Forest Ecology and Management 285 (2012) 20–28

Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Gap recruitment and partitioning in an old-growth beech forest of the Dinaric Mountains: Influences of light regime, herb competition and browsing

Jurij Diaci *, Tomaz Adamic, Andrej Rozman

Department of Forestry, Biotechnical Faculty, University of Ljubljana, Vecna pot 83, 1001 Ljubljana, Slovenia

ARTICLE INFO

Article history:
Received 12 May 2012
Received in revised form 12 July 2012
Accepted 7 August 2012
Available online 6 September 2012

Keywords:
Old-growth forest
Natural regeneration
Fagus sylvatica
Acer pseudoplatanus
Allium ursinum
Light climate

ABSTRACT

Canopy gap recruitment in beech (*Fagus sylvatica* L.) old-growth forests is influenced by the interplay of the canopy gap disturbance regime, site factors, and stand history. Persistent seedling and sapling banks of beech and other shade tolerant species often play a major role in canopy gap closure. To gain more insight into interactions between medium-sized gaps and pre-gap ground vegetation patterns, we studied beech regeneration over a 10-year period on a site rich in wild garlic (*Allium ursinum* L.) in a Dinaric beech old-growth forest. In 1999 we selected the five largest newly created gaps ($\sim$200 m^2) and systematically established 13 permanent plots (1 × 2 m) in each gap. In 1999, 2004, and 2009, we sampled tree species regeneration (density, cover, and growth), ground vegetation (composition and cover), and light climate. Beech regeneration slowly increased in density and cover despite an overall decrease in light (11.0–5.7%). The same was not true for maple. While beech was present in all regeneration classes, dominant maple seedlings rarely reached 50 cm. Beech also had a significantly greater height increment. Regeneration of both species was negatively affected by *Allium* cover, low light levels, and ungulate browsing. Gap partitioning was observed among shade tolerant Allium, which preferred microsites under closed canopy and low light levels, beech regeneration, which preferred gap periphery, and other less shade tolerant herbs, which favoured gap centres. The slow development of the regeneration indicated the importance of several gap releases. The high maple seedling density and less abundant beech advance regeneration in this study site compared to other beech sites suggests that *Allium* dominated managed forests might present an opportunity for growing less shade-tolerant species, if managed with a gap-oriented silvicultural system (e.g. irregular shelterwood).

1. Introduction

Natural regeneration in beech (*Fagus sylvatica* L.) is a result of the complex interactions of many biotic and abiotic factors (Wagner et al., 2010). Studies have shown that limited seed dispersal, seed predation, the formation of a seedling bank, shade tolerance, susceptibility to competition from herbs, susceptibility to drought, vulnerability to frost, and browsing are among the most important characteristics of beech regeneration ecology (e.g. Watt, 1923; Mosandl and el Kateb, 1988; Schmidt, 1997; Collet et al., 2001; Pages et al., 2003; Diaci, 1997; Mountford et al., 2006; Mihok et al., 2007; Hahn and Emborg, 2007; Petritan et al., 2007). A challenge for studying beech regeneration ecology, however, is that because beech often forms a seedling bank due to its high shade tolerance and overall resource use efficiency during the regeneration phase, making it difficult to accurately assess the effects of various ecological factors and their interplay (Madsen and Hahn, 2008). Thus, in old-growth forests, where stands were not influenced by silviculture, beech seedlings are subjected to extremely low light levels and therefore provide ideal test beds for studying the various ecological factors that influence beech regeneration (Emborg, 1998).

