similar proportions.

A common characteristic of the gaps we encountered in Perucica was that multiple gapmakers formed individual gaps. Moreover, while some of the gaps with multiple gapmakers formed in a single event, 70% showed evidence of subsequent expansion after their initial formations. Larger gaps and extensive disturbance areas, for example, often had gapmakers in each decay class representing both standing mortality as well as multiple windthrow events and likely formed from the coalescence and expansion of several smaller openings. Thus, large canopy openings in our study formed from several mortality agents and were mainly a result of multiple expansion events rather than a single disturbance. Similarly, large openings found in old-growth *F. sylvatica*-dominated forests in central Europe and *Picea–Abies* forests in the United States were also a result of gap expansion rather than of single disturbance events (Drösser and von Lüpke 2005; Splechtna et al. 2005; Worrall et al. 2005).

The fact that nearly half of all the gaps showed evidence of multiple formation events suggests that secondary gap expansion is an important process in Perucica. It seems that once a small opening is formed, the canopy is likely to re-stabilize if lateral crown expansion of trees at the gap margin close the gap prior to a subsequent disturbance. If not, mortality of exposed trees at the gap margin may expand the opening, which in turn may lead to further expansion. The large number of snapped and uprooted gapmakers in our study suggests that increased wind exposure of trees at the gap margin was the primary cause of gap expansion. Gap expansion due to chronic wind stress has also been reported in *Picea–Abies* forests of the northeastern United States (Foster and Reiners 1986; Worrall and Harrington 1988; Worrall et al. 2005) as well as in temperate *Nothofagus* spp. forests in Argentina (Rebertus and Veblen 1993). Aside from an increased risk of windthrow, there are several possible indirect reasons why trees at the gap margin, especially *F. sylvatica*, are more susceptible to mortality. First,
because the crowns of these trees are often damaged by wind, these individuals are more vulnerable to fungi attack through broken branches (Worrall et al. 2005). Second, the cambium of F. sylvatica is vulnerable to direct sunlight, causing the bark to split open, which acts as a further entrance for pathogens (Jenssen and Hofmann 1996). Although we did not record the presence of pathogens for the gapmakers in our study, we did observe extensive heartrot and fungi fruiting bodies on many gapmakers.

The complex etiology of gaps coupled with multiple expansion events was also evident in the evidence of gap shape, which became increasingly irregular with gap size. The increase in the irregularity of gap shape in relation to complex gap formation and gap expansion processes has also been found elsewhere (Lertzman and Krebs 1991; Battles and Fahey 1996). This is notable, as gap shape can have an important influence on forest recovery. For example, gaps with a large perimeter to area ratio (e.g., a long, narrow gap) are more likely to be closed by lateral crown expansion of trees at the gap margin (Battles et al. 1996). In addition, gaps with complex shapes influence the gap light environment differently than gaps shaped like circles or ellipses, which in turn affects gap regeneration patterns (Rozenbergar et al. 2007).

**Management implications**

A thorough understanding of natural disturbance processes is central to developing silvicultural prescriptions aimed toward maintaining the structure, composition, and heterogeneity found in natural forests (Franklin et al. 2002; Mitchell et al. 2002), all of which are important for maintaining forest biodiversity (Angelstam 1998). In most managed forests, however, there needs to be a balance between social, economic, and ecological objectives. As such, it is unlikely that forest managers will always be able to precisely emulate the patterns and processes found under old-growth reference conditions (Palik et al. 2002).

Under close-to-nature management of mixed F. Sylvatica – A. alba forests in central and southeastern Europe, managers attempt to balance both economic and ecological goals. However, an ecological approach to forest management is difficult without quantitative information on disturbance processes. Therefore, the results of this study could provide important baseline information used to guide management. We suggest the following silvicultural guidelines to more closely emulate the gap disturbance regime found in mixed F. Sylvatica – A. alba forests: (i) managers should maintain between 10% and 20% of the forest in canopy gaps; (ii) managers should create a range of gap sizes, in which approximately two thirds of the gaps are small openings (<100 m²) created from one to two gapmakers, one third are intermediate sized openings (mostly <500 m²) created from approximately 3 to 10 gapmakers, and a few openings are large (but not >0.5 ha) with standing trees remaining in the gap interiors; (iii) The majority of intermediate to large sized openings should be created by expanding smaller gaps during stand re-entry; (iv) Larger multiple-tree gaps, especially those formed by expanding old openings, should not be shaped like simple circles or ellipses; (v) gapmakers should generally be canopy trees >50 cm DBH; and (vi) some large canopy trees should be left to die naturally, to create important structural features (i.e., snags and downed logs).

The variability created by gap disturbance processes in Perucica would be difficult to emulate with only one silvicultural system. Therefore, forest managers need a more flexible strategy, which chooses from a variety of silvicultural models (i.e., single-tree selection, group selection, and irregular shelterwood). This type of uneven-aged forest management, often termed a “freestyle” approach, is already being practiced in parts of Slovenia (Mlinsek 1968) and could be a useful approach in other F. sylvatica – A. alba forests in central Europe.

**Conclusions**

The disturbance regime in mountain forests of central and southeastern Europe has traditionally been thought of as a small-scale, endogenous tree mortality process (Prusa 1985; Leibundgut 1987; Korpel 1995). Our data suggest the disturbance regime is characterized by the formation of small gaps as well as the creation of large canopy openings, especially through expansion of existing gaps. Moreover, most gaps were formed by snapped and uprooted trees rather than trees that died standing, indicating the importance of wind-driven gap formation. Much of the gap formation in Perucica is likely associated with localized thunderstorms with winds strong enough to cause moderate canopy damage, ranging from damage to scattered trees to more severe, stand level damage. The episodic nature of these storm events likely causes high temporal variation in the gap formation rate (Splechtna et al. 2005; Nagel et al. 2007). We emphasize that gap formation in Perucica is a complex process, resulting from various mortality agents, and gapmaker mortality is often asynchronous within individual gaps. The different pathways to gap formation, such as multiple tree-fall gaps formed in one event or gaps that slowly expand over time, will likely influence within gap recovery (Battles and Fahey 2000; Worrall et al. 2005). Forest management that aims to emulate the complexity of the gap disturbance regime in Perucica would need to use a variety of silvicultural approaches.

**Acknowledgements**

The authors wish to thank the park administration of Sutjeska National Park for providing access to the Perucica forest reserve. The second author received support from the NAZV 1G58031 project. For help with field work, the authors thank Tihomir Rugani, Katrine Hahn Kristensen, and Anders Busse Nielsen. Finally, we thank two anonymous reviewers for their helpful comments on an earlier version of the manuscript.

**References**


Battles, J.J., and Fahey, T.J. 2000. Gap dynamics following forest
Diacci, J. (Editor). 1999. Virgin forests and forest reserves in Central and East European countries. Biotechnical Faculty, Department of Forestry and Renewable Forest Resources, University of Ljubljana, Ljubljana, Slovenia.