Available online at www.sciencedirect.com
SCIENCE DIRECT
Forest Ecology and Management 226 (2006) 268–278
Forest Ecology and Management
www.elsevier.com/locate/foreco

Regeneration patterns after intermediate wind disturbance in an old-growth *Fagus–Abies* forest in southeastern Slovenia

Thomas A. Nagel [a,*], Miroslav Svoboda [b], Jurij Diaci [a]

[a] *University of Ljubljana, Biotechnical Faculty, Department of Forestry and Renewable Forest Resources, Vecna Pot 83, 1000 Ljubljana, Slovenia*
[b] *Czech University of Agriculture in Prague, Faculty of Forestry and Environment, Kamycka 129, 16521 Prague 6, Czech Republic*

Received 1 September 2005; received in revised form 24 January 2006; accepted 30 January 2006

Abstract

We studied patterns of tree regeneration in relation to canopy structure in a 1-ha plot damaged by an intermediate windstorm in 1983 and a 1-ha control plot regulated by small-scale canopy gaps in an old-growth *Fagus sylvatica–Abies alba* forest, southeastern Slovenia. In the windthrow plot, a maze of interconnected gaps covered 55% of the plot, while more discrete canopy openings covered 27% of the control plot. The different canopy structures resulted in marked differences in the density and spatial patterns of tree regeneration in the two plots. *Fagus* dominated the regeneration layer in both plots, while *Abies* occurred infrequently. For *Fagus*, there were nearly six-fold less seedlings, but twice as many saplings and understory trees in the windthrow plot compared to the control plot. Overall, the spatial patterns of *Fagus* seedlings, saplings, and understory trees were clumped in both plots, but only saplings and understory trees were aggregated under canopy gaps in the control plot, whereas saplings in the windthrow plot were distributed irrespective of canopy gaps. *Abies* individuals also had an aggregated spatial distribution, but were growing under a closed canopy. We suggest that infrequent, intermediate windstorm disturbance plays an important role in the structure and dynamics of central European forests by creating more coarse-grained forest structures than in stands regulated by smaller-scale gap processes.

Keywords: Forest dynamics; Canopy gaps; Tree regeneration; Blowdown; Forest structure; Windstorm

1. Introduction

The importance of canopy gaps for tree regeneration processes in temperate forests has received much attention from ecologists (Runkle, 1981; Canham, 1990; Nakashizuka, 1991; Lertzman, 1992). In temperate, old-growth forests of central Europe, gap formation by death of individual or small groups of canopy trees is often noted as the dominant process driving forest dynamics (Prusa, 1985; Leibundgut, 1982; Korpel, 1995). In these forests, wind seems to be the dominant source of canopy disturbance, yet surprisingly few studies have examined the role of wind disturbance on the structure and dynamics of near-nature or old-growth temperate forests in Europe (Falinski, 1978; Mayer and Neumann, 1981; Pontailler et al., 1997; Reich et al., 2004; Wolf et al., 2004). What little is known about wind disturbance comes mostly from coniferous forests, plantations, and managed forests (Gardiner and Quine, 2000; Lässig and Mocalov, 2000; Ulanova, 2000; Fischer et al., 2002), so the effects of wind damage on old-growth forest structure and dynamics remain poorly understood.

Variation in the frequency and intensity of wind disturbance events that reduce canopy cover should influence recruitment of canopy trees and overall stand dynamics. In central Europe, with the exception of the extraordinary storms in 1990 and 1999 that caused unprecedented damage to forests throughout the region (Schönenberger et al., 2002; Angst et al., 2004), storms that cause large-scale catastrophic blowdowns are infrequent, while strong winds associated with local thunderstorms are more common (Schelhaas et al., 2003). These events may play an important role in creating canopy disturbance intermediate between scattered canopy gaps and large, catastrophic blowdowns, both of which have received much attention from ecologists (Lorimer, 1980, 1989; Runkle, 1982, 2000; Canham and Loucks, 1984; Glitzenstein and Harcombe, 1988; Peterson and Pickett, 1991; Foster et al., 1998). Less, but more recent studies have documented the role of intermediate wind disturbance on temperate forest structure and dynamics (Webb, 1989; Greenberg and McNab, 1998; Canham et al., 2001; Woods, 2004). These events damage moderate portions of a

* Corresponding author. Tel.: +386 1 423 11 61; fax: +386 1 257 11 69.
E-mail addresses: tom.nagel@bf.uni-lj.si (T.A. Nagel), svobodam@fle.czu.cz (M. Svoboda).

0378-1127/$ – see front matter © 2006 Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2006.01.039

stand (i.e. 5–30%), creating a fine-grained mosaic of canopy damage in a matrix of undisturbed forest. Disturbances of this type can create a range of canopy gap sizes (i.e. 100–2000 m^2), including ''messy'' intermediate sized openings without discrete edges and standing trees remaining in gap interiors (Greenberg and McNab, 1998).