Although old-growth forests are rare in Europe, beech regeneration ecology has been intensively studied in old growth (Leibundgut, 1982; Korpel, 1995; Emborg, 1998; Zeibig et al., 2005; Commarmot et al., 2005; Nagel et al., 2006; Drössler and von Lüpke, 2007; Mihok et al., 2007). Such studies reveal important processes that could be used to improve silviculture in beech forests. Nevertheless, and despite beech's growing importance for its role in mitigating climate change and for its role in close-to-nature silviculture, repetitive measurements of beech regeneration in old-growth forests are rare (sensu Runkle and Yetter, 1987; Hahn and Emborg, 2007). Because one-time observations can be strongly influenced by yearly climatic changes, they may yield only limited insight into the long-term regeneration process. Moreover, since research on stand regeneration patterns is specialised, gap dynamics research rarely includes measurements of ecological factors (sensu Drössler and von Lüpke, 2005). Likewise, specialised research on regeneration ecology rarely

---

* Corresponding author. Tel.: +386 1 320 3533; fax: +386 1 257 11 69.
E-mail address: jurij.diaci@bf.uni-lj.si (J. Diaci).

0378-1127/$ - see front matter © 2012 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.foreco.2012.08.010

takes into account the whole regeneration cycle, which includes small trees and potential gapfillers.

Research on disturbance dynamics in European old-growth beech forests has revealed relatively small average gap sizes (Tabaku and Meyer, 1999; Zeibig et al., 2005; Drössler and von Lüpke, 2005), suggesting that these forests are predominantly driven by endogenous events with occasional intermediate disturbances, especially windthrows. Because of the prevalence of small gaps and the fast lateral crown growth of beech canopy trees, it seems likely that the dominant pathway to canopy recruitment involves a combination of beech advance regeneration and several gap releases. However, beech regeneration strategies may be well adapted to different site conditions, especially in its optimum growing range, where it can be found on a variety of substrates and geomorphologic types in an altitudinal gradient from the lowlands to the upper timberline. Research on gap dynamics has often neglected the fine scale site differences and ground vegetation patterns that may significantly influence the establishment and early growth of seedlings.

Many eutrophic and mesotrophic beech forests in Europe are characterised by an early spring herb layer consisting of geophytes. This herb layer is occasionally extremely dense, especially where wild garlic (*Allium ursinum* L.; hereafter *Allium*) dominates. *Allium* can have a strong allelopathic effect on other herbaceous plants and presents a very challenging environment for the growth of woody regeneration (Ernst, 1979; Ellenberg, 1988; Djurdjevic et al., 2004). Geophytes such as *Allium* are characterised by fast growth made possible by the nutrients stored in perennial bulbs and a short aboveground life-cycle that usually lasts less than 3 months. This life history strategy takes advantage of the bounty of early spring resources, such as the light transmitted through bare crowns and the humid, nutrient-rich soils that result from melting snow and little competition from other summer-green plants (Ernst, 1979; Jandl et al., 1997). Competition from *Allium* may influence beech regeneration, especially the formation of seedling banks, although tree regeneration profits from a longer growing season and variability of ground vegetation throughout many years. To better understand the link between these special forests sites and the canopy gap disturbance regime, we studied beech regeneration over a 10-year period in an old-growth beech forest rich in *Allium*. The main objectives of this study were (1) to document changes in light climate and ground vegetation patterns over the observed period, (2) to analyse competition and gap partitioning patterns among *Allium* and woody regeneration, (3) to compare the recruitment success of beech and maple (*Acer pseudoplatanus* L.), and (4) to describe possible scenarios of gap recruitment in medium gaps in *Allium*-rich beech forests.

