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Estonian University of Life Sciences

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TORMIKAHJUSTUSE KÄIGUS TEKKINUD MIKROALADE DÜNAAMIKA JA HÄIRINGUJÄRGNE PUURINDE UUENEMINE HEMIBOREAALSES SEGAMETSAS

FLOORTJE VODDE

A Thesis
for applying for the degree of Doctor of Philosophy in
Forestry

Väitekiri
Filosoofiadoktori kraadi taotlemiseks metsanduse erialal

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers, which are referred to in text by their Roman numerals.

I **Vodde, F.**, Jõgiste, K., Kubota, Y., Kuuluvainen, T., Köster, K., Lukjanova, A., Metslaid, M., Yoshida, T. 2011. The influence of storm-induced microsites to tree regeneration patterns in boreal and hemiboreal forest. Journal of Forest Research 16(3): 155–167.

II Ilisson, T., Köster, K., **Vodde, F.**, Jõgiste K. 2007. Regeneration development 4-5 years after a storm in Norway spruce dominated forests, Estonia. Forest Ecology and Management 250: 17–24.

III **Vodde, F.**, Jõgiste, K., Gruson, L., Ilisson, T., Köster, K., Stanturf, J.A. 2010. Regeneration in windthrow areas in hemiboreal forests: the influence of microsite on the height growths of different tree species. Journal of Forest Research 15: 55–64.

IV **Vodde, F.**, Jõgiste, K., Engelhart, J., Frelich, L.E., Moser, W.K., Sims, A., Metslaid, M. Does position matter in wind-induced microsites for tree seedling establishment, growth and survival? Submitted to Journal of Vegetation Science.

The contributions of the authors to the papers were as follows:

	I	II	III	IV
Original idea	FV, KJ	KJ, TI	FV, KJ	FV, KJ
Study design	FV, KJ	KJ, KK, TI	FV, KJ, KK, TI	FV, JE, KJ, LF
Data collection	All	FV, KK, TI	FV, LG, TI, KK	FV, JE, MM
Data analysis	FV	TI	FV, KJ, KK	AS, FV
Manuscript preparation	All	FV, KK, TI	FV, JS, KJ, TI	All

AS - Allan Sims; FV - Floortje Vodde; JE - Jeroen Engelhart; JS - John A. Stanturf; KJ - Kalev Jõgiste; KK - Kajar Köster; LF - Lee E. Frelich; LG - Loïc Gruson; MM - Marek Metslaid; TI - Triin Ilisson

ABBREVIATIONS

BA	Basal area, m^2
CI	Competition index, based on H and D
CWD	Coarse woody debris
dbh	Diameter at breast height (130 cm), cm
D	Density, regeneration trees m^{-2}
i	i^{th} regeneration tree
j	j^{th} microsite
H´	Shannon diversity index
H	Tree height, cm
HI_n	Annual height increment calculated as (H in year *n*) minus (H in year *n*-1), cm
HI_{nx}	Annual height increment in the x^{th} year before current (*n*)
HI_{xn}	Averaged height increment over the previous *x* years until current (*n*)
SSI	Storm severity index

1. INTRODUCTION

Disturbance by windthrow is one of the main drivers of natural origin of forest development in central and northern European forests (Gromtsev, 2002; Schelhaas *et al.*, 2003; Shorohova *et al.*, 2009). Variation in storm size and intensity, in conjunction with pre-disturbance forest diversity, results in a range of post-storm initial conditions for regeneration and accordingly, stands can have varying reactions in terms of successional trajectories. Windthrow occurs with increased frequencies and magnitudes and this trend, most probably due to climate change (e.g. Schelhaas *et al.*, 2003; Usbeck *et al.*, 2010), is expected to persist (Goldenberg *et al.*, 2001; Stanturf *et al.*, 2007).

Current forest policy strives to incorporate natural disturbances in management planning and hence adapt silvicultural activities in order to minimize negative disturbance effects and to take advantage of the positive effects by relying on a system's natural resilience. One of these benefits could be obtained in post-disturbance regeneration. Nevertheless, salvage logging after windthrow is still common practice in most countries. Among the main motives are mentioned sanitation, i.e. limiting the risk of insect outbreaks (Eriksson *et al.*, 2005) and fungus infestations (Moykkynen and Miina, 2002; Jactel *et al.*, 2009) from weakened trees and coarse woody debris (CWD), reducing potential future fire fuel load, mitigating the economic loss from woody resources, and facilitating subsequent artificial forest regeneration (Lindenmayer and Noss, 2006; Lindenmayer *et al.*, 2008; Palik and Kastendick, 2009). To illustrate this, the Estonian Forest Act requires salvage logging and reforestation when the damage surpasses a threshold of 70% of the pre-storm stand canopy density on the basis of live trees (§24 and §25, Forest Act, 2006).

However, the actual risk for forest health of sustained high levels of damaged trees and CWD is a topic prone to controversy (Eriksson *et al.*, 2005). In some recent publications the logic is turned around by stating that insect outbreaks and pathogen infestations are indicators that forest vigour was already fragile in the first place. Logging would, in that case, not prevent insect outbreaks but rather increase the susceptibility of epidemics (Black, 2005; Lindenmayer *et al.*, 2008).

On ecological as well as economic grounds, it is attractive to explore options for relying on natural regeneration in non-salvaged areas after abiotic disturbances. It would save the trouble of harvesting the often less valuable wood in damaged areas (Ruel *et al.*, 2010) and of preparing them for artificial regeneration by planting or sowing. Furthermore, a naturally regenerated stand is often more species rich, contributing to the heterogeneity and, hence, the stability of the stand (*e.g.* Mason, 2002).

Disturbance terminology has undergone rapid development over the last few decades. Where initially a definition of disturbance (White and Pickett, 1985) and the components of a disturbance regime (Blackburn *et al.* 1988; Lorimer and Frelich, 1989; Rogers, 1996; Armstrong, 1999) were identified, subsequently the approach became more process-oriented, including spatial distribution of disturbance patterns and interactions with disturbances of the same or a different type (Angelstam and Kuuluvainen, 2004; Seidl *et al.*, 2011). As an important link in the chain of disturbance dynamics, post-disturbance regeneration both reflects the response of a forest stand to the disturbance, based on the disturbance severity and the pre-disturbance stand characteristics, and the basic elements determining the susceptibility to subsequent disturbances (Lässig and Močalov, 2000; Lugo, 2008).

Compared to other disturbances, windstorm occurrence is less influenced by site and stand properties and hence the storm regime is less predictable. Uniform even-aged stands with low canopy roughness are, from an aerodynamic point of view, considered more wind-resistant (Quine *et al.*, 1995; Achim *et al.*, 2005). On the other hand, multi-layered forests with high canopy roughness, developed as a result of natural cohort dynamics (Angelstam and Kuuluvainen, 2004; Shorohova *et al.*, 2009) or under continuous cover forest management, are probably better acclimated to heavy wind in the upper canopy (Dhôte, 2005). Furthermore, tree species composition and forest development phase do not always provide an indication of stand susceptibility to wind damage (Lässig and Močalov, 2000; Zhao *et al.*, 2006; Shorohova *et al.*, 2008; Yoshida and Noguchi, 2009). Analogous to the differences in predictability between disturbance types, the disturbance legacies vary considerably as well. Whereas fire may devastate understory plants as well as canopy trees, the main impact of windstorm is generally on overstory trees (Reyes *et al.*, 2010), although studies on storm damage to the understory are rare (Foster, 1988; Xi and Peet, 2011). Nevertheless, the origin and spatial distribution of disturbance legacies are of crucial importance for the direction of post-disturbance stand development (Kuuluvainen and Juntunen, 1998; Palik and Kastendick, 2009; Grenfell *et al.*, 2011; Xi and Peet, 2011).

2. REVIEW OF LITERATURE

This section reflects updated and synthesised parts of the more extensive literature review presented in paper **I** and is supplemented with an overview, from recent literature, of approaches to study post-storm forest development, and the resulting research needs.

2.1 Storm-induced microsites: availability and suitability for tree establishment

The legacies of a windstorm can be categorised as 1) structure and composition of remaining canopy trees (both intact and damaged), determining light, water and nutrient availability for new and advance regeneration, also constituting the seed and sprouting sources for post-storm regeneration; 2) damage status and position of advance regeneration, supplemented with the stumps and root systems that will later develop sprouts and 3) microsites that are a specific result of the storm, among which the most important are the pit and mound complexes resulting from the uprooting of trees, and decaying CWD in different positions (e.g. Peterson and Carson, 1996; Franklin *et al.*, 2002; Mitchell, 2013). The wide range of combinations of these legacies illustrates the variation in potential starting points for post-disturbance forest development.

The presence of storm-induced microsites can be detected up to a century after disturbance based on the vegetation composition (Gromtsev, 2002; Ulanova, 2006) and up to several centuries in the local topography and pedogenic composition (Lyford and MacLean, 1966; Beatty and Stone, 1986; Hofgaard, 1993; Ulanova, 2000; Gromtsev, 2002; Šamonil *et al.*, 2010). Depending on the initial species composition, forest development stage, soil conditions and storm characteristics (Figure 1), a certain percentage of the forest blows down, either by stem breakage or uprooting (Foster, 1988; Ilisson *et al.*, 2005). Pits form where the root systems and soil were pulled out; mounds consist of the root-plates including the attached organic soil. The type of tree-fall (Beatty and Stone, 1986), tree species and soil properties determine the pit area and depth (Šamonil *et al.*, 2010), and the mound height and thickness (Schaetzl *et al.*, 1989).

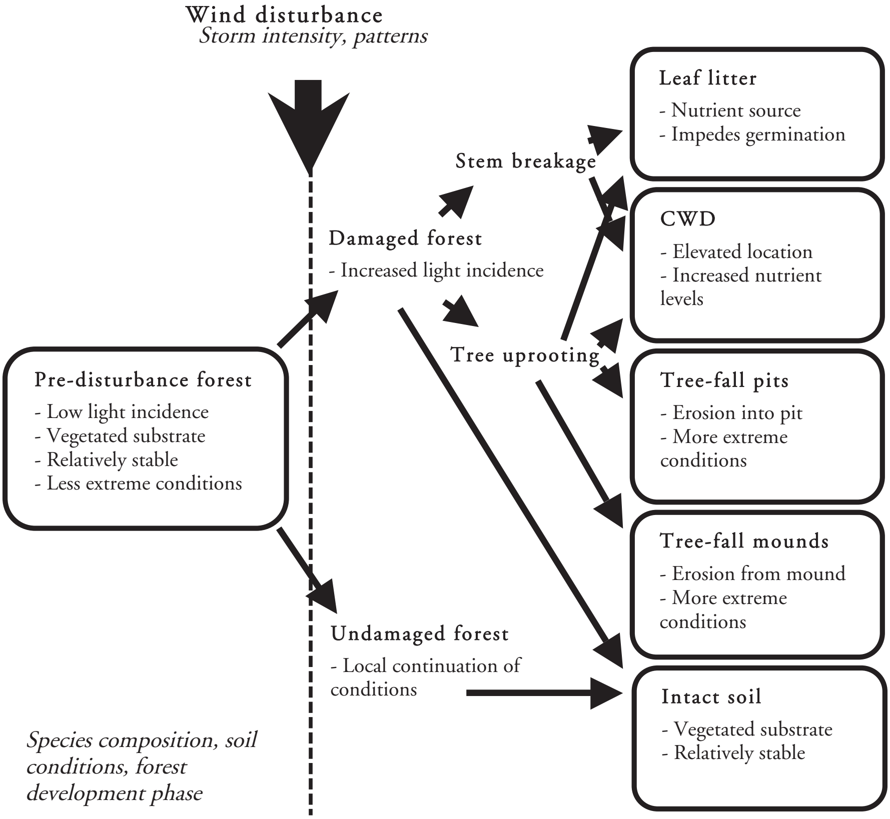

Figure 1. Pre- and post-storm microsites and characteristics relevant to tree regeneration establishment and development (frames), driving agents (italics) and interactions (arrows)

Microclimate on storm-induced microsites is generally different, in most cases more extreme than on intact soil (Bonan and Shugart, 1989; Peterson *et al.* 1990; Clinton and Baker, 2000).

Mounds and CWD generally provide more elevated establishment sites for regeneration, offering increased light incidence and reduced competition from surrounding vegetation and advance tree regeneration (Peterson and Pickett, 1991; Noguchi and Yoshida, 2004; Mochalov *et al.*, 2005). Furthermore, large-sized CWD in more advanced stages of decay offers softer, humid substrates facilitating root penetration (Skvortsova *et al.*, 1983; Harmon, 1986; Eriksson and Eriksson, 1997; Takahashi *et al.* 2000). The relatively moist conditions in pits can be beneficial in dry forest types, whereas flooded pits in wet site types can be detrimental to tree seedlings (Hörnberg *et al.*, 1997; Skvortsova *et al.*, 1983). Storm-induced microsites are relatively unstable over time, susceptible to erosion, litter accumulation, physical movement, and decay (Putz et al., 1983; Skvortsova *et al.*, 1983; Beatty and Stone, 1986; Nakashizuka, 1989; Peterson *et al.* 1990; Ulanova, 2000; Mori *et al.*, 2004). It may take decades for microsites to become sufficiently solid to provide for tree seedling establishment (Skvortsova *et al.*, 1983; Nakagawa *et al.*, 2003). Moreover, the nutrients released from CWD debris are not always suitable and often a limited amount is initially available for uptake by tree regeneration (Harmon *et al.* 1986; Krankina *et al.*, 1999; Narukawa and Yamamoto, 2003; Zielonka, 2006). Leaching of nutrients from mounds and in some cases even from pits, was reported, although pits generally accumulate more humus (Skvorstsova *et al.*, 1983; Schaetzl et al,. 1989; Kramer *et al.*, 2004).

