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9/Gap regeneration patterns in Carpathian old-growth mixed beech forests – Interactive effects of spruce bark beetle canopy disturbance and deer herbivory

Olga Orman[a,*], Dorota Dobrowolska[b], Jerzy Szwagrzyk[c]

[a] Department of Silviculture, Forest Ecology and Silviculture Institute, Faculty of Forestry, University of Agriculture in Kraków, Al. 29 Listopada 46, 31-425 Kraków, Poland

[b] Department of Forest Ecology, Forest Research Institute, Braci Leśnej 3, Sękocin Stary, 05-090 Raszyn, Poland

[c] Department of Forest Biodiversity, Forest Ecology and Silviculture Institute, Faculty of Forestry, University of Agriculture in Kraków, Al. 29 Listopada 46, 31-425 Kraków, Poland

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ABSTRACT

The combined effects of various disturbance types have lasting consequences on forest ecosystems and the services they provide. We examined inter-specific differences in the responses of European beech, silver fir and Norway spruce to canopy disturbance across four life stages (small seedlings, tall seedlings, saplings and pole-sized trees) in two Carpathian old-growth mixed beech forests located in the Gorce National Park (GNP) and Babia Gora National Park (BGNP), Poland. Both study sites were recently affected by spruce bark beetle outbreak. We compared the composition of tree regeneration between forest plots, canopy gaps and expanded areas (i.e. areas located under tree crowns). Moreover, we studied how various gap properties (size, expanded gap to canopy gap size ratio, shape) and other factors (browsing, plant and advanced regeneration cover) shaped regeneration patterns. Inter-specific differences in species abundance relative to gap properties and intra-specific differences in species response across various life stages to gap properties were found. Gap properties had more pronounced effects on saplings and pole-sized trees than on small and tall seedlings. Gap size had the most noticeable effect on beech across all regeneration classes. However, its effect varied from negative to positive depending on life stage. Pole-sized trees of all species responded positively to gap size. Thus, it seems that large gaps provided an opportunity for all species to recruit to canopy. Fir and spruce responded contrastingly to expanded gap to canopy gap size ratio, which reflects differences in their ability to adapt to high-intensity solar radiation. With the exception of beech, the 'forest-gap' gradient only affected trees in the advanced life stages (saplings and pole-sized trees). Beech and fir sapling densities and fir pole-sized tree densities were higher when under forest canopy, but spruce pole-sized trees were slightly more abundant in expanded areas. Browsing rates differed between the two study sites; they were more severe in BGNP, where deer densities in the last twenty years have been significantly higher. This intense deer browsing kept silver fir regeneration below the height of 0.5 m and prevented any recruitment to sapling stage. We conclude that even though the recent spruce mortality caused by bark beetle outbreak improved light conditions in both study areas, thus providing good regeneration opportunities to both beech and fir, deer browsing may have long-lasting effects on successional patterns by hindering fir recruitment in BGNP.

1. Introduction

The drivers, magnitude and frequency of changes in natural disturbances have recently drawn attention from researchers, society and policy makers. Climate change, long-term land use practices, changes in pathogens and insect dynamics have been altering disturbance regimes and producing new spatial vegetation patterns across local and regional scales (Adams et al., 2009; Anderegg et al., 2013; Seidl et al., 2014). Fine-scale gap dynamics have been recognized as a crucial process in determining stand structure and development in many forest ecosystems worldwide (Pickett & White, 1985). Even small canopy releases can alter environmental conditions due to an increase in light heterogeneity, spatial and temporal variations in soil water content, soil/ air temperature and availability of nutrient elements (Ritter et al., 2005;

* Corresponding author.
E-mail address: olaorm@gmail.com (O. Orman).

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Gálhidy et al., 2006; Rozenbergar et al., 2007). Moreover, they can provide diverse microsite patches for the establishment of tree regeneration (Nakashizuka, 1989; Zielonka, 2006; Orman & Szewczyk, 2015). Microclimates inside such gaps can speed up the germination of tree species' seeds; but, on the other hand, an increase in light and nutrients can stimulate the growth and reorganize the structure and composition of herbaceous plants and shrubs that compete with tree seedlings for resources (Holeksa, 2003; Diaci et al., 2012). Previous studies have shown that some tree seedlings exhibit more frequent occurrence and higher survival rates when located below adult trees or in patches with a higher proportion of larger trees than in gap openings, likely via the mechanism of indirect facilitation (Levine, 1999; Slocum, 2001; Paluch, 2005; but see Pagès et al., 2003).

Although some authors have suggested that various canopy gap properties (e.g. shape, orientation, age etc.) may affect species-specific differences in establishment, survival and growth (Mihók et al., 2007; Garbarino et al., 2012), the majority of studies from European mixed mountain forests have focused on comparing differences in the composition and structure of tree regeneration under forest canopy vs. in gaps as well as on species-specific responses to various light regimes caused by different tree-fall gap sizes (Rozenbergar et al., 2007; Nagel et al., 2010; Petritan et al., 2013; Čater et al., 2014; Feldmann et al., 2018). However, gap properties may not be the only influence on vegetation patterns in canopy gaps. For instance, the spatial distribution of resources along forest-gap gradients may also affect long-term tree growth and mortality (Gray et al., 2012; Stan & Daniels, 2014). Moreover, it is essential for regeneration studies to take into account the life stages both before and after sapling establishment because different mechanisms work at different life stages (Nakashizuka, 2001; Kneeshaw et al., 2006).