2. Materials and methods

2.1. Stand and site characteristics

Our study was carried out in the Krokar old-growth forest reserve (74.5 ha) in the Dinaric Mountains of southern Slovenia (45°32′25″N, 14°45′57″E). The parent material is composed of limestone and dolomite. Karstic phenomena such as sinkholes and rocky outcrops are common. The soil type is calcocambisol of variable depth. The elevation of the reserve ranges from 840 to 1170 m a.s.l. Mean annual precipitation often exceeds 2000 mm, and mean annual temperature is about 6° C. In 2004 the growing stock was 636 m^3/ha and was composed of 93% beech, 6% silver fir (*Abies alba* Mill.; hereafter fir), and 1% other broadleaves (Diaci et al., 2011). The average volume of coarse woody debris was 154 m^3/ha, 43% of which was snags and 57% of which was logs. Several site types exist within the reserve (Accetto, 2002). This study focused on a pure beech site on a flat dolomite Karstic plateau (*Isopyro-Fagetum*; hereafter IF). In contrast to the limestone surroundings, there was very little aboveground rockiness and stoniness. The mean inclination of the research plots was 2°. The upper canopy height of gap edge trees was 42 m. In 2000 a total of 49 canopy gaps were inventoried on the IF site. These gaps covered 5.6% of the sampled area and varied from 6 to 833 m^2 (Zeibig et al., 2005). Stand structure was relatively homogeneous on the IF site and gaps were beginning to form in the closed canopy. This structure may be related to stand development following past natural (e.g. windthrow) or anthropogenic disturbances (e.g. logging for charcoal burning). However, based on the historical archival evidence, the stand was not disturbed by humans; the entire forest reserve has been protected for more than 100 years and the upper most area, which includes the IF site, has been protected since 1885 (Hocevar et al., 1985). We did not find any signs of logging or any other human intervention in the research area. However, past changes in the forest structure of the adjacent *Omphalodo-Fagetum* forest site, the decline of silver fir in particular, indicated the indirect influences of air pollution and overbrowsing (Diaci et al., 2011). During the sampling period (1999–2009), a few new gaps were created, but not in the near vicinity of the gaps under research.

2.2. Recordings

In 1999 we selected the five largest gaps on the IF site (average size was about 200 m^2). The relatively recent formation (5–10 years old) of the gaps allowed subsequent comparison of regeneration development. Within each gap we systematically established 13 rectangular permanent plots 1 × 2 m in size with the shorter side facing north. The first plot was located in the gap centre, and an additional three plots were located in each direction of the compass (Fig. 1). Plots were located 2 m apart, except when obstacles (i.e. CWD, root plates, large trees) were present, in which case plots were moved by 1 metre in the direction of the transect. Using this sampling design, approximately five plots were located in the gap centre, four at the gap edge, and four below closed canopy. All plots were permanently marked with iron stakes for location with a metal detector at the next inventory. In 1999, 2003, and 2009, we recorded the species composition and percent cover of vascular plants on the plots. Plant cover was estimated visually from above and was recorded to the nearest 10% from 10 to 100%, and to the nearest 1% from 1% to 10%, excluding mosses. In 1999 plant cover was recorded in late July, when *Allium* had already begun to wither. Subsequent recordings in 2003 and 2009 were therefore carried out in early July. Most analyses were based on the most recent recording; however, the coverage of geophytes could still be slightly underestimated. Regeneration density was recorded per species in four height classes: small seedlings ($h \leqslant 20$ cm; excluding 1-year-old seedlings), seedlings ($20\text{ cm} < h \leqslant 130$ cm), saplings ($130\text{ cm} < h \leqslant 250$ cm), and small trees ($h > 250$ cm and dbh < 5 cm). In 1999 and 2009, all beech and maple plants were scored for browsing damage. They were classified as unbrowsed or lightly browsed if less than or equal to 10% of the lateral shoots were damaged. If more than 10% and less than or equal to 50% of lateral shoots were browsed, including the terminal shoot, seedlings were classified as moderately browsed, while plants with even more damage were categorised as heavily browsed.

In 1999 and 2003 we measured the length and last height increment of the two dominant beech or maple plants in each plot. In 2009 the three dominant beech plants in each plot were analysed in the same way. Plants were considered dominant only if they were not overtopped by nearby regeneration or herbs and only if the terminal shoot had not been browsed in the previous 2 years, thus the tallest plants were usually, but not always, dominant. Dominant individuals were not permanently marked, such that dif-