The relative coverage of wind-induced microsites of the total stand area depends on the severity and spatial pattern of the storm, as well as the tree species creating the pit and mound complexes. Estimates from literature range 1-16% for pits, 1-36% for mounds, 7-23% for CWD and 45-89% for intact ground including already existing microsites such as stones, depressions, etc. (Nakashizuka, 1989; Schaetzl *et al.*, 1989; Kuuluvainen and Juntunen, 1998; Peterson and Pickett, 2000; Ulanova, 2000 and 2006; Narukawa and Yamamoto, 2003; Kuuluvainen and Kalmari, 2003; Šamonil *et al.*, 2010).

2.2 Regeneration strategies and post-disturbance forest succession

Successful regeneration strategies in storm areas depend to a large extent on the pre-disturbance tree species and the ability of species, besides from seeds and as advance regeneration, to establish through vegetative regeneration as root suckers or sprouts from crushed, buried, snapped or uprooted trees (Peterson and Pickett, 1991; Clinton and Baker, 2000). Inter-specific variation in tree regeneration traits in relation to forest disturbances can be the key to explaining the direction of post-disturbance stand development. Tree functional groups based on shade-tolerance (Figure 2) are linked to certain areas of the gradient of disturbance severity (e.g. Nakashizuka, 1989). Among the shade-tolerant species, many are able to establish and maintain below canopy, and at release resume growth, as advance regeneration under a partly opened canopy profiting from reduced competition (Metslaid *et al.*, 2007; Nagel *et al.*, 2010). Therefore, at different storm severities, but also considering the survival of pre-storm vegetation (Castelli *et al.*, 1999), e.g. advance regeneration (Nagel *et al.* 2006) and the sun-blocking effects of CWD (Kurulok and MacDonald, 2007), conclusions regarding the retarding (Hytteborn *et al.*, 1987; Nishimura, 2006; Lugo, 2008), or acceleration (Arevalo *et al.*, 2000; Webb and Scanga, 2001; Zhao *et al.* 2006; Hanson and Lorimer, 2007; Rich *et al.*, 2007) of succession can be divergent.

Between and also within microsites, circumstances can be highly variable (Skvortsova *et al.*, 1983; Beatty and Stone, 1986; Peterson *et al.*, 1990; Kuuluvainen and Juntunen, 1998; Clinton and Baker, 2000; Ulanova, 2006; Burney *et al.*, 2007; Grenfell *et al.*, 2011), potentially resulting in a pattern of spatial partitioning. On the other hand, locally, post-disturbance regeneration densities are high. There are signals that intraspecific density-dependent competition may be stronger than interspecific competition, hence in this way favouring species coexistence (Queenborough *et al.*, 2007; Clark, 2010; Metz *et al.*, 2010).

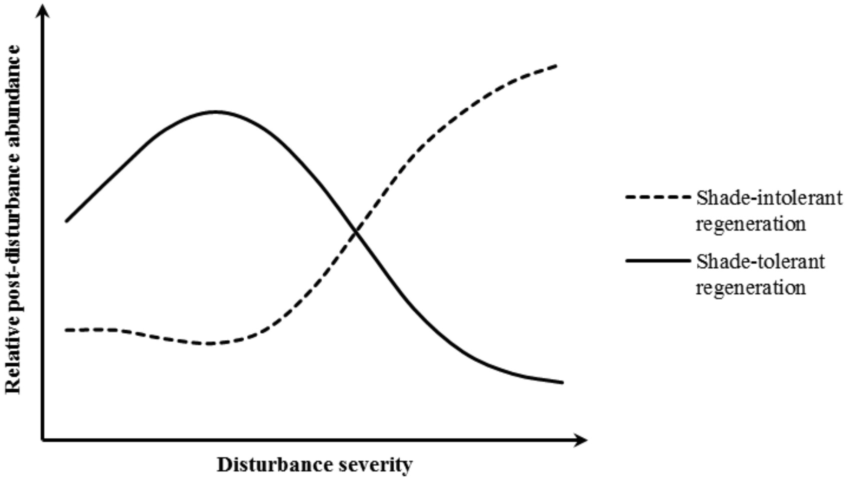

Figure 2. Hypothetical relation between disturbance severity and the relative abundance of shade-tolerant vs. shade-intolerant species in the early post-disturbance stand

Although microsites can be suitable as establishment substrates at a certain stage after disturbance, the appearance of seedlings and the conditions to grow into the canopy do not necessarily match (DeLong *et al.*, 1997). A major example is the large supply of CWD from the storm event, which, in terms of seedling colonisation, is initially in a less favourable early stage of decay, whereas in time, along with CWD decomposition, the stand reaches canopy closure and light incidence decreases (Zielonka, 2006). Timing of regeneration establishment to achieve resource congruence seems crucial for subsequent successional development (Carlton and Bazzaz, 1998b; Ishizuka *et al.*, 1998; Arevalo *et al.*, 2000; Iijima *et al.*, 2007; Kathke and Bruelheide, 2010).

2.3 Approaches in post-storm forest development research

The majority of publications on post-disturbance natural forest regeneration report case studies, several using a combination of different storm severities (Harrington and Bluhm, 2001; Nishimura 2006), cascading effects of several storm events (Hiura *et al.*, 1996; Peterson, 2000), or comparing natural disturbance types or post-disturbance management (Schönenberger, 2002; Wohlgemuth *et al.* 2002; Schulze *et al.*, 2005; Peterson and Leach, 2008; Palik and Kastendick, 2009; Jonášová *et al.*, 2010; Reyes *et al.*, 2010; Grenfell *et al.*, 2011), as pseudo-treatments in the analyses. In general, successional development during the first years since disturbance is analysed, whereas only few studies are based on data collected over a period of ten years or more since disturbance (Ishizuka *et al.*, 1998; Arevalo *et al.*, 2000; Schönenberger, 2002; Zhao *et al.*, 2006; Fischer and Fischer, 2012). Some studies evaluate storm impact at a certain advanced stage since the event (Kuuluvainen and Kalmari, 2003, Schulze *et al.*, 2005, Nagel *et al.*, 2006), but may, due to the lack of data on earlier regeneration demography, encounter difficulties to identify which other processes were involved in creating the current structural and species composition. Backdating of disturbances is sometimes applied, based on determination of the decay stage of CWD or on dendrochronology techniques (Narukawa *et al.*, 2003, Šebkova *et al.*, 2012).

Study design is mostly plot-based, though some studies are oriented explicitly on individual seedlings or microsites to identify species-specific substrate associations (Nakashizuka, 1989; Peterson *et al.*, 1990; Kuuluvainen and Juntunen, 1998; Castelli *et al.* 1999; Clinton and Baker, 2000; Kuuluvainen and Kalmari, 2003; Burney *et al.*, 2007; Iijima *et al.*,

2007). At larger scale, above the microsite level, some studies infer storm impact on stand development from stand structure (Schulze *et al.*, 2005; Shorohova *et al.*, 2008). Stand-replacing disturbances and gap dynamics have been widely studied, whereas few focus on storms of moderate severity (Nagel *et al.* 2006).
Experimental designs are limited to seeding and planting experiments in different storm-induced microsites (Carlton and Bazzaz, 1998a; Peterson and Pickett, 2000) and storm simulations by pulling down individual trees or groups of trees (Carlton and Bazzaz, 1998a; 1998b; Cooper-Ellis *et al.*, 1999).

In literature reviews post-storm regeneration does get attention (e.g. Schaetzl *et al.*, 1989; Kuuluvainen, 1994; Ulanova, 2000; Gromtsev, 2002; Lugo, 2008; Xi and Peet, 2011), but it has not been the main topic yet.

Modelling studies involving forest disturbance dynamics (e.g. Peltola *et al.*, 1999; Mitchell *et al.*, 2001; Gardiner *et al.*, 2008) are mainly intended to predict wind damage risk (Seidl *et al.*, 2011). Some models are extended with regeneration modules, but these generally serve to simulate next generation susceptibility. Papaik and Canham (2006) integrate models of windstorm mortality, seed mass dispersal and recruitment, and spatial forest dynamics, to highlight the importance of species-specific characteristics in successional trajectories.

2.4 Research needs

Considering that wind is among the principle disturbances in European forests causing major damage, post-storm effects on regeneration development have so far received relatively little attention compared to other disturbance types. The difficulty of predicting windthrow, due to its stochastic nature, generally limits the options to design adequate field trials. Furthermore, the pre-storm stand conditions are often unknown or can only partly be reconstructed.

Comparison of post-disturbance development among different disturbance types is generally the main study aim, whereas within disturbances the impact of severity, frequency and size as well as the regeneration substrate may be considerable. Regeneration development in both storm-cleared areas and single tree falls have been studied more intensively than in the intermediate-sized group or cohort replacement (Papaik and Canham, 2006; Hanson and Lorimer, 2007). Besides the stand-replacing events, cohort and gap phase dynamics in natural boreal and hemiboreal forests are regularly initiated by strong winds. The importance of these perturbations is often underestimated (Kuuluvainen, 2002), and they do not fit well in the more traditional even-aged forest management systems. Additionally, most studies have focused on immediate impact of storm damage, during the first few years after windthrow (Lindenmayer and Noss, 2006; Palik and Kastendick, 2009; Caquet *et al.*, 2010; Fischer and Fischer, 2012). However, in the extended initial period retarded establishment and mortality among tree regeneration can be high (*e.g.* Leemans, 1991) and these fluxes are crucial for predicting future stand development. As a result of the variation in both the storm severity among studies and time since disturbance, in combination with the different functional groups examined, conclusions regarding the direction of post-disturbance succession are highly divergent. Therefore, the consequences of windthrow for forest successional dynamics remain largely indistinct (Gromtsev, 2002; Schulze *et al.*, 2005). An overview of studies would contribute to the understanding of post-storm dynamics. Furthermore, the necessity of long term monitoring for increased understanding of post-disturbance stand development was recently highlighted (Xi and Peet, 2011; Fischer and Fischer, 2012).

3. AIMS OF THE STUDY

The aims of the present doctoral thesis were:

1. To provide a literature-based overview of the consequences of wind-induced microsites for forest development in the boreal and hemiboreal zone **(I)**;

and, based on studies established in two windthrow areas in Estonia:

2. To investigate the impact of storm severity and microsite type on establishment, height, height growth and composition of regenerating tree species of different functional groups **(II–IV)**;
3. To model post-disturbance mortality probability of regeneration of four tree species **(IV)**;
4. To analyse changes in the impact of factors affecting post-disturbance regeneration performance **(III, IV)**; and
5. To evaluate the importance of storm-related microsites relative to other microsites for post-disturbance stand development **(I, IV)**.

Hypotheses:
1. Shade-intolerant species are dominant in areas with higher disturbance severity (**I, IV**);
2. Abandonment of salvage logging, retaining the storm-induced diversity in microsites, increases species diversity (**II, IV**);
3. Disturbance severity influences tree species diversity: the combination of microsites and light incidence is most heterogeneous at moderate levels of disturbance, creating the most variable conditions for seedling establishment, growth and survival (**II**);
4. More stable microsites (intact ground, large shallow pits, low mounds) provide better prospects regarding regenerating tree species' growth and survival than unstable microsites (small deep pits, high mounds) (**III, IV**); and
5. In the years immediately following windthrow, site-related factors such as light incidence, flooding and substrate determine tree regeneration occurrence, growth and mortality, whereas later, at around one decade after disturbance, these processes are mainly directed by species' competitive traits (**II-IV**).

4. MATERIALS AND METHODS

4.1 Approach literature review

The compilation of an overview (**I**) of the importance of storm-induced microsites for post-storm forest development in the boreal and hemiboreal zone was based on the results of 163 studies from northern America and Eurasia, traced by searching electronic databases, and the contents of review reference lists and peer-reviewed online journals. A synthesis combined 1) the factors contributing to wind-damage and hence to the changed post-storm environmental conditions, and 2) the characteristics and occurrence of storm-induced microsites. Within this frame, the regeneration strategies of shade-intolerant and shade-tolerant species were considered along the trajectory of microsite colonisation, growth and mortality. The results were discussed in the perspective of different theories on species coexistence and successional development.

4.2 Study areas

Field study (**II–IV**) was carried out in two windthrow areas 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) resulting from summer storms in 2001 and 2002, respectively (Figure 3).

Both sites had mature to old mixed spruce-broadleaf 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 severely-, moderately- and lightly damaged patches. Main 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 species at the time of the storm ranged from 110–158 years. The storm was locally so destructive that no specific tree species was hit more or less than any other. The gleyed podzolic soils showed significantly more stem breakage than tree uprooting, whereas in the gley soil type the difference was negligible (Ilisson *et al.*, 2005). More details on storm damage and vegetation community changes can be found in Ilisson *et al.* (2005) and Ilisson *et al.* (2006), respectively.

In the Tudu unit, within the borders of the Suigu nature protection area (82 ha), no active management took place since 1976 in order to maintain the mature to old-growth forest and provide habitat for several protected animal species, including the flying squirrel (*Pteromys volans*). The passive-management strategy was continued after the 2001 storm event, regardless of the damage severity. In the Halliku unit, agreements with the former and current Forest District offices preserved several areas from salvage logging, some already protected as woodland key habitats.

