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Canopy gap dynamics and tree understory release in a virgin beech forest, Slovakian Carpathians

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ABSTRACT

Canopy gaps play a crucial role for forest dynamics processes, as they largely determine light transmission to lower canopy strata, thereby controlling the turnover of tree individuals in the stand. Even though their functional importance is undisputed, quantitative data on the rate of gap creation and gap closure, and the temporal change in gap size distribution patterns in temperate virgin forests are scarce. We used a repeated inventory (line-intercept sampling) of gap size frequency and fraction in a virgin beech (*Fagus sylvatica*) forest in the Slovakian Carpathians over a 10-year interval (2003–2013) to test the hypotheses that (i) disturbance intensity and thus gap creation and gap closure rate change only little over time, (ii) gaps persist or even expand, until they are filled primarily by vertical ingrowth of trees from lower strata, and (iii) gap creation promotes the height growth of released saplings and sub-canopy trees. In the 2003 and 2013 inventories, 37 and 30 gaps > 20 m^2 size were mapped along a total of 3217 m transect line investigated. The large majority of gaps was < 100 m^2 in size; large gaps > 500 m^2 were very rare. Gap fraction decreased significantly from 13.6% in 2003 to 8.2% in 2013 (associated with a reduction in mean gap size from 261 to 96 m^2), indicating considerable variation in disturbance intensity in the past decades. Before 2003, both large gaps (probably caused by wind throw) and small gaps (from dying trees) have been formed, while only small gaps developed in the period 2003–2013. Small gaps were closed within a few years through rapid horizontal canopy expansion of neighboring beech trees, while vertical gap filling through ingrowth of lower canopy layers and regeneration was the dominant process in larger gaps. Saplings and trees in lower canopy layers formed a heterogeneous understory in large parts of recently formed gaps and responded to this process with increased height growth. We conclude that, despite considerable variation in disturbance intensity over time, this beech virgin forest responds to gap formation with high resilience through rapid lateral canopy expansion in small gaps and ingrowth of saplings and sub-dominant tree layers in larger gaps.

1. Introduction

In the prospect of climate change and global biodiversity loss, understanding the structure and dynamics of virgin forests is of great importance for forest ecosystem research from both a conservation and management perspective (Leuschner and Ellenberg, 2017). Various questions of forest ecology can only be answered in virgin forests (sensu Hunter, 1990), as management activities can imprint on forest structure for centuries (e.g. Tabaku, 2000). When investigating the structural dynamics of natural forests, the study of the disturbance regime is of high significance, as it largely determines the turnover of tree individuals in the canopy. The disturbance regime of forest ecosystems is characterized by several, partly interacting factors, including the type of disturbance, its magnitude, frequency and size, as well as the spatio-temporal dispersion of disturbances (Frelich, 2002; Nagel et al., 2007; White and Jentsch, 2001). Similar to many temperate forests in eastern Asia and North America (e.g. Coates and Burton, 1997), forests of European beech (*Fagus sylvatica* L.) are mainly exposed to small-scale disturbances (Peters, 1997) while medium and large-scale disturbance events are rare and most often related to wind throw (Peters, 1997; Schelhaas et al., 2003). Small-scale disturbances result in canopy gaps of < 100 to several hundred m^2 size that drive the forest cycle through their control on light transmission to the lower strata (Whitmore, 1989). Adjacent and formerly suppressed trees as well as seedlings and saplings in gaps benefit from the reduction in competition intensity. Further, gaps are an important habitat for

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many woodland plant and animal species (Coates and Burton, 1997; Lachat et al. 2016; Muscolo et al., 2014). Emulating natural gap dynamics in forestry offers opportunities for close-to-nature management and forest ecosystem restoration (Seymour et al., 2002), notably in beech-dominated forests (e.g. Nagel and Svoboda, 2008; Schütz et al., 2016).

Several authors have studied canopy gaps in beech-dominated virgin forests in the recent past. Approaches using terrestrial methods reported gap areas ranging from 3 to 19% (Bottero et al., 2011; Drößler and von Lüpke, 2005; Kenderes et al., 2009; Kucbel et al., 2010; Nagel and Svoboda, 2008; Petritan et al., 2013; Tabaku and Meyer, 1999; Zeibig et al., 2005), whereas remote sensing approaches found canopy gap percentages of 1% (Garbarino et al., 2012) or even less (Hobi et al., 2015a). However, these remote sensing approaches are constrained by only identifying those gaps that do not contain tree regeneration. Irrespective of the method applied, size-frequency distributions of canopy gaps generally show an exponential decline in the number of gaps with increasing gap size. This means that most gaps in beech forests result from the mortality of single or a few trees. Nevertheless, large gaps, if they are present, can account for a large fraction of the total gap area (Bottero et al., 2011; Kucbel et al., 2010; Nagel and Svoboda, 2008; Zeibig et al., 2005).

Early studies on the stand structure of beech virgin forests suggested that these forests are in a structural equilibrium condition at the stand scale (e.g. 30 ha; Korpeĺ, 1995). In contrast, dendroecological studies in beech-dominated virgin forests indicate a high variability in the frequency and intensity of disturbances (e.g. Nagel et al., 2014). Time series of aerial photographs from beech forests covering a few decades document both, low variation (Kenderes et al., 2009) or high variation (Splechtna and Gratzer, 2005) in disturbance intensity. Both scenarios seem plausible against the background of variation in local climate and site conditions, and they are not necessarily contradictory, as return intervals of high intensity disturbances might be longer than a few decades.