Mountain forests of Central Europe are among the most important ecosystems in the region. The disturbance history of these forests varies across mountain ranges and is influenced by past human activities, i.e. deforestation and land use patterns (Kulakowski et al., 2017). The last century has brought an increase in chronic disturbance processes, such as air pollutants (Elling et al., 2009), insect outbreaks (Sproull et al., 2015; Holeksa et al., 2017) and/ or prolonged herbivory (Klopcic et al., 2010; Nagel et al., 2015; Winter et al., 2015). Yet, many of the studies from this region have focused on only a single disturbance type or agent (Nagel et al., 2006, 2010; Mihók et al., 2007; Motta et al., 2011; Petritan et al., 2013). Given that the disturbance regimes of Central European montane forests are the result of complex interactions between natural and anthropogenic factors, a comprehensive approach is needed. This approach must consider multiple agents since the interplay between various agents may shift forest communities to alternative stable states by changing successional pathways (Paine et al., 1998; Kulakowski et al., 2013; Winter et al., 2015). Moreover, ongoing global environmental changes will likely escalate the frequency of interactions among and between both natural perturbations (e.g. windthrows, fires, a single canopy tree death as a result of senescence) and chronic disturbances (e.g. overbrowsing of regeneration, infection of trees by pathogens or insects) (Turner, 2010; Holm et al., 2013).

From the mid-2000s to the early 2010s, spruce bark beetles (*Ips typographus* (L.)) attacked a large area of monodominant natural and managed Norway spruce (*Picea abies* (L.) Karst.) forests in the Western Carpathians (Fujak, 2004; Grodzki, 2010). The outbreak affected not only upper montane belts but also mixed stands in lower montane zones (Loch & Armatys, 2014), resulting in a complex pattern of small sized gaps in the latter (Orman & Dobrowolska, 2017). The share of spruce among gapmakers was reported to be 3–6 times higher than its share in the canopy, making this species the most abundant gapmaker. Although our understanding of the role of bark beetle outbreaks in monodominant spruce stands has greatly improved in recent years, regeneration processes following an outbreak in mixed stands are still not well understood and data from mixed forests are scarce (Winter et al., 2015). Yet, the study of interactions between various disturbance factors is especially crucial in mixed stands, where they can result in unexpected vegetation pathways, for instance by giving a certain species a competitive advantage (Hart et al., 2014; Nagel et al., 2015). In this study, we examined tree regeneration responses to canopy disturbances induced by spruce bark beetle and deer browsing in two old-growth montane mixed beech forests composed of European beech (*Fagus sylvatica* L.), silver fir (*Abies alba* Mill.), Norway spruce and interspersed with sycamore maple (*Acer pseudoplatanus* L.) and rowan (*Sorbus aucuparia* L.). Primarily, we studied species-specific responses to various gap properties and the 'forest-gap' gradient. Secondly, we examined how species composition and height structure are affected by deer browsing. Specifically, we asked the following three questions: (i) how do tree species vary in their response to gap properties and 'forest-gap' gradient?; (ii) how do gap properties affect the composition of regeneration across different life stages (seedlings, saplings, pole-sized trees)?; (iii) how do other factors (herbaceous plant and advanced regeneration cover, browsing) shape the composition and structure of tree regeneration in gaps and under forest canopy?

2. Materials and methods

2.1. Research sites

The study was conducted in two old-growth mixed beech stands in the lower montane zones of the Babia Gora National Park (BGNP) and Gorce National Park (GNP), located in the Western Carpathians, southern Poland. The distance between the study sites is about 35 km. Both sites are located in the mixed montane forest zone, and the geological substrate in both cases is the so-called Carpathian flysch, consisting of layers of sandstone and shale. Dystric and eutric cambisols developed from Carpathian flysch are the dominant soil types in the mixed beech forests of both national parks. The main difference between the two sites is exposure; the BGNP site is located on northern slopes, while the GNP site is on south-facing slopes. European beech dominated both locations in terms of stem density and basal area, while silver fir and Norway spruce were two main codominant species (Orman & Dobrowolska, 2017). There is no historical evidence of regular forest management in either study site. Similar to other parts of Central Europe, the fir population in the Western Carpathians suffered from a significant decline in growth and high mortality from the 1960s to the late-1980s, mainly due to high SO_2 emissions (Elling et al., 2009). This period was followed by a subsequent recovery beginning in the early 1990s (Chwistek, 2008). Browsing by red deer (*Cervus elaphus* L.) and to a lesser extent by roe deer (*Capreolus capreolus* L.) is reported to have reduced the regeneration densities in these areas, particularly of fir and some other species, such as rowan and sycamore maple (Kalisz, 2015). Gray wolves (*Canis lupus* L.) and Eurasian lynxes (*Lynx lynx* L.) are present in both areas. Moderate to severe wind disturbances were recorded in both national parks in the early-2000s (Fujak, 2004; Grodzki et al., 2006) and likely triggered the ensuing bark beetle outbreak. However, severe wind damage was not observed in the old-growth stands, where no canopy openings larger than > 1500 m^2 were recorded (Orman & Dobrowolska, 2017).

The study area in GNP was situated in a 112 ha old-growth patch protected since 1970 (N 49°32′ E 20°07-08′) with elevation ranging from 920 to 1120 m. The climate is cold and humid: mean annual temperatures vary from 6.3 °C in the lower parts to 2.9 °C at the highest peak. Annual rainfall ranges from 920 mm to 1200 mm (Różański et al., 2006). The BGNP study area consisted of three strictly protected areas with a total size of about 100 ha (N 49°35′ E 19°28-29′ & 33–34′). Portions of mixed beech stands have been protected since 1934, even before the establishment of BGNP in 1954. The areas were located on the northern slopes of the Babia Gora Mt., with elevation ranging from 860 to 1010 m. The mean annual temperature is around 4.0 °C (Obrębska-Starklowa, 1983).