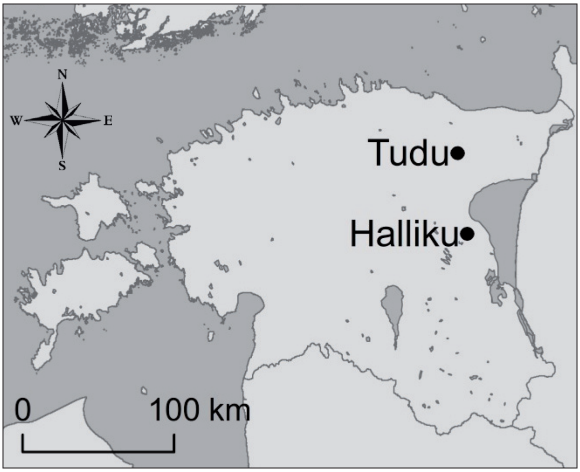

Figure 3. Location of the two study areas in Estonia

Study plots were initially selected to represent all three damage severity degrees, heavy (H), moderate (M) and control (C). In surrounding areas with comparable stand characteristics, where harvesting of completely downed stands took place, the impact of this superimposed anthropogenic disturbance on stand development was assessed in harvested (S) plots (Figure 4).

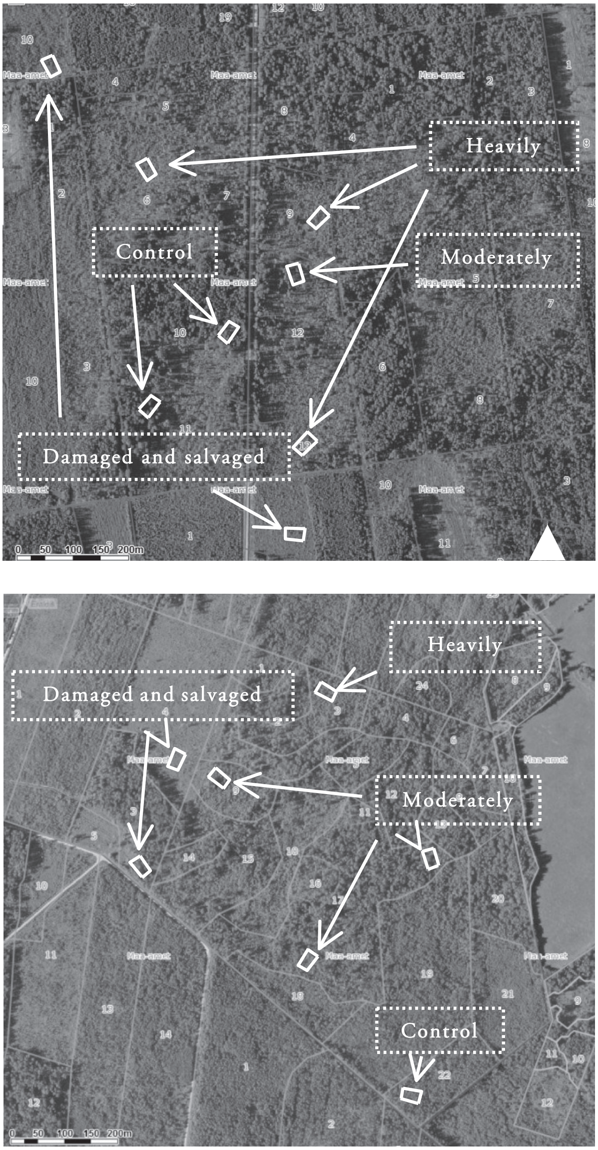

Figure 4. Location of the study plots

4.3 Field data collection

The permanent sample plots (20 × 40 m) were established in 2002 (Tudu) and 2003 (Halliku). As a basis for determining damage severity (**IV**), storm legacies were investigated in terms of canopy tree locations, position and vitality conditions. Characteristics of storm-induced microsites from trees that, in an upright position, would be located within the plot borders were reported in 2004. These included size measurements, pit depth, mound height and width, location, orientation, uprooted tree species and, for CWD, decay stages I–V, varying from fresh stems without signs of decay to stems which are almost entirely decomposed (e.g. Palviainen *et al.*, 2008). Regeneration surveys were carried out in summer, in successive years in the period 2004–2012, except for 2008 and 2011.

In a selection of 15 plots, four in each 'treatment' and three control plots (Figure 4), tree regeneration, defined as established seedlings (height 5 cm – 1.3 m), saplings (height 1.3 m – 6 m), and understory tree regeneration (height >6m), was inventoried in all wind-induced microsites and an additional series of ten 1 × 1m squares on intact soil along the middle line of each plot (Figure 5). The number of living regeneration was recorded per microsite. Additionally, for each individual regenerating tree, species, height, incidence of physical damage (i.e. caused by browsing and insects), mortality, and microsite type were reported. On intact soil the regeneration position was measured relative to the middle line. Pit and mound perimeters and regeneration were mapped using a surveyors compass and electronic distance meter Vertex III (Haglof, Inc.) from a fixed measuring point at the pit edge opposite the middle of the root plate of the uprooted stem ('reference point', Figure 1 in **III**).

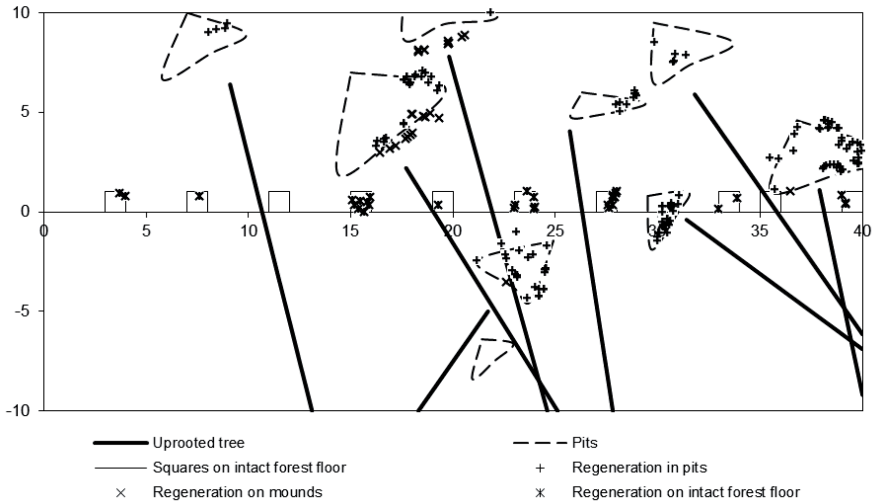

Figure 5. Example of a study plot (**II**)

The 95 pit-and-mound complexes covered 13.3–29.8% of the total plot area in heavily damaged areas (70 pairs) and 4.4–14.4% in moderately damaged areas (25 pairs). Within plots practically all pit and mound complexes were monitored, whereas the samples on intact soil only covered up to 2% of the total microsite area available. In order to expand the sample area of the underrepresented substrate intact soil and to support the findings on species composition and height of regeneration on different microsites, additional supplots were investigated in the years 2011 and 2012.

4.4 Data processing and statistics

Regeneration density was calculated as the number of individuals per square meter per microsite (**II**–**IV**). Pit area was estimated as the sum of two circle sections (described in **III**) and mound area as the projection as viewed from above, of a rectangle with mound width and diameter as its sides. Based on literature (**I**) and the repeated personal observations of extremely low regeneration numbers on CWD, it was decided to exclude the substrate from the study at this stage. Shannon diversity index (H') and evenness (E_h) were calculated for regeneration microsites and treatments (**II**). Annual height increment was represented as the difference in height in two successive years (**II-IV**) and average height increment as the difference in height over more years (**IV**). Factors tested for effects on regeneration height and height increment comprised damage level (moderate and heavy damage), microsite type, regeneration tree species, uprooted tree species, regeneration age and year of observation (**II**–**IV**). For regeneration in pits, pit area and pit depth were included (**III**). Browsed individuals were excluded from height and height increment analyses. A multilevel random coefficient model in software package MLwiN Version 2.1 (Rasbash *et al.*, 2009) assisted in determining the significance of different levels in the analysis of height increment (**III**).

As an approximation of disturbance intensity, a storm severity index (SSI, adapted from Rich *et al.*, 2007) was calculated for all plots, based on the ratio of post-disturbance basal area (BA) of storm-damaged trees and pre-disturbance plot BA (Table 1). Post-disturbance BA of damaged trees consisted of the plot sum of cross-sectional stem areas at *dbh* or 1.3m from the stem base for all dead trees, consisting of standing and hanging trees and snags of decay stage I, as well as stumps and lying trees or parts of trees of decay stages I and II of which the roots, in an upright position, would be located within the study plot. Pre-disturbance BA consisted of the BA sum of storm-damaged trees and surviving trees. Trees in more advanced stages of decay were not considered in calculating the SSI.

Table 1. Storm severity index (**IV**)

Damage level	BA (m^2/ha) of storm-damaged lying trees	BA (m^2/ha) of storm-damaged standing trees	post-storm BA (m^2/ha) -undamaged standing trees	pre-storm BA (m^2/ha)	Storm severity index
Control	1.01	2.41	34.42	37.84	0.090
Control	0.00	6.82	37.11	43.93	0.155
Control	1.31	1.00	36.47	38.78	0.059
Mod.	4.99	1.83	21.90	28.72	0.237
Mod.	2.81	6.29	17.51	26.61	0.342
Mod.	7.94	9.55	10.47	27.96	0.626
Mod.	2.59	9.58	27.65	39.82	0.306
Heavy	10.74	0.07	0.59	11.41	0.948
Heavy	19.59	10.44	0.00	30.03	1.000
Heavy	14.56	10.84	0.00	25.40	1.000
Heavy	21.66	24.62	1.31	47.58	0.973
Salvage	3.42	27.67	0.00	31.09	1.000
Salvage	2.10	32.38	0.08	34.56	0.998
Salvage	6.76	28.24	0.00	35.00	1.000
Salvage	4.23	33.37	0.00	37.60	1.000

Although initially pre- and post-disturbance established regeneration were separated visually (**II**), throughout the years and especially after a (destructive) tree ring analysis in adjacent subplots in 2011, it became obvious that many more seedlings and saplings established before the storm than previously assumed (**IV**). Due to the difficulty to identify regeneration type visually at a few years after disturbance, and the fact that several individuals have perished in the meantime, eliminating the option of reclassification, advance and new regeneration were not analysed as distinct groups.

Competition indices for each regenerating tree were based on regeneration tree height and density as a combination of previous calculations of tree (Hegyi, 1974; Sims *et al.*, 2009) and regeneration (Kuuluvainen and Kalmari, 2003; Metslaid *et al.*, 2005; Collet and Moguedec, 2007) competition indices:

$$CI_i 1 = \frac{\bar{h}_j}{h_i} * D_j \qquad (1)$$

$$CI_i 2 = \ln\left(\frac{\bar{h}_j}{h_i}\right) * D_j \qquad (2)$$

where CI_i is the competition index of regenerating tree i, $\bar{h}_j$ represents average tree height in microsite j, h_i is the height of tree i and D_j is regeneration density in microsite j. The latter equation gives a better expression of the competition experienced by a single regenerating tree: positive values indicate that the tree experiences probably more competition than average in that specific microsite and *vice versa*. For regeneration in pits, also the distance to the deepest point of the pit, based on observations at one fourth of the distance from the root plate to the other side of the pit, was calculated as a proxy for substrate humidity in pits.

Factors tested for effects on regeneration mortality probability (**IV**) were categorised on the basis of their presumed correlation (Table 2). As the response variable is binary, we used a logistic regression model, where the logistic transformation of p_i is expressed as a linear function composed of the explanatory variables:

$$\text{logit}(p_i) = \ln\left(\frac{p_i}{1 - p_i}\right) = \beta \cdot X_{ijk} \qquad (3)$$

where β is a matrix representing $m + 1$ grouped regression coefficients of the explanatory variables at the regenerating tree level (i), the microsite level (j) and the plot level (k), grouped in matrix X_{ijk}. Correlated factors are employed in separate model runs.

Two main, partially overlapping subsets were created in order to have sufficient data to compare mortality among microsites, among damage types, among regenerating tree species and over the years, and to evaluate the effects of factors on regeneration mortality.

Differences in regeneration tree mortality between microsites were analysed only in heavily damaged areas (microsites-subset), whereas specific microsite-level factors and differences between the damage levels heavy and moderate were analysed only in pits (severities-subset). Although we seek generalities for all species throughout the years, species sets were analysed as well to determine the explanatory power of individual variables for each of four main regenerating species or species groups: Norway spruce, silver and downy birch, European rowan (*Sorbus aucuparia* L.) and black alder. Additionally, to test for changes in time in the impact of factors involved in different stages since disturbance, the years 2006 and 2009/2010 were tested separately using the linear mixed effects R function lmer from the package lme4 (Bates *et al.*, 2011). All years together are analysed with the SAS procedure GLIMMIX (Schabenberger, 2005), which can handle a response variable with binomial distribution, as well as the hierarchic structure and the longitudinal character of the database, recognising repetitively recorded individuals of the same regenerating tree as dependent samples. Akaike's Information Criterion (AIC) in combination with the number of observations and the significance of factors were used to select the best two to four models per subset. Conventional parametric and, where appropriate, non-parametric statistics (t-test, Mann-Whitney *U* test, various types of ANOVA, GLM, Kruskal-Wallis ANOVA), several post-hoc tests and model comparisons were used for hypothesis testing. Height data were logarithmically transformed.

