Forest Ecology and Management 348 (2015) 174–185

Contents lists available at ScienceDirect

Forest Ecology and Management

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

Impact of wind-induced microsites and disturbance severity on tree regeneration patterns: Results from the first post-storm decade

Floor Vodde [a,*], Kalev Jõgiste [a], Jeroen Engelhart [a], Lee E. Frelich [c], W. Keith Moser [d], Allan Sims [b], Marek Metslaid [a]

[a] Department of Forest Biology, Estonian University of Life Sciences, Kreutzwaldi 5, 51014 Tartu, Estonia
[b] Department of Forest Management, Estonian University of Life Sciences, Kreutzwaldi 5, 51014 Tartu, Estonia
[c] Department of Forest Resources, University of Minnesota, St. Paul, MN, USA
[d] Forest Inventory & Analysis Unit, Northern Research Station, USDA Forest Service, St. Paul, MN, USA

ARTICLE INFO

Article history:
Received 30 December 2014
Received in revised form 30 March 2015
Accepted 31 March 2015
Available online 20 April 2015

Keywords:
Mortality
Competition
Establishment sites
Regeneration dynamics
Windthrow

ABSTRACT

In two hemiboreal mixed spruce–hardwood forests in north-east Estonia, we studied (1) which factors affect tree regeneration survival and development during the first post-storm decade and (2) how these effects change in time. Regeneration height and mortality of the tree species black alder (*Alnus glutinosa* (L.) J. Gaertn.), birch (*Betula pendula* Roth., *Betula pubescens* Ehrh.), Norway spruce (*Picea abies* (L.) Karst.) and European rowan (*Sorbus aucuparia* L.) were analysed in moderately and heavily damaged stands, in two types of windstorm-created microsites, i.e. root-plate pits and mounds of uprooted trees, and on intact soil at different stages since disturbance.

Regeneration was significantly taller in heavily damaged areas and species traits regarding tree height only became noteworthy at later stages since disturbance. Mortality probability was initially indifferent to microsite type and increased later for regeneration on intact soil compared to regeneration on the storm-induced microsites. Mortality increased with storm severity for *A. glutinosa* and *Betula*, whereas mortality of *P. abies* was initially low and became higher with time since disturbance in areas with increased levels of coarse woody debris. Eventually, height and height increment in previous years were clearly negatively related to mortality probability and competition levels in previous years increased chance of death. The relatively high spatial heterogeneity and trends in dominance of post-storm microsites by different tree species increase disturbance-emulating management options. In conclusion, regeneration mortality and species composition are initially directed by exogenous factors linked to storm severity and microsite heterogeneity, generating a degree of spatial partitioning within a microsite, whereas gradually species' life-history traits and competition take over.

1. Introduction

Microsites in forests consist of spatially delineated areas of specific climatic and pedological characteristics. Here, we concentrate on those microsites important for tree regeneration establishment, such as undisturbed, vegetated forest floor and tree stumps. Windthrow can contribute to forest microsite heterogeneity by increasing the amount of coarse woody debris (CWD) and adding root mounds and pits. This, in turn, may increase within-stand diversity of regenerating tree species and stand vertical and horizontal structure (Peterson and Pickett, 1990; Kuuluvainen, 1994; De Grandpré and Bergeron, 1997). Most studies of post-storm stand development focus on the first few years of regeneration development after disturbance (Caquet et al., 2010; Vodde et al., 2011; Fischer and Fischer, 2012), a period when mortality is often high (Peet and Christensen, 1987) and highly variable (Nakashizuka, 2001; Queenborough et al., 2007). Nevertheless, early mortality is regarded as a key process in forest development (Lutz and Halpern, 2006). In combination with other differences, such as the spatial extent of the study and forest type, it is complicated to extrapolate the findings to the long term, resulting in varied conclusions on the role of wind-induced microsites on forests (Vodde et al., 2011; Xi and Peet, 2011).

In the first decade after windthrow, surviving mature trees struggle with radical changes in environmental circumstances, including increased exposure to radiation, wind, fungus outbreaks

---

* Corresponding author.

E-mail addresses: floorvodde@hotmail.com (F. Vodde), kalev.jogiste@emu.ee (K. Jõgiste), jeroenengelhart@gmx.com (J. Engelhart), freli001@umn.edu (L.E. Frelich), moserk@safnet.org (W.K. Moser), allan.sims@emu.ee (A. Sims), marek.metslaid@emu.ee (M. Metslaid).

http://dx.doi.org/10.1016/j.foreco.2015.03.052
0378-1127/

and insect infestations. Simultaneously, several groups of regeneration compete for a place in the future canopy: (1) surviving advance regeneration, (2) new sprouts and basal shoots from downed, broken or buried tree stems or root systems, and (3) new seedlings germinating post-disturbance. Vitality of surviving individuals, their size and spatial distribution depend on their pre-storm status and storm characteristics (e.g. Kuuluvainen, 1994; Collet et al., 2008). Seed source availability, tree species' traits and the size of disturbance gaps determine the potential share of newly regenerating trees. Branches and logs of fallen trees may safeguard new and advance regeneration from ungulate browsing (Krueger and Peterson, 2006; de Chantal and Granström, 2007). Furthermore, the aftermath of the disturbance may influence stand development: survivors that eventually die, delayed falling of dead wood and persistently blocked sunlight as a result of the accumulated logs or surviving vegetation (Castelli et al., 1999; Kurulok and Macdonald, 2007; Lugo, 2008).