Change in gap area over time with gap formation, gap expansion or gap closure is driven by processes of tree growth and population dynamics, which are not well understood in virgin forests. Some terrestrial studies in virgin beech forests described a successive expansion of canopy gaps, driven apparently through the death of bordering trees as indicated by snags in different stages of decay ('gap makers') (Drößler and von Lüpke, 2005, Nagel and Svoboda, 2008; Bottero et al., 2011). These findings suggest that gaps may destabilize the bordering stand through mechanical damage, exposure to wind, or direct sunlight overheating the bark. In contrast, Tabaku and Meyer (1999) found gaps to be formed only by single disturbance events. In an old-growth beech-sugar maple forest in Ohio (USA), Runkle (2013) observed tree mortality over 32 years; tree mortality was not higher in the trees neighboring a gap than in the canopy trees in the closed stand. As for the process of gap closure, the distinction between lateral crown expansion of adjacent trees and vertical ingrowth from lower layers is crucial for the interpretation of gap dynamics, as only the latter is connected with a generational turnover in the canopy. The structure and species composition of formerly suppressed tree layers is supposed to play an important role in the process of gap closure. Studies on gap regeneration in (mixed) beech virgin forests reported a high presence of advanced regeneration (Nagel et al., 2010; Kucbel et al., 2010; Diaci et al., 2012). Even though it is undisputed that canopy gaps influence tree understory dynamics, this relationship has rarely been quantified.

In this case study, we conducted a repeated inventory of canopy gaps (2003 and 2013) in a virgin beech forest in the Carpathians. Our study bases on an earlier inventory by Drößler and von Lüpke (2005) that was conducted in 2003, representing one of the pioneering works on gap dynamics and disturbance patterns in European temperate broadleaf forests. As far as we know, our analysis represents the first ground-based repeated inventory of canopy gaps in a virgin beech forest. We addressed several questions in the field of canopy gap dynamics research, which arose from recent studies in temperate virgin forests.

Studies in virgin forests of *F. sylvatica* document a high variability in gap fraction among different stands. It is not yet clear whether this variation is caused by (i) the use of different inventory methods and gap definitions, (ii) regional differences in disturbance frequency and intensity, or (iii) possible temporal variation in disturbance frequency and intensity. With the repeated inventory approach, factors (i) and (ii) can be excluded, allowing us to focus on the temporal variation in canopy structure. Our work was guided by three hypotheses:

(H1). Based on the observation that large-scale, stand-replacing disturbances are rare in the climate of eastern-central Europe and old-growth forest may develop a dynamic equilibrium state in the long intervals between two external disturbance events (Korpel' 1995), we hypothesized that in the period between two large-scale events, the imprint of disturbance on stand structure should remain relatively constant over time, resulting in similar gap formation and gap closure rates on the stand scale. For our 10-yr observation period we thus predict similar total gap areas and gap size patterns for the 2003 and 2013 inventories.

(H2). Conclusions on the size development of gaps, once formed, are vague and different trends have been reported. The importance of different processes behind gap closure, i.e. horizontal ingrowth or vertical gap filling, in beech virgin forests has not been quantified yet. To test the general assumption, that gaps induce the turnover of tree-generations in the canopy, we formulated the hypothesis that gaps persist or expand, until they are filled mainly by vertical ingrowth of trees from lower layers into the upper canopy.

(H3). By addressing the assumed response of sub-canopy layers to gap formation we hypothesized that gap formation and the associated increase in light transmission to lower strata promote the development of the understory via two pathways, (i) facilitation of the establishment of new seedlings which increases the regeneration layer cover, and (ii) the release of existing advanced regeneration from competition through the upper canopy, causing a shift in canopy density towards taller sub-canopy layers.

2. Methods

2.1. Study site

The study was conducted in the virgin forest reserve Kyjov at 700–820 m a.s.l. in the Vihorlat Mountains in the eastern Slovakian Carpathians (48°53′N, 22°06′E). The forest reserve covers an area of 53 ha on a north- to north-east-facing slope (21% mean inclination). Mean annual temperature ranges from 5.2 to 5.7 °C and mean annual precipitation from 950 to 1000 mm in the sloping terrain with 120 m altitudinal distance (Kucbel et al., 2012). The bedrock is andesite, on which Dystric Cambisols with good water-holding capacity have developed. The forest community was assigned to the Fagetum dentarietosum glandulosae beech forest association. European beech was the dominant tree species, which formed almost pure stands (99% of the tree individuals) in the reserve with a small share of sycamore (*Acer pseudoplatanus* L.), Norway maple (*Acer platanoides* L.), common ash (*Fraxinus excelsior* L.), and wych elm (*Ulmus glabra* L.). Stand height was approximately 30 m. According to local foresters (personal communication), stand-replacing disturbances have not occurred during the last 60 years in this mountainous forest region, which is made accessible since about 1950. As a consequence, records from the more distant past do not exist.

2.2. Gap definition

As this study is a gap inventory repeating an earlier investigation of Drößler and von Lüpke (2005) in the year 2003 in the same forest, we largely adopted the method and gap definition used in that study. Canopy gaps were defined as openings in the canopy layer that were caused by the death of canopy trees. The maximum height of the vegetation, which filled the gap, was allowed to reach up to 2/3 of stand height. Thus, the canopy was considered to be closed, if tree height exceeded 20 m, corresponding to a diameter at breast height (dbh) ≥ 20 cm in this stand (see Fig. 1 in Drößler and von Lüpke 2005). In our