Table 2. Potential mortality factors and hierarchical structure (**IV**)

Model term	*Description, values, units*	*Level*
Response variable	Regeneration tree mortality - binary	*ijk*
Explanatory variables (candidates)		*ijk*
Storm severity	Plot level	*k*
Storm severity level	Moderate (contrast), Heavy	*k*
Storm severity index	0-100 (no damage - all trees dead)	*k*
CWD volume	In m^3ha^{-2}	*k*
CWD basal area	In m^2ha^{-1}	*k*
Microsite	Microsite level	*jk*
Microsite type	Intact soil (contrast), mound or pit	*jk*
Pit characteristics	Microsite level	*jk*
Species uprooted tree	Hardwood (contrast) or Norway spruce	*jk*
Uprooted tree dbh	In cm	
Pit area	Two circular sections, in m^2	*jk*
Pit depth	At former stem base, in m	*jk*
Mound area	In m^2	
Mound height	From ground level at stem base, in m	*jk*
Mound width	At stem base, in m	*jk*
Regeneration	Regeneration level	
Regeneration species	Birch (contrast) versus rest	*ijk*
Regeneration age	Regeneration level	
Age category	Age cat A (contrast) – C	*ijk*
Regeneration height	Regeneration level	
Hn1-Hn6	Height in yr-1 - yr-6	*ijk*
H2n-H6n	Average height over 2-6 years	*ijk*
Regeneration height growth	Regeneration level	
HIn1-HIn4	Annual height increment yr-1 to yr-4	*ijk*
Competition	Regeneration level	
CI1n1-CI1n6	Competition index 1 in yr-1 to yr-5	*ijk*
CI2n1-CI2n6	Competition index 2 in yr-1 to yr-5	*ijk*
Browsing	Regeneration level	
Browsing in past	Binary	*ijk*
No. of years browsed	In number of years	*ijk*
Time since disturbance		
Inventory year	Longitudinal aspect of the dataset	*i*

5. RESULTS

5.1 Synthesis of the review results (I)

Agents and conditions determining the storm impact and consequently the starting point for post-disturbance stand development in the boreal and hemiboreal zone were presented in section 2.1 of this thesis. Regeneration strategies and the general findings on forest succession after storm were discussed in section 2.2.

5.1.1 Regeneration strategies and storm-induced microsites

The specific importance of storm-induced microsites for stand development was acknowledged in many studies, referring to the proportion of regeneration on these microsites relative to the proportion on undisturbed soil. Subdividing the regeneration process into the components colonisation, growth and mortality on storm-induced microsites facilitated in classifying the findings.

Colonisation depends on species-specific requirements that can be mainly connected to seed size. Under circumstances that seed sources are not limiting, dispersal traits such as seed weight and wings determine which microsites can be physically reached. Subsequently, conditions for the actual germination depend largely on the microclimate, which can be highly variable among different post-storm microsites. Germination is in some cases also more dependent on light with decreasing seed mass (Milberg *et al.*, 2000). As the final stage in establishment, rooting species depend on the ability to penetrate a microsite, which can be constrained by substrate hardness and vegetation. Generally, heavy seeded species have an advantage at rooting in thick moss layers and less decayed CWD.

Once established, growth conditions are mostly related to light availability, though early growth can still partly rely on resources stored in seeds, or roots in the case of vegetative reproduction. Shade-tolerant species have better capacities to maintain low growth rates under canopy and resume regular rates with some delay after release by subsequent disturbances. On the other hand, shade-intolerant species generally grow faster to reach the canopy before closure and are better capable of producing sprouts from roots or stumps. Some species are plastic in their requirements and can adapt to the microsite conditions. However, generally differences in performance of regeneration among microsite types can be related to species shade tolerance.

Both light conditions and microsite stability are affecting the mortality probability in post-storm regeneration. Storm-induced microsites tend to be initially less stable than intact soil due to high erosion risk, more extreme microclimate and substrate decay (Skvortsova *et al.*, 1983). Conversely, regeneration may find shelter against browsing (Peterson and Picket, 1995; de Chantal and Granström, 2007), and extreme conditions (Kuuluvainen and Kalmari, 2003) when situated in areas with dense coverage of storm-torn branches.

5.1.2 Relation with disturbance regimes and species coexistence

Species of different functional groups are often capable of establishing on similar microsite types, whereas subsequent selection can in many cases be linked to the degree of canopy openness at a later stage, e.g. induced by a disturbance. Setting-back and acceleration of forest succession are generally connected with the difference in reactions among functional groups after stand-replacing and gap-creating disturbances respectively. Associated with this, the significance of storm induced microsites for successional development is more often recognised in studies on moderate to stand-replacing disturbance than on gap dynamics. However, the importance of surviving pre-storm vegetation, regeneration through sprouting and root suckers, and advance regeneration should be considered in the light of timing of species establishment and disturbance frequency. Applicability of elements from the many theories on species coexistence, such as the difference in intra- and interspecific competition (e.g. Clark, 2010) after multi-species post-disturbance recruitment and the trade-off between seedling growth rate and mortality (Hiura *et al.*, 1996) also depend on the spatial extent covered.

5.2 Height and height increment (II–IV)

A multilevel random coefficient model, respecting the hierarchy of observations on the storm area study sites, indicated that variables at the microsite and regeneration tree levels exerted significant influence on height growth (**III**). Mounds of hardwood species, when compared to Norway spruce, were significantly thicker and their pits deeper.

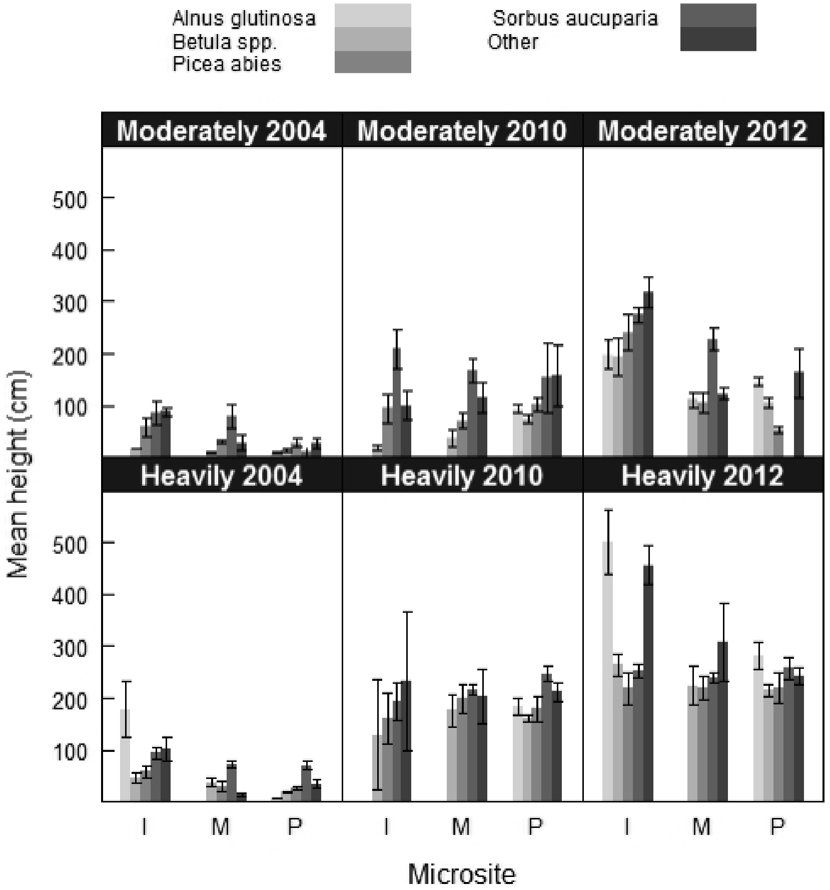

Figure 6. Regeneration height development by species under varying growth circumstances on intact soil (I), mounds (M) and in pits (P). The 2012 survey includes the additional subplot data, which particularly enlarged the sample area of intact soil. Error bars represent standard error (**IV**)

Initially height increment was found significantly correlated with microsite type (Table 4 in **II**), whereas subsequently, damage level (earlier not significant) and species of the uprooted tree (not tested before) constituted significant effects (Table 3), and regeneration tree species remained significant throughout the years (**II**–**IV**): rowan had fastest height growth; differences between other species were not significant

(Figure 3 in **III**). Regeneration density was significantly negatively correlated with increment of birch (One-way ANOVA, $p = 0.0058$) and rowan ($p = 0.0099$, Table 5 in **II**). Most favourable circumstances for height growth for all species and for all years up to 2007 pooled occurred on spruce mounds in heavily damaged areas (**III**). Growth rate slowed down after the first survey year and then accelerated again after three years for spruce and birch (Figure 4 in **III**). Pits created by spruce were significantly better for birch growth than pits created by hardwood species (**III**).

Table 3. The effects of damage level (moderate/heavy), microsite forming species (spruce/hardwood), and microsite type (pit/mound) on the annual regeneration height increment (multiple ANOVA, **III**)

Source of variation	D.F.	Sum of squares	*F*-value	*p*-value
Damage level (a)	1	2178.79	5.15	0.0233
Microsite forming species (b)	1	6698.04	15.85	0.0001
Microsite type (c)	1	7880.52	18.64	<0.0001
Interactions				
ab	1	18.28	0.04	0.8375
ac	1	64.54	0.15	0.7002
bc	1	1.81	0.00	0.9486
Error	1524	644170.35		
Corrected total	1530	664557.91		

At the start of the surveys in 2004, the difference in regeneration height between the storm severity levels heavy and moderate was not significant (**II**), whereas in 2010 and at taking all years together, regeneration in heavily damaged areas was significantly taller (Figure 6, **IV**). Although rowan and black alder were initially among the significantly tallest and shortest species respectively, these differences disappeared with time in the heavily damaged areas (**IV**). Birch seedlings remained significantly lower than spruce in the moderately damaged areas (**IV**).

5.3 Species occurrence and regeneration density (II, IV)

Regeneration densities varied among microsite types and disturbance severity levels by regeneration species throughout the surveys. Harvested sites were significantly most densely populated, with birch as the dominant species (**II**, **IV**). The undamaged control areas were least populated (**IV**). The difference in regeneration tree densities between heavily and moderately damaged areas was overall negligible, but the differences appeared when separating by species and microsite (**IV**). At the start of the surveys, the intact soil was most densely populated, before pits and mounds (**II**). In 2010, differences between microsites were no longer significant (Figure 7, **IV**).

Pits in heavily damaged areas hosted mainly birch regeneration and in moderately damaged areas, black alder dominated pits. On mounds in heavily damaged areas, rowan dominated and in moderately damaged areas Norway spruce and rowan were the most represented species. On intact soil regenerating species are more equally distributed than on wind-induced microsites where species dominance differs between treatments and microsites (Figure 7, **IV**).

Birch and black alder were more selective regarding microsite than were Norway spruce and rowan (**III**). Not one species showed a significant preference for locations close to the pit centre than further away from it, although birch was more abundant in pits created by spruce uproots (**IV**). Regeneration species composition turned out most diverse in moderately damaged areas and in pits early after disturbance (Shannon index, Table 4, **II**), whereas in time, regeneration species were more equally distributed on intact soil than on wind-induced microsites (Figure 7, **IV**). Among the sprouting regeneration, European rowan and birch were most abundant and among advance regeneration, Norway spruce and European rowan were prevalent (**IV**).

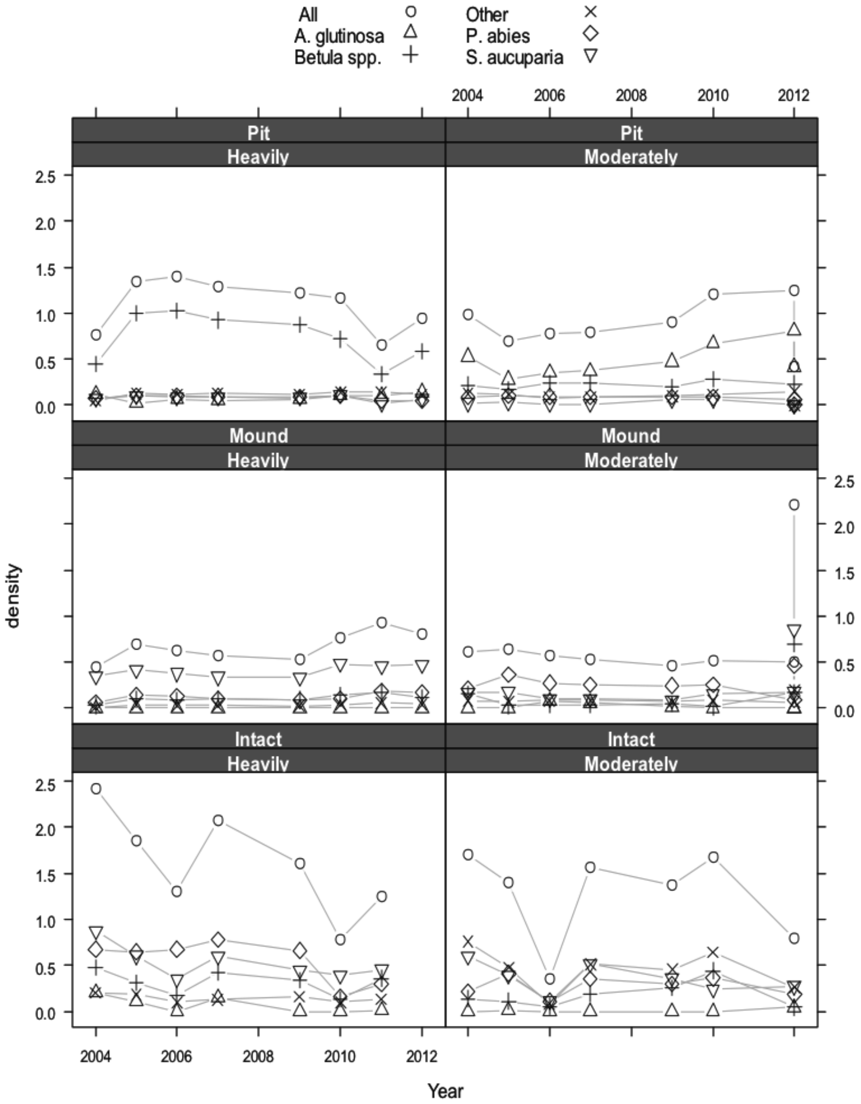

Figure 7. Density development of regenerating trees per species (# m^{-2}), arranged by damage severity level and regeneration microsite. Data in heavily damaged areas were supplemented with additional subplots in 2011 and data in moderately damaged areas in 2012 (**IV**)

5.4 Mortality (IV)

Based on the two to four best models (dependent on Akaike's Information Criterion and taking into consideration the number of observations) per column (Table 2), the main differences among variables affecting mortality probability were evaluated for regenerating tree species at different stages since disturbance (Table 4 in **IV**).