Under circumstances that seed sources of the main pre-storm tree species are not limiting, new regeneration of these species emerges where it finds the conditions to germinate, mainly colonising the newly-created microsites. These may comprise pit-and-mound complexes created by uprooted trees, and logs in various stages of decay. Small-seeded species generally require less-vegetated sites or surface mineral soil for germination (Sayer, 2006) and in some cases also higher light levels (Milberg et al., 2000), whereas average to large-seeded species, with the capacity to penetrate better through moss or humus layers, have more potential establishment sites (Eriksson and Eriksson, 1997; Leishman et al., 2001). The somewhat more favourable germination conditions notwithstanding, post-storm natural tree regeneration generally suffers from relatively high mortality rates (Vodde et al., 2011) and also the conditions that influence growth at these locations may be variable. Elevated sites such as mounds offer the best light conditions (Kuuluvainen and Kalmari, 2003), especially for small-seeded and light-demanding tree species, whereas flat sites are more stable. However, new regeneration on flat sites can experience burial by litter and soil erosion from adjacent mounds and pit walls, as well as extreme microclimatic circumstances that limit growth and survival. The interaction between soil moisture and tree species' traits determine the optimal location for survival in the face of flooding and drought (Beatty, 1984; Beatty and Stone, 1986). Regeneration in pit centres on wet sites may suffer mortality due to inundation, whereas on dry sites, pits may be the only place to survive summer droughts. Therefore, microsite location, regeneration location within the microsite, competition from other new regeneration and storm severity (status of adjacent surviving trees) contribute to seedling performance. Finally, the dynamic character of the conditions in wind-induced microsites, the timing of seedling germination (Nakagawa et al., 2003; Kathke and Bruelheide, 2010) and early seedling mortality (Maher and Germino, 2006) all may influence post-storm stand development.

To better predict survival of regeneration in wind-impacted microsites, it is important to understand how seedlings, saplings and understorey trees perform in different areas of a given microsite type and among types. We analysed growth and mortality of tree regeneration in two types of wind-impacted microsites, pits and mounds, and on intact soil to find out which factors are most important for survival and growth during the first post-storm decade. Furthermore, we compare final tree height and abundance a decade post storm, and relate this to microsite availability to illustrate the importance of wind-induced microsites. After germination in pits or on mounds, we expect that within-microsite variability in light conditions, soil stability and moisture influence growth and mortality of functional groups differently, resulting in spatial partitioning within a microsite. The latter effects could become neutralised as pits get more homogeneous over time. In addition, we expect that the regeneration tree layer in a given microsite and its surroundings becomes denser over time, implying that initially, microsite conditions determine growth and mortality, whereas later on, competition gradually takes over.

2. Materials and methods

2.1. Study area

Two summer storms caused major blow-down in north-east Estonia, in the former forest districts of Tudu (59°11′N, 26°52′E) and Halliku (58°43′N, 26°55′E) in 2001 and 2002, respectively (Fig. 1). Both areas are situated in the hemiboreal zone with a moderately cool and moist climate. The average annual temperature is 4–6 °C, ranging from a monthly average of −6 °C in February to 17 °C in July. Annual precipitation varies between 500 and 750 mm, of which 40–80 mm falls as snow. The active vegetation period (daily air temperature above 5 °C) lasts between 170 and 180 days per year. Both sites had mature mixed spruce–hardwood forests on flat, humid, though locally drained, mainly gleyed podzolic and gley soils of the *Myrtillus* and *Filipendula* forest site types (Lõhmus, 2004). The storms created an irregular disturbance pattern, with heavily, moderately and scarcely damaged patches. In the Tudu unit, within the borders of the Suigu nature protection area (82 ha), no active management took place since 1976. The passive management strategy was continued after the 2001 storm, regardless of the damage severity. In the Halliku unit, agreements preserved several areas from salvage logging and some sites were already protected as woodland key habitats. The most prominent tree species in the pre-storm stands were Norway spruce (*Picea abies* (L.) Karst), silver and downy birch (*Betula pendula* Roth. and *B. pubescens* Ehrh.), European aspen (*Populus tremula* L.) and black alder (*Alnus glutinosa* (L.) J. Gaertn.). Age of the dominant tree species at the time of the storm ranged from 110 to 158 years. More details on storm damage and vegetation community changes can be found in Ilisson et al. (2005) and Ilisson et al. (2006). Study plots were initially selected to represent four treatments; heavy, moderate and control (i.e. scarcely damaged) wind severity levels, plus heavy wind damage followed by salvage harvest.

2.2. Field methods

In 2002 (Tudu) and 2003 (Halliku), permanent 20 × 40 m sample plots were established, followed by mapping canopy tree locations, position and vitality to estimate damage severity. To minimise edge effects, plots were placed in the centre of patches of a given storm severity. Four plots were placed in each 'treatment' and three in control areas (total 15 plots).

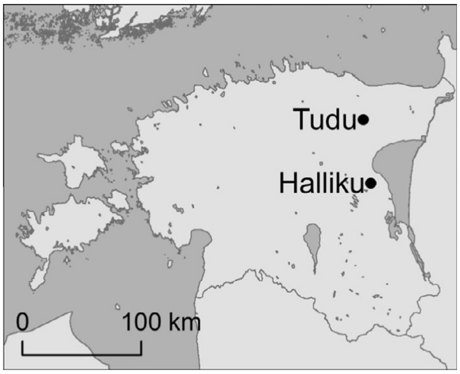

Fig. 1. Location of the study areas in Tudu and Halliku forest districts in Estonia.