The direct effects of intermediate wind disturbance may have long-lasting and distinctive effects on stand structure and composition compared to more frequent, small-scale gap disturbance processes resulting from the death of individual canopy trees. For example, the larger canopy openings created from multiple tree fall gaps may create even-aged patches of trees at the scale of the gap, resulting in a more coarse-grained forest structure. Increased understory light levels in large gaps also play an important role in maintaining shade intolerant species (Peterson and Pickett, 1995). Moreover, uprooted trees are more common in windthrow gaps than in gaps formed during the slow death of canopy trees from background mortality processes. These uprooted trees are a major source of soil turnover, and treefall pits, mounds, and decaying boles create small-scale environmental heterogeneity that help to maintain species diversity (Falinski, 1978; Nakashizuka, 1989; Peterson et al., 1990; Szewczyk and Szwagrzyk, 1996). Therefore, an examination of the post-disturbance vegetation response to intermediate wind damage will contribute to understanding long-term forest dynamics in central European old-growth forests.

During the summer of 1983, an intense, local thunderstorm caused intermediate damage (10% of the canopy trees were killed) to approximately 12 ha of an old-growth, *F. sylvatica–A. alba* forest in Slovenia. In an earlier paper, we described the immediate effects of the storm on patterns of tree mortality (Nagel and Diaci, 2006). In this paper, we describe the effects of the windthrow on forest structure and composition 21 years after the event, with a focus on the relationship between canopy gaps and the spatial patterns of seedlings, saplings, and understory trees. Measurements were made in two permanent plots, one located in an area of the stand affected by the windthrow and another in an adjacent undisturbed area that served as a control. This approach allowed a comparison of the regeneration patterns following intermediate wind disturbance with those regulated by smaller-scale gap dynamics.

2. Materials and methods

2.1. Study area

This study was conducted in the Pecka forest reserve, a 60 ha old-growth European beech (*F. sylvatica* L.) and silver fir (*A. alba* Mill.) forest remnant located on a high karst plateau (900 m) in the Dinaric Alps, southeastern Slovenia (45°754′N, 14°995′E) (Fig. 1). Micro-topography on the site is very diverse, with abundant sinkholes typical of karst geology. Calcareous brown soils on the site are derived from the limestone parent material, and soil depth can vary between 30 and 70 cm depending on micro-topographic position. The region experiences a combination of a continental and Mediterranean climate, with an annual precipitation of ca. 1400 mm. Mean monthly temperatures range from −4 °C in January to 20.3 °C in July.

The forest is dominated by *F. sylvatica* (81%) and *A. alba* (19%), but other species, including Norway spruce (*Picea abies* Karst.), maple (*Acer pseudoplatanus* L.), and elm (*Ulmus glabra* Huds.), occur infrequently. *F. sylvatica* regeneration is abundant throughout much of the understory, mainly because there is little competition from herbaceous vegetation (Diaci et al., 2003), seed sources are abundant, and understory light levels have increased due to a recent decline in the *A. alba* population. Long-term inventory studies in the reserve indicate that the *A. alba* population substantially declined over the second half of the 20th century (Turk et al., 1985; Rozenbergar, 2000), which is a trend reported throughout *F. sylvatica–A. alba* forests in Slovenia and Central Europe (Boncina et al., 2003; Bigler et al., 2004). Reasons for the decline are unclear, but may be partly due to anthropogenic factors, such as climate change, pollution, and soil acidification. People have influenced the forest in other ways as well. Long-term changes in deer populations regulated by hunting have strongly influenced *A. alba* demography through browsing pressure on regeneration (Debeljak, 1997; Diaci and Boncina, 2003). Also, a few scattered *A. alba* in parts of the reserve were selectively cut during late 1940s.

There is little meteorological information for the 1983 storm event, especially regarding wind speeds, as most weather stations in Slovenia did not measure wind speed until 1993. A second storm on July 23, 2004 that caused widespread damage in the reserve recorded wind speeds up to 24.4 m/s at the closest weather station (Novo Mesto-14 km from the study site) (Nagel and Diaci, 2006). However, it is impossible to speculate about wind speeds in the reserve during the storm, due to significant variation in wind intensity over scales of kilometres in storm events (Everham and Brokaw, 1996). Wind speed data compiled from weather stations located in regions of the country near the study site show that strong-wind events occur rather frequently in some years (Fig. 2), suggesting wind may be an important disturbance agent in this area.

2.2. Field sampling

In the summer of 2004 we set up a 1-ha (100 m × 100 m) permanent plot in part of the stand affected by the 1983 windthrow and another 1-ha (100 m × 100 m) permanent plot in an adjacent undisturbed area that served as a control. The location of the two plots was based on the following criteria: (1) plots should be away from the edge of the reserve to avoid edge effects; (2) plots should not include parts of the stand affected by subsequent windthrow events; (3) the windthrow plot should be representative of the overall 1983 storm damage severity in the reserve; (4) the control plot should be located near the windthrow plot and should have similar site conditions; and (5) both plots should be located in areas that had similar stand structures before the 1983 storm. To determine the pre-storm forest structure, we used a detailed inventory of forest development phases, which were mapped in the entire reserve in 1980 (Turk et al., 1985). According to the map, the forest