Table 4. Shannon diversity (*H'*) and evenness (E_h) indices of five recruitment tree species (**II**)

	H'	E_h
Damage severity		
Harvested	0.7414	0.5348
Heavy	1.1358	0.7057
Moderate	1.1691	0.7264
Microsite		
Pit	0.8185	0.5086
Intact	0.5954	0.3700
Mound	0.5455	0.3935

Initially only mortality of birch and rowan regeneration was influenced by individual height and height increment, whereas later on, taller individuals of all species had increased survival probability (Figure 8, **II**, **IV**).

Higher levels of competition increased mortality probability as time since disturbance increased. Rowan was the only species on all microsites that initially suffered from higher competition (Table 4 in **IV**). In pits the difference between the stages was remarkable: initially, higher competition implied better conditions for germination, establishment and survival of many seedlings, whereas in later years, high competition levels increased mortality (Table 4 in **IV**). Taking all microsites together, birch and rowan initially benefited slightly from higher disturbance severity; in later stages, birch survival was positively related to the amount of dead wood. In contrast, spruce incurred more mortality later on by higher amounts of dead wood. However, when pits were analysed separately, birch later suffered from higher disturbance severity including high dead wood levels, whereas black alder and spruce seemed to profit initially from higher amounts of dead wood. For all years together, black alder had higher mortality probability in pits with higher storm severity (Table 4 in **IV**).

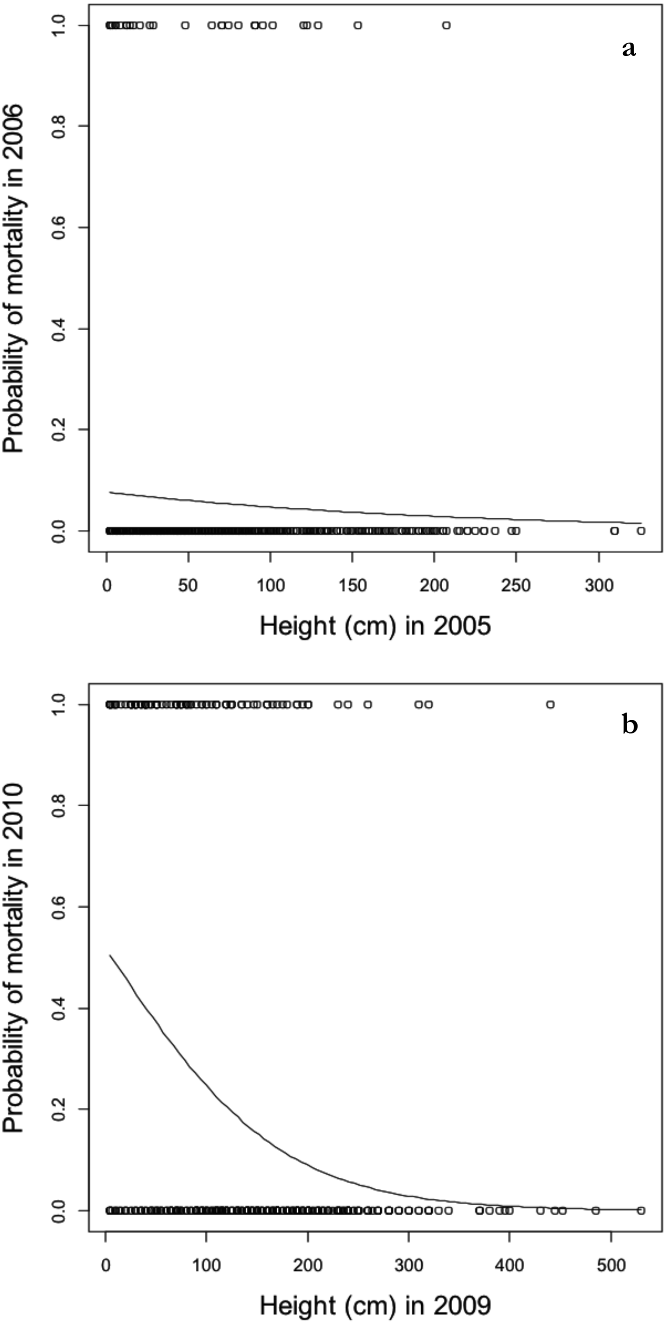

Figure 8. Mortality probability in year *n* as a function of regeneration tree height in year *n*-1 at 3 years (**a**) and 8 years (**b**) since disturbance. Dots represent single observations and the curve reflects the modelled probability (**IV**)

The regeneration microsite did not clearly influence regeneration mortality. In two of the models for the later stages, the storm-induced microsites displayed greater survival, especially for birch, than did intact ground (Table 4 in **IV**), which may be due to competing vegetation. Spruce generally had a greater probability of mortality in pits when microsite was evaluated as the sole factor. Survival probability was higher in the larger pits (based on significance of individual effect, data not shown) for black alder throughout the years and for birch during the later years. Deeper pits seemed to be safer for birch (not shown) and less so for spruce (Table 4 in **IV**), but spruce as the uprooted tree species, creating shallower pits with a larger area than the hardwood species involved (**II**), enhanced survival probability of birch and spruce regeneration. Black alder generally profited from the presence of higher, wider and larger mounds as single model terms. The distance of a regenerating tree to the pit centre (i.e. deepest point) may also influence regeneration mortality. Nevertheless mortality probability was only significantly higher closer to the pit centre for black alder (Table 4 in **IV**). Birch (followed by rowan) was the most vulnerable regeneration species, when analysing all microsites together, especially at a later stage since disturbance. In pits only, black alder had higher mortality probabilities than birch and spruce (Table 4 in **IV**). Recruitment registered as advance regeneration, mainly present on mounds and intact soil, generally had higher survival chances, except, initially, birch advance regeneration (data not shown).

6. DISCUSSION

6.1 Functional groups and resource congruence

Wind disturbance alters resource availability in forests, in particular light incidence, nutrients and soil organic matter (**I**; Ulanova, 2006). The balance in resource levels, i.e. resource congruence (Carlton and Bazzaz, 1998b), determines the suitability of a microsite for colonisation by and growth of tree regeneration of a certain species or functional group. The actual timing of tree species germination depends on seed source availability, meteorological conditions and dispersal traits (Ishizuka *et al.* 1998; **I**). In the current case study, seed source availability was assumed not limited. However, the nearest canopy trees to heavily damaged plots are found at 30–120m from the plot border, which could be a constraint for some species.

The results of the field study, when tree functional groups are considered on the basis of shade-tolerance, comply in part with the associated traits (see also Figure 2). As the most shade-intolerant group, both birch species exposed higher mortality probability with relatively lower tree height in the previous years. In contrast, other, more shade-tolerant species only exhibited this relation at a later stage since disturbance (**IV**). In association, Löf *et al.* (2007) found no relation between Norway spruce mortality and degree of canopy closure at four years since planting, but acknowledged that a longer monitoring period may have changed the results.

Although densities of regeneration overall did not differ between storm severity classes, shade-intolerant species were better represented in heavily damaged areas and established more frequently on exposed mineral soil and elevated sites than on vegetated substrates (**II**, **IV**). Moreover, the species with smaller seeds, birch, black alder and willow, established better on the exposed mineral soil of pits, whereas mounds and intact soil were more often populated by middle-sized seeded Norway spruce (in accordance with Skvortsova *et al.*, 1983), large-seeded rowan and advance regeneration (**II–IV**). Mortality was highest in most abundant species birch, which confirms the trade-off between a species' tolerance to stressful conditions and fecundity (Muller-Landau, 2010). Remarkably, at later stages since disturbance, mortality of birch regeneration in pits increased with storm damage. This may be explained by the augmented level of competition at the transition into the stem exclusion phase (Oliver and Larson, 1996; Krumm *et al.*, 2012).

Sun-blocking by CWD probably inhibited height growth rate during the first years after germination, whereas both birch and Norway spruce showed accelerated height growth after the third year since establishment (**III**). However, in areas with a higher density of CWD, mortality probability of Norway spruce increased at later stages since disturbance (**IV**). This can have several reasons, *e.g.* competition by other species (Holeksa *et al.*; 2012), birch and rowan establishment on higher locations in our case, or the potentially closer establishment position to CWD of Norway spruce, which is thus more limited by sun-blocking and potential physical damage due to delayed falling or sliding of dead wood (Schönenberger, 2002). Nevertheless, the establishment on or in the vicinity of CWD may be restricted to more advanced stages of wood decay (Kuuluvainen and Kalmari, 2003; Grenfell *et al.*, 2011). Besides that, in some cases hardwood species, and not spruce, were found closer to CWD (de Chantal *et al.*, 2009). Thus, although CWD levels and damage severity are generally assumed correlated, subtle differences, as recorded in this study, indicate that both factors exert differential effects on species performance.

Functional groups characterised by soil moisture responses explain the preference of black alder for pits formed by hardwood species (**II**), its almost-absence from mounds (**II**, **IV**), indifference in height growth of black alder between pits formed by hardwood and spruce species (**III**), and the significant positive relation between black alder regeneration survival and distance to pit centre, which was considered the deepest point (**IV**). On the other hand, Norway spruce may, due to harsh environmental conditions rather than lower light availability, be entirely absent in pits (Skvortsova *et al.*, 1983) or establish later (**II**) and accomplish poor height growth. As the high variability in conditions of storm-induced microsites becomes gradually less pronounced, more species could be expected, unless the more moist-tolerant species already dominate the area.

At the start of regeneration inventories in 2004, an attempt was made to distinguish between the sprouting, the advance (pre-disturbance) and the new (post-disturbance) regeneration types. In correspondence with the literature (e.g. Peterson and Pickett, 1991; Oliver and Larson, 1996; Arevalo *et al.*, 2000), the main species exhibiting sprouting from stumps were the hardwood species rowan and birch and the most represented species in advance regeneration were the more shade-tolerant species Norway spruce and rowan. Tree-fall mounds have a vegetated outer side, whereas the inner side exposes the root system and the attached mineral soil (Skvortsova *et al.*, 1983). Most regeneration on mounds in this study was recorded on the tops, on the border of both sides, although a part of the advance regeneration was capable of redirecting stem or apex from a vertical position on the outer part of the mound into a horizontal position. The species which were most abundant among advance regeneration were also mostly dominant on vegetated substrates (**IV**). However, throughout the years and especially after a destructive study in 2011, it appeared that many more seedlings and saplings were established before the storm than previously assumed. More intensive collection of control data would have provided a better baseline of the pre-disturbance forest, especially regarding the presence and performance of advance regeneration. The above section illustrates the complexity of determining the type of regeneration even only a few years after disturbance. Moreover, tremendous demographic changes may take place directly after disturbance (e.g. Maher and Germino, 2006). As a consequence, comparison between the three regeneration types in the study areas was ruled out at this stage. Nevertheless, it can be assumed that in tree-fall pits, advance regeneration is much less represented than in the other, more vegetated microsites.

6.2 Importance of wind-induced microsites for forest succession

The range of microsite types available for regeneration establishment becomes proportionally more heterogeneous at intermediate to high disturbance severity (Figure 9). In combination with the heterogeneity in light intensities offered at each severity level, areas with intermediate disturbance host the highest diversity in establishment conditions. The differences in soil moisture regime may not be significant among severity levels, though in moderately damaged areas, conditions may be more stable. According to Skvortsova *et al.* (1983), species composition 'normalises' in most cases at 80-100 years since disturbance, maintaining a multi-age structure. In the current study, the highest species diversity throughout the monitoring period was found in moderately damaged areas (Table 4, Figure 7).

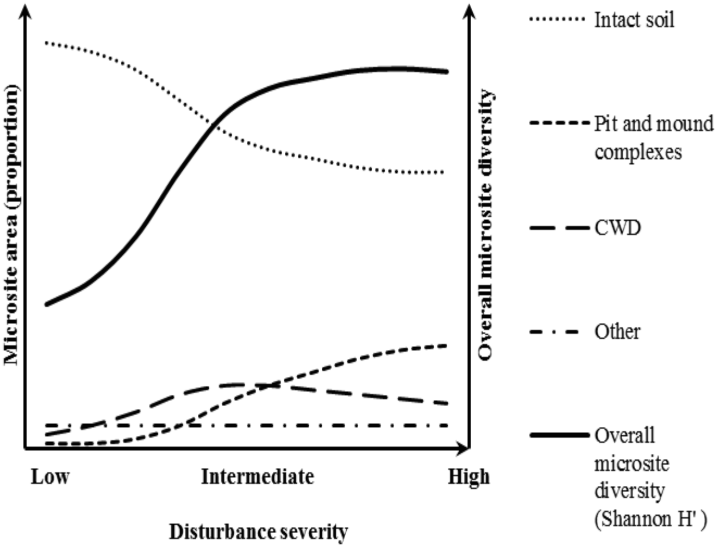

Figure 9. Proportional area of microsite types in wind-disturbed forest, based on the study areas (**IV**), and in correspondence with findings in the literature (**I**). Overall microsite diversity was approximated by calculating Shannon diversity index

For forest succession, besides the availability and colonisation of microsites by different tree species, the development of height and mortality probability between and within species are of crucial importance. Although height increment of birch and rowan was initially negatively correlated with overall seedling density (**II**), for the mortality analysis the effect of density was indirectly evaluated through competition indices (**IV**). Here, birch and black alder initially showed higher survival rates and rowan had lower survival rates with increased competition levels, whereas later, for all species in pits, mortality probability increased with competition. The situation of pits, surrounded by higher edges, mound and CWD may explain the increased mortality levels. Another cause could be higher intraspecific than interspecific competition (Queenborough *et al.*, 2007; Metz *et al.*, 2010), but this should be tested with a spatial study design or a competition index acknowledging the species' competitive traits. The role of rowan in future succession is restricted to early competition, due to its limited maximum height (e.g.

Skvortsova *et al.*, 1983). Nevertheless, the consequences of the presence of ground vegetation, shrubs and bushes can be critical for the direction of post-disturbance succession (Arevalo *et al.*, 2000).

Acknowledging the favourable starting position of advance regeneration, it can be expected that regeneration in intact ground and on mounds continues to be taller relative to the regeneration of mainly post-disturbance origin in pits. In this study the share of regeneration types initially recorded were comparable throughout the severity levels. Regeneration on intact ground in moderately damaged areas was indeed significantly higher (**IV**). However, with all severity types pooled, regeneration height in pits has clearly caught up with the regeneration height in other microsites (**III**, **IV**). An explanation can be that more trees in the larger size classes survive in less severely damaged storm areas (e.g. Dyer and Baird, 1997; Peterson, 2007; Canham *et al.*, 2001; Rich *et al.*, 2007), and thus there the difference in advantage for regeneration types is more explicit. Furthermore, the better survival of regeneration in storm-induced microsites (**IV**), can be due to the fact that birch regeneration was most abundant and birch survives better on mounds and pits than on intact soil (Skvortsova *et al.*, 1983).

The importance of CWD could not be reliably evaluated on the basis of this field study, due to the limited monitoring period since disturbance juxtaposed with the generally more advanced decay stage at which logs and stumps get suitable for colonisation by tree seedlings (Takahashi *et al.*, 2000; Wohlgemuth *et al.*, 2002; Zielonka, 2006; Bace *et al.*, 2011). In general, shade-intolerant regeneration can only profit from the presence of CWD resulting from earlier disturbances at the occurrence of a subsequent considerable disturbance event. In forests with abundant understory vegetation, CWD and other elevated sites constitute the primary substrate for post-storm tree regeneration of shade-tolerant as well as shade-intolerant regeneration (Simard *et al.*, 1998; Takahashi *et al.*, 2000; Noguchi and Yoshida, 2004; Iijima *et al.*, 2007). However, the establishment of new regeneration on intact soil in the current field study areas implies that CWD contributes to the long-term heterogeneity of regeneration substrates, especially for shade-tolerant species such as spruce, but that it is not a precondition for tree recruitment in these regions. Skvortsova *et al.* (1983) found the abundance of seedlings established on elevated substrate positively correlated with the soil moisture level.

6.3 Risks of generalising findings on succession in storm areas

Generalising findings on post-storm forest succession from single or multiple studies is important to detect certain patterns contributing to theory development (White and Jentsch, 2001). However, this brings along several risks.
Firstly, along with increasing latitudes (and altitudes), forests under natural conditions generally get a more open, less dense structure (Kuuluvainen, 2002). This may contribute to the reason why studies in temperate zones (e.g. Nagel *et al.*, 2006; Peterson and Leach, 2008; Kathke and Bruelheide, 2010) attribute less importance to storm-induced microsites than studies in boreal zones (e.g. Kubota and Hara, 1996; Kuuluvainen and Kalmari, 2003; Narukawa *et al.*, 2003). In forests with denser canopies the microsite suitability and availability of sufficient incoming radiation may more often not match than under open canopies. Besides that, under the latter type, also more competitive vegetation may impede tree species regeneration on intact soil, further illustrating the importance of elevated sites. Another spatial factor that may influence post-disturbance ecosystem development is the lack of connectivity of forest areas, e.g. in many parts of Europe, which limits species, particularly those related to old forests, in colonising disturbed soil (Moola and Vasseur, 2004).

Secondly, the timing of a study can, as mentioned before, be the underlying cause of divergent conclusions. In addition to the high rate of changes in species composition and growth conditions in early post-storm succession (Rydgren *et al.*, 2004), the majority of the plots are selected after the storm, thus impeding the reconstruction of pre-storm conditions. In the current field study, regeneration monitoring started with some delay after the disturbance, therefore early colonisation and mortality were not part of the study. Furthermore, delayed storm effects such as the rate of death of canopy trees due to the storm or subsequent disturbances (Ulanova, 2006; Köster *et al.* 2009), and hence the accumulation of CWD in moderately damaged areas, were not taken into account.

Thirdly, the pre-disturbance management can have a major impact on post-disturbance stand recovery. The forests in the current study areas, although unmanaged for some time, still did not show the structure of old-growth stands in the sense of a multilevel canopy and larger amounts of CWD in more advanced stages of decay. If this were the case, then probably more and older advance (or sub-canopy) regeneration may have survived the storm initially (e.g. 31% of the second layer at total canopy destruction in Ulanova, 2006), casting locally more shade then without such a dense cover. Additionally, the presumably larger amount of more decomposed units of CWD would likely have hosted a denser population of spruce regeneration then was currently the case.

Finally, the difficulty to reproduce storm research often puts constraints on the statistical soundness. However, the stochastic character of wind disturbance often does not leave much choice. On top of that, in many countries the forest act requires salvage logging in areas with considerable damage, which in fact even demonstrates a privileged position in the current study, of having two areas with comparable forest site types in which the heavily damaged areas are left untouched. Also growing season variability and climate change, may have differential consequences for both disturbance regimes and regeneration development (different species or species combinations). Furthermore, factors such as frost heaving on loamy soils and burial by litter in pits in some site types (Skvortsova *et al.*, 1983), subsequent stress or disturbance by browsing, insect outbreaks, pathogen infestations etc. can be of crucial importance to forest development, but may vary considerably between sites.

6.4 Implications for forest management

Forest management actions at different pre- and post-storm stages can influence forest succession to a certain extent, dependent on the initial storm severity.

- Pre-disturbance tree species composition has a major impact on prevailing species in the recruitment (Peterson and Pickett, 1991; Lässig and Močalov, 2000; Lugo, 2008).
- Pre-disturbance management (e.g. thinning, prescribed fire) can determine the share and species composition of advance regeneration in post-disturbance stands and influence response to sudden release (Kneeshaw *et al.*, 2002; Zald *et al.*, 2008).
- Salvage logging will increase the share of shade-intolerant species (**II**, **IV**), whereas non-management or the preservation of certain microsites may contribute to heterogeneity in species diversity. Nevertheless, the impact of salvage logging probably also depends on salvage intensity, as Peterson and Leach (2008)

found that after clear-felling, the microsite availability became more diverse.

- Height growth, mainly affected by light incidence (**III**), can be directed for certain species by the execution of pre-commercial thinning of surrounding trees.
- Prolonged retention of CWD of pre- and post-disturbance origin (most suitable are logs with diameter >20 cm, Skvortsova *et al.*, 1983) in post-disturbance stands can increase options for shade-tolerant species such as Norway spruce to germinate at a later stage since disturbance on this substrate when CWD decay is advanced.

7. CONCLUSIONS

1. Wind-induced microsites offer contrasting conditions, which vary in favourability for establishment, development and survival of post-disturbance regeneration. The range of microsite types available for regeneration contributes to increased heterogeneity in the future tree (and vegetation) species composition and spatial distribution. Generally, stands which experienced intermediate to heavy disturbance offer better circumstances for shade-intolerant species than stands with gap dynamics. The coupled effects of disturbance severity and microsite availability, the stand's disturbance history, disturbance legacy, the timing of establishment and life history traits of occurring species constitute the key to understanding post-disturbance regeneration dynamics (**I**).

2. The occurrence and performance of tree species in wind-induced microsites is influenced by a series of co-occurring gradients, interacting differentially with tree functional traits. Seedling establishment is mainly directed by seed size, dispersal traits and soil cover, ranging from bare mineral soil to vegetated soil. Small-seeded and/or air-borne dispersing species rely on elevated sites (birch) and on disturbed soil in pits and on mound tops (black alder and birch, **II**, **III**). The majority of rowan and Norway spruce seedlings on mounds consisted of advance regeneration. Soil moisture influences both germination and performance according to a species' drought or moisture tolerance. Substrate moisture is, especially in heavily damaged areas, subject to substantial variations due to meteorological and day-to-night variability. Pits and mounds can be persistently wet and dry, respectively. Especially black alder benefitted from the lower moisture tolerance of other species in pits. The gradient of light incidence is most important for seedling height and height growth. Both elevated sites and heavily damaged storm areas are most favourable for the growth of shade-intolerant species. However, this gradient is also influenced by the amount and distribution of CWD, the survival of advance regeneration and other competitive vegetation (**II**–**IV**). Nutrient availability has in this study received minor attention.

3. Analogous to the sequence of germination, establishment and growth, regeneration tree performance and mortality were expected to be influenced predominantly by microsite conditions initially, and later by inter- and intra-specific competition. Best germination conditions occurred in stable areas with soil disruption: rather in large shallow pits (Norway spruce uproots) than in deep pits, and rather on low thick mounds (uproots of broadleaved species) than on high thin mounds. The factors affecting regeneration mortality in the current field study varied considerably among regeneration species, microsites and inventory years. Survival of shade-intolerant species silver and downy birch was consistently positively correlated with factors related to disturbance severity and individual height in the past. Good performance and limited competition in the past were only later positively associated with survival of more shade-tolerant species black alder, Norway spruce and rowan. Although CWD and browsing had a clear impact on regeneration mortality, the interrelated effects should be further investigated before the importance of these factors can be evaluated relative to other factors (**II**, **IV**).

4. This study indicates that the prediction of post-storm successional pathways should be based on several years of inventory or at least on a number of investigations at distinct moments in time. There are many processes which play a contradictory role for species performance at different stages since disturbance. Notwithstanding these differences, species' preference for a particular microsite-severity combination was maintained in the current study, although species' performance altered. This can be partly explained by the distinct responses of pre- and post-disturbance regeneration. Storm perturbations, such as delayed tree mortality and falling of CWD, persist during more than 10 years after the event. Therefore, it is recommended to prolong monitoring to a range of at least a decade since disturbance (**IV**).

5. The presence of storm-induced microsites increases long-term tree species diversity on the stand level, due to spatial partitioning. Harvesting considerably encourages dominance by shade-intolerant species. A decade of post-storm regeneration inventories implies that, when aiming at disturbance-emulating management, relying on natural regeneration provides a wide range of opportunities (**I**, **IV**).

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SUMMARY IN ENGLISH

Wind disturbance is a major driver of forest development in Europe's temperate and boreal forests. Sustainable forest management attempts to include windthrow as a natural process, relying on a system's resilience by natural post-disturbance regeneration. Variation in storm characteristics and pre-disturbance conditions initiates a wide range of potential post-disturbance succession trajectories. Findings on the impact of wind disturbance on the direction of succession are therefore often contradictory. Low disturbance severities, beneficial to shade-tolerant species, have been suggested to accelerate succession and high disturbance severities, promoting shade-intolerant species, to retard succession. However, severity alone is not sufficient to explain the controversy. The composition and spatial distribution of biological storm legacy, i.e. surviving trees, advance regeneration, ground vegetation, coarse woody debris (CWD) and the variability in abiotic microsites may assist in the detection of patterns.

Windstorms cause breakage of biological tree matter (foliage, branches, stems) and tree uprooting. Therefore, in addition to the undamaged (intact) forest soil, a range of storm-related microsites are created, such as the pit and mound complexes caused by the uplifting of root-plates, and accumulations of CWD of various size. The conditions within and between these microsites are highly variable.

This thesis presents an overview of microsites in storm-damaged areas, discussing availability and relevant conditions at different stages of tree regeneration development. Furthermore, post-disturbance regeneration performance is evaluated based on a series of field inventories in two mature spruce-broadleaf mixed forests on humid, eutrophic soils in Estonia.

Two major storms left behind a heterogeneous pattern of storm damage in the areas in 2001 and 2002 respectively. The focal species in this study were Norway spruce (*Picea abies* (L.) Karst.), silver and downy birch (*Betula pendula* Roth. and *B. pubescens* Ehrh.), black alder (*Alnus glutinosa* (L.) J. Gaertn.) and European rowan (*Sorbus aucuparia* L.). Starting in 2004, regeneration characteristics and site conditions were investigated in patches with different disturbance severities: sample plots were

established in areas having no, moderate or heavy damage, and in damaged + harvested areas.

Microsite conditions, availability and occupancy at different storm severities

Elevated sites such as tree-fall mounds and CWD, especially when unvegetated, reduce competition at the initial post-disturbance stage, which is beneficial for shade-intolerant species. Both substrates encompass the risk of instability. The increased availability of bare mineral soil after windthrow, mainly located in tree-fall pits and on the top and inner part of mounds, facilitates germination and establishment of small-seeded species. Pits accumulate litter and nutrients and, at a more advanced decay stage, CWD releases nutrients and becomes more suitable for germination and physical anchorage of regeneration roots. With time since disturbance, light incidence generally decreases while CWD gets more suitable as a germination substrate, which implies that timing of establishment and optimal growth conditions do not always match.

Based on literature and current field study, pits and mounds are most available immediately after storm (1–16% and 1–36% of the total area, respectively), whereas the amount of CWD can increase during subsequent decades due to delayed storm effects (7–23%). With increasing disturbance intensity, the share of storm-induced microsites increases and the share of intact ground including pre-disturbance microsites (45–89%) declines. Throughout inventories in the two storm areas in Estonia, pits in heavily damaged areas were dominated by birch, pits in moderately damaged areas by black alder and the mounds in heavily and moderately damaged areas by (for a large part advance) regeneration of rowan and Norway spruce, respectively. Regeneration species composition turned out most diverse in moderately damaged areas (compared to areas with other disturbance severities) and in pits (compared to other microsite types) early after disturbance, whereas in time, at the last inventories for this thesis, regeneration species were more equally distributed on intact soil than on wind-induced microsites. Harvested sites were significantly most densely populated, with birch as the dominant species, whereas control areas hosted least regeneration. Differences in regeneration density between heavily and moderately damaged areas were not significant.

Consequences for post-storm succession

Wind disturbance alters resource availability in forests, in particular light incidence, nutrients and soil organic matter. Whilst the initial microsite conditions regulate regeneration species germination, species traits regarding shade-tolerance are mostly responsible for further growth and mortality. Field study results in this thesis indicate that shade-intolerant species experience a continuous influence of light availability, as disturbance severity, expressed as the ratio of post-disturbance basal area (BA) of storm-damaged trees and pre-disturbance plot BA, exerted significant effect on height and height growth. Past performance, in its turn, was negatively linked to mortality probability. In contrast, more shade-tolerant species only started to feel the impact of past competition at later stages (i.e. around 10 years) since disturbance. Advance regeneration, dominated by rowan and, to a lesser extent, spruce, was analysed together with new regeneration. According to logistic regression modelling, the factors affecting regeneration mortality probability varied considerably among regeneration species, microsites and inventory moments since disturbance. Soil moisture explains occurrence and good performance of black alder in pits. The amount of CWD may have inhibited initial height growth rate through sun-blocking in the first years after germination, whereas it may have protected birch from ungulate browsing in later stages. Although CWD is abundant, but initially not yet as a suitable substrate, its presence may turn out crucial for stand development at subsequent disturbances. The presence of storm-induced microsites is expected to increase long-term tree species diversity on the stand level, due to the species' preferences. However, future research is necessary to judge whether the observed trends are persistent.

Implications for forest management

Forest managers who rely on natural regeneration can, dependent on the storm severity, exert a certain influence on post-disturbance stand development. Pre-disturbance stand management including thinning affect future species composition and the post-disturbance presence, composition and dimensions of advance regeneration. Post-disturbance salvage logging will increase the share of shade-intolerant species, whereas stands that were left untouched may have increased species diversity and, in the case of CWD retention, an extended offer in substrates suitable for shade-tolerant species. Finally, pre-commercial thinning can be applied to promote height growth of preference species.

SUMMARY IN ESTONIAN

Tormide ja tugeva tuulega seotud häiringud on väga olulised faktorid, mis mõjutavad metsaökosüsteemide arengut Euroopa parasvöötme metsades ja boreaalses metsavööndis. Jätkusuutlikus/säästvas metsamajanduses käsitletakse tormikahjustust kui looduslikku protsessi, mis tähendab ka süsteemi isetaastumist, ehk looduslikku häiringujärgset uuenemist. Varieeruvus tormi erinevates karakteristikutes ja ökosüsteemi häiringueelses olukorras põhjustab väga erinevaid häiringujärgseid suktsessioonilisi arengusuundi. Seetõttu ongi häiringujärgselt kirjeldatud erinevad suktsessioonistsenaariumid ja mudelid vastuolulised. Nõrgad tormid, mis soosivad varjutaluvate puuliikide uuenemist, kiirendavad suktsessiooni, samas kui suure intensiivsusega tormid, mis soosivad pioneerliike, arvatakse olevat suktsessiooni aeglustavad. Samas ei ole häiringu intensiivsus üksinda piisav näitaja selgitamaks erinevusi. Häiringu jäänukelemendid, nagu ellujäänud puud, eeluuendus, alutaimestik, lamapuit ja mitmesugused abiootilised häiringuelemendid (häiringu käigus tekkinud mikroreljeefi, mulla ja pinnasemoodustised, mida võib nimetada uuenemise mikroaladeks) ning nende ruumiline paigutus on aluseks oluliste metsa uuenemisprotsesside kirjeldamisele ja modelleerimisele.

Tugev tuul põhjustab puittaime mehaanilist kahjustust, murdumist (lehed, oksad, tüved) ja tuuleheidet. Viimane tekitab suurel hulgal erinevaid uuenemise mikroalasid, nagu juuremättad ja -augud, mis tekivad juurestiku ülespööramisel pärast puu heitmist tormituulte poolt. Samuti tekib tuuleheite tagajärjel erinevate dimensioonidega lamapuitu. Tingimused nende mikroalade sees ja vahel on väga varieeruvad.

Käesolevas väitekirjas analüüsitakse erinevates kasvuetappides oleva uuenduse olemasolu ja seisundit tormikahjustatud alade mikroaladel. Häiringujärgset uuenduse dünaamikat hinnati kordumõõtmiste käigus Eestis kahel häiringualal (Tudus ja Hallikul), kus viljakatel gleistunud ja gleimuldadel kasvavad hariliku kuuse – lehtpuu segapuistud.

Tormid, mis leidsid aset 2001. ja 2002. aastal, kujundasid antud uuringualadel väga heterogeense taimkattemustri. Peamisteks puuliikideks käesolevas uuringus olid harilik kuusk (*Picea abies* (L.) Karst.), aru- ja sookask (*Betula pendula* Roth. ja *B. pubescens* Ehrh.), sanglepp (*Alnus* *glutinosa* (L.) J. Gaertn.) ja harilik pihlakas (*Sorbus aucuparia* L.). Alates 2004. aastast on uuritud puurinde uuenduse ja alustaimestiku dünaamikat erineva kahjustusastmega proovialades, mis rajati kahjustamata metsa (kontroll), mõõduka ja tugeva kahjustusega metsaosadesse ja kahjustatud ning seejärel tormikahjustatud puudest koristatud aladele.

Uuenemise mikroalade olemasolu, nende iseloomustus ja uuenduse teke erineva tormikahjustuse astme korral

Häiringu käigus tekkinud mikroreljeefi kõrgematel osadel (juuremättad, mis moodustuvad juurestiku, mulla ja pinnase ümberpaigutumisel, aga samuti lagmapuit), eriti kui seal esineb vaid vähesel määral puittaimedega konkureerivat taimestikku, on soositud kiirekasvuliste lehtpuude uuenemine. Nii juuremättad kui lagunev lamapuit on osutunud ebastabiilseks substraadiks. Tormiheite tagajärjel juureaukudes ning juuremätaste üla- ja keskosas tekkinud mineraalpinnasega taimedeta mikroalad osutuvad heaks uuenduskohaks kergete ja väikeste seemnetega pioneerliikidele. Juureaukude olemasolul võib nendes täheldada varise ja mullatoitainete mõningast akumuleerumist. Puittaimede tüvede järkjärgulisel lagunemisel vabaneb toitaineid ja puidu tihedus kahaneb, ning puit on selliselt uuenduse kasvavatele juurtele kergemini läbitav. Tavaliselt häiringu järgselt tekkiva uuenduse all valgustatus väheneb, samas muutub lagunev puit taimedele paremaks kasvupinnaseks. Metsauuenduse kasvu mõjutavate erinevate tegurite optimumid ei lange sageli kokku.

Uuenemise mikroaladest on juuremättad- ja augud kõige suurema osakaaluga vahetult pärast tormi (vastavalt 1–16% ja 1–36% häiringuala pindalast). Lagupuidu osakaal võib suureneda häiringu järgselt 7–23% (lisandub ellujäänud puude suremine). Tormi intensiivsuse suurenedes kasvab ka vahetult tormi tagajärjel tekkivate häiringuelementide osakaal, samas väheneb kahjustamata pinna ja häiringu eel olemas olnud mikroalade osa. Kahe tormi puhul tekkinud häiringualal tõdeti kordusmõõtmiste käigus, et suure kahjustusastmega alade juureaukudes on enim uuenenud puuliigiks kask, mõõduka kahjustuse puhul domineerib aga sanglepp. Juuremätastel on kõrge kahjustusastme korral enamlevinud liigiks harilik pihlakas, mõõduka kahjustuse puhul harilik kuusk. Puittaimede uuenduse liigiline koosseis oli kõige rikkalikum vahetult häiringu järel (mõõtmiste alguses) mõõdukalt kahjustatud aladel (võrreldes teiste kahjustusastmetega) ja juureaukudes (võrreldes teiste mikroaladega). Aja möödudes (10 aastat pärast tormi) tekib uuendus ühtlasemalt ka tormi poolt mehaaniliselt mõjutamata mullapinnale. Tormijärgselt puidust koristatud aladel oli uuendus kõige arvukam, seal domineeris kask. Kontrollaladel oli uuendust kõige vähem. Uuenduse arvukus mõõduka ja tugeva kahjustusastmetega aladel ei erinenud oluliselt.

Tormijärgne suktsessiooniline dünaamika

Tormikahjustus muudab metsaökosüsteemi aineringet, valgustingimusi ja mullaga seotud protsesse. Algsed, häiringu käigus tekkinud mikroreljeefi ja mullaga seotud häiringuelemendid (juuremättad ja -augud, lamapuit) määravad ära uuenevate puuliikide seemnete idanemise. Hilisemalt muutub oluliseks puuliikide kohastumine (varjutaluvus), mis määrab ära noorte puude suremuse ja kasvukiiruse. Käesoleva töö tulemused näitavad, et muutunud valgustingimustes (seda iseloomustab häiringueelse ja -järgse puistu rinnaspindalade suhe), kiireneb varjutaluvate ja eeluuendusena olemasolevate liikide kasv. Puutaimede kasvukiirust on negatiivses korrelatsioonis puude suremusega. Varjutaluvamate liikide kasvu hakkab konkurents mõjutama alles häiringujärgse koosluse arengu hilisemas staadiumis. Käesolevas töös analüüsiti puuliikide eeluuendust, mille suuremas osas moodustab harilik pihlakas (vähesel määral ka harilik kuusk) ja häiringujärgset uuendust koos. Logistiline regressioonimudel toob esile suure varieerumise uuenenud puude suremuses, mis sõltub puuliigist, kasvukohast ja vaatluse teostamise ajast. Tormikahjustuse käigus juuremätaste üleskerkmisel tekkinud pinnaseaukudes esineb sageli ja näitab head kasvu sanglepp, selle peamiseks eelduseks võib pidada häid niiskustingimusi. Suur lamapuidu kogus loob tõenäoliselt varjestusefekti (langenud tüved katavad kinni osa valgusest), mille tõttu idanenud puutaimede kasv pidurdub. Ka koosluse arengu hilisemas faasis loob lamapuit takistuse metsloomade liikumisele, vähendades seega uuendusel nende toitumisega seotud kahjustusi. Kuigi lamapuit ei mängi olulist rolli seemnete idanemispinnasena vahetult häiringu järel, võib see muutuda oluliseks hilisemates koosluse arengufaasides ja korduvate häiringute puhul. Eeldatavalt suurendavad pikemas perspektiivis tormikahjutuse käigus tekkinud häiringuelemendid puurinde liigilist mitmekesisust, mis on seotud liikide erineva nõudlusega kasvukeskkonna suhtes. Edasised uuringud aitavad selgitada, kuivõrd kestvad on algselt kirjeldatud arengutrendid tulevikus.

Uurimistulemuste kasutamine metsade majandamisel

Kui majandamisel planeeritakse metsa uuendada looduslikult, saab seejuures rakendada teadmisi häiringujärgse metsa uuenemise kohta (tekkiv liigiline koosseis, vajadus selle reguleerimiseks). Häiringule eelnenud majandusvõtted puistus, näiteks harvendusraied, muudavad liigilist koosseisu ja loovad tingimused eeluuenduse tekkeks, mis häiringu järgselt määravad koosluse arengu. Olukorras, kus majandusskeem näeb ette häiringu poolt mõjutatud (kahjustatud) metsa koristamise, uuenevad looduslikult peamiselt valgusnõudlikud puuliigid. Kui häiringujärgse metsaökosüsteemi areng jätkub ilma otseste majandusvõtete rakendamiseta (looduslikult), on kujuneva koosluse puurinde liigirikkus suurem. Säilitatud lamapuit moodustab varjutaluvate liikide uuendusele idanemis- ja kasvupinnase ja loob eeldused mitmerindelise puistu tekkeks. Soovitud liigilise koosseisu saavutamiseks võib rakendada metsakasvatuslikke võtteid, näiteks harvendusraiet.

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I

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SPECIAL FEATURE: REVIEW

Approaches for forest disturbances studies: natural variability and tree regeneration

The influence of storm-induced microsites to tree regeneration patterns in boreal and hemiboreal forest

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Abstract We reviewed studies dealing with regeneration under variable conditions in boreal and hemiboreal forests as affected by different microsite types by tree species functional groups. Generally, the importance of storm-induced microsites for regeneration dynamics in boreal forests depends on several factors: (1) distribution and type of microsites (generated by storm characteristics and stand conditions); (2) viable seed supply (stand history, species dispersal traits and status of surviving trees) and their species' life history strategy; (3) climatic and site conditions (pre-storm conditions and storm-induced changes); and (4) delayed storm effects, such as retarded falling of trees, favoured vegetation growth, etc. Studies acknowledging the significance of microsites were mostly related to intermediate or severe events, causing sufficient changes in resource levels and growth conditions, and influencing extrinsic factors such as frost heaving, erosion and browsing. Also, the dispersal traits of available tree species, including sprouting and response of surviving trees, such as canopy expansion, should be considered in evaluating microsite importance in individual cases. In intermediate to severe windstorm events, pioneer species are generally profiting most from the additional offer in microsites, requiring bare mineral soil and elevated locations for their establishment and growth. Under gap dynamics, shade-tolerant species benefit from dead wood and elevated locations as these offer safe sites in stands with abundant understorey vegetation.

Keywords Dead wood · Pit and mound structure · Regeneration dynamics · Shade-tolerant/intolerant species · Wind disturbance

Introduction

In many models and theories on forest development, disturbances are regarded as a factor that sets back or retards succession and rejuvenate the forest (e.g. Hytteborn et al. 1987; Nishimura 2006; Lugo 2008). Obviously, the impact of disturbance also depends on the disturbance regime and type (Kneeshaw and Bergeron 1998; Papaik and Canham 2006), as forests subject to frequent disturbance will not

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exceed the early successional stage. Moreover, stand-replacing disturbances do not distinguish between tree species or dimensions (Mason 2002), generally devastating the majority of the canopy dominants and hence favouring colonisation by pioneer species, in addition to promoting released advance regeneration and sprouts from stumps, roots and seeds. In contrast, smaller perturbations may provide circumstances, which are mainly favourable to advance regeneration of shade tolerant species, thus potentially accelerating succession (Webb 1999; Arevalo et al. 2000; Zhao et al. 2006; Hanson and Lorimer 2007; Rich et al. 2007). Furthermore, disturbance types may have differential impacts on the forest: where fire generally starts from the understorey, and may kill understory plants and regeneration as well as mature trees (Reyes et al. 2010), windstorm affects mainly canopy trees, sometimes taking down advance regeneration with them, but—initially—hardly damaging understory vegetation (Angelstam and Kuuluvainen 2004).

The importance of windthrow in boreal forests is often recognised, especially in areas with relatively long fire cycles (Ulanova 2000; Gromtsev 2002; de Chantal et al. 2003b; Schulze et al. 2005), although the role of fire may still have been overemphasised in recent studies (as confirmed by Kuuluvainen and Kalmari 2003; Achim et al. 2005; Fraver et al. 2008). Wind damage has a more stochastic character than most other natural disturbance agents, less influenced by site and stand properties. Where natural fires can be literally absent from a humid area (see, e.g., ASIO-model as described by Angelstam 1998; Wallenius et al. 2004, 2005, 2007; Liu et al. 2010), topography can only influence chances of windthrow events to take place in a stand (several modelling studies; e.g. Gardiner et al. 2008; Moser and Nelson 2009). This implies that all stands experience a wind disturbance regime, which contributes to a certain degree to its dynamics. The relative impact of storm may increase further due to an expected rise in storm frequency and intensity as a result of climate change (Schelhaas et al. 2003; Usbeck et al. 2010) and a local decrease in fire frequency resulting either from climate change (Bergeron et al. 1998; McCoy and Burn 2005) or from altered anthropogenic fire suppression and other interactions (Wallenius et al. 2005).

The legacies of a storm can generally be described in terms of (1) the structure and composition of the intact and damaged canopy trees, determining light, water and nutrient availability for new and advance regeneration and constituting the seed (and sprouting) sources for post-storm regeneration; (2) damage status and position of advance regeneration; and (3) storm-related microsites such as pit and mound complexes and decaying coarse woody debris (CWD). The wide range of potential combinations of these legacies, depending on several factors presented in the next section, form the basic conditions for post-disturbance stand development. Additionally, regeneration is subject to seed dispersal strategies of current and preceding tree and vegetation species (Barnes et al. 1998; Papaik and Canham 2006).

The consequences of windthrow for forest successional dynamics still remain largely unknown (Gromtsev 2002; Schulze et al. 2005). Generally, tree successional dynamics depend upon species' dispersal and establishment traits, competitive ability (usually shade-tolerance) and disturbance resistance (e.g. Papaik and Canham 2006). That microsites after storm can be important for regeneration and soil formation has been recognised in many studies (e.g. Nakashizuka 1989; Kuuluvainen 1994; Kuuluvainen and Juntunen 1998; Pozdeev 2000; Ulanova 2000; Wohlgemuth et al. 2002; Kuuluvainen and Kalmari 2003; Ilisson et al. 2007; Šamonil et al. 2010; Vodde et al. 2010). However, an overview of these studies, synthesising the consequences of storm-induced microsites for forest development and analysing their relative importance with regard to other disturbance types/circumstances, is, so far, lacking. This review intends to do this, by discussing findings in regeneration patterns within storm-induced microsites of the boreal and hemiboreal zone, following the establishment, growth and mortality of functional groups (1) the shade-intolerant pioneer (early-successional) species, and (2) the shade-tolerant (late-successional) species in different microsites in boreal and hemiboreal forest zones.

The most important limitations of these studies and thus for interpreting and comparing the results are (1) the often less well-documented pre-storm conditions versus post-storm conditions, (2) the limited time period of most studies, complicating long-term development predictions, and (3) the varying definitions of 'recruitment size' as the threshold in registering emerging seedlings, which has significant consequences for the study outcomes (e.g. Leemans 1991 reported a 99% mortality rate of seedlings <5 cm in the subsequent year). We take these difficulties into account in our considerations of regeneration patterns.

Storm-induced changes in environmental conditions

Factors influencing wind damage

Besides the individual storm event characteristics (Peltola et al. 1999; Gardiner et al. 2000, 2008; Canham et al. 2001; Achim et al. 2005; Usbeck et al. 2010) and the prevailing storm regime (Takahashi 1994; Nagel and Diaci 2006), the traces a storm leaves behind depend on several other factors (Fig. 1). Abiotic factors include topography and soil of the area, influencing the stands' exposure, and tree anchorage and growth rate (Schaetzl et al. 1989; Takahashi 1994; Mitchell et al. 2001; Ruel et al. 2001; Scott and Mitchell 2005; Nicoll et al. 2006; Gardiner et al. 2008; Shorohova et al. 2008). Biotic factors can be subdivided into tree level and stand level traits. Individual species have certain strength and architectural properties regarding branches, stem and roots (Kato and Nakatani 2000; Wolf et al. 2004; Achim et al. 2005; Nicoll et al. 2006; Gardiner et al. 2008), which often depend on tree age and growth circumstances, hence also inducing within-species variation at the tree level (Kato and Nakatani 2000; Achim et al. 2005; Gardiner et al. 2008). Furthermore, pioneer species are commonly regarded as relatively more vulnerable to wind disturbance than late successional shade-tolerant species (Foster 1988; Wolf et al. 2004; Rich et al. 2007), although several studies report no significant differences between tree species (Lässig and Močalov 2000; Zhao et al. 2006; Shorohova et al. 2008; Yoshida and Noguchi 2009).

In mixed forests, a higher vulnerability of pioneer species to moderate windthrow would decrease the number of pioneers in the stand and favour shade-tolerant regeneration. In addition to the species, individual tree health (Schaetzl et al. 1989), dimensions (Arevalo et al. 2000; Kuboyama and Oka 2000; Lässig and Močalov 2000; Lekes and Dandul 2000; Peterson 2000; Ulanova 2000; Canham et al. 2001; Wolf et al. 2004; Nagel and Diaci 2006; Rich et al. 2007; Gardiner et al. 2008; Yoshida and Noguchi 2009) and position in the stand (Peltola et al. 1999; Lekes and Dandul 2000; Mitchell et al. 2001; Ancelin et al. 2004; Nagel and Diaci 2006; Gardiner et al. 2008) also contribute to its vulnerability to wind damage, having different effects on both stem breakage and windthrow (Ishizuka et al. 1998).

Stand factors influencing windthrow risk are comprised of the sum of the tree level factors, resulting in a stand with a certain overall vigour, containing wind susceptible or resistant species—although a late-successional stand phase is regarded as more vulnerable by, e.g., Hytteborn et al. (1987), trees of the same or different dimensions, certain spatial distribution patterns, etc. But stand density, gap mosaic (Gardiner et al. 1997, 2008; Ruel et al. 2001; Scott and Mitchell 2005; Zeng et al. 2009), presence of relatively new, sharp cutting edges versus older, natural coulisse-like edges (Stathers et al. 1994) and the storm behaviour also impact of one species to another (e.g. swaying crowns) highly influence a stand's vulnerability to wind.

Different aspects of forest management influence tree and stand windthrow susceptibility (Schaetzl et al. 1989; Jactel et al. 2009). As we have argued before, there is no consensus on the effects of species choice and composition, including the mixture versus monoculture discussion, on windthrow risk. Methods of regeneration include dependence on natural regeneration from seeds or advance regeneration and several sowing and planting options, where it seems most likely that natural regeneration yields the most resistant individuals. Considering stand structural

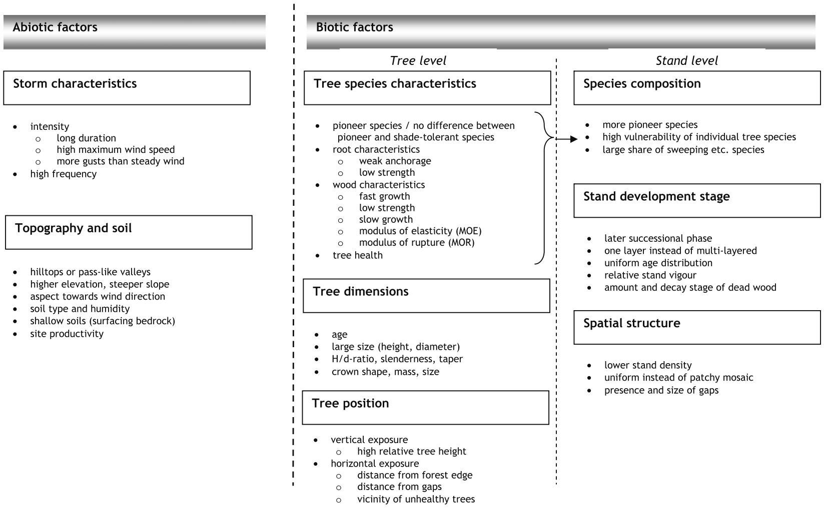

Fig. 1 Factors influencing wind-damage (both windthrow and breakage) risk

issues, regeneration after clear-cut generally results in uniform even-aged stands, with low canopy roughness and, from an aerodynamic point of view, more wind-resistance (Quine et al. 1995; Achim et al. 2005). In contrast, under continuous cover forest management, multi-layered stands develop, with high canopy roughness, but probably better acclimated trees in the upper canopy (Dhôte 2005). Site preparation methods such as drainage, tilling and evenly distributed resources may increase rooting depth, symmetrical and vigorous root development and, hence, improve tree stability (Schaetzl et al. 1989; Coutts et al. 1999; Nicoll et al. 2006). Finally, thinning intensity (Schaetzl et al. 1989; Quine et al. 1995), execution of harvesting operations (Schaetzl et al. 1989) and silvicultural system with respect to cutting intensity, rotation length and shape of harvested area affect acclimation of remaining trees (Quine et al. 1995; Gardiner and Quine 2000).

Consequences of windthrow for environmental conditions

Establishment and juvenile growth of tree species largely depend on the availability of resources as light, water, temperature and nutrients, which are generally subject to the local climatic conditions, topography, soil humidity and texture, and depth of the humus layer (Tegelmark 1998; Diaci et al. 2000; de Chantal et al. 2003a, 2004). The rate of death of individual trees and groups of trees after natural disturbances, either as a delayed effect or due to subsequently evoked disturbances, determine the pace at which these resources are reorganised and become available for species with different life history traits (Suzuki et al. 1987; Kneeshaw and Bergeron 1998; Kozlowski 2002). Therefore, the gradient in light conditions, and hence the changed temperature, nutrient levels and humidity along gap formation after storm, either suddenly and drastically or slowly progressing, have large consequences for regeneration patterns (Papaik and Canham 2006). Another pattern displays when storm-induced gaps favour growth of specific understory species, hence inhibiting tree regeneration. A major example is dwarf bamboo (*Sasa senanensis* Rehd.) in boreal Japan (e.g. Takahashi et al. 2000; Iijima et al. 2007), but other cases, especially *Rubus* spp., have been reported in North America (Castelli et al. 1999; Arevalo et al. 2000).

Storm events generally decrease canopy closure by windthrow and stem breakage. Besides causing mortality, storms often weaken a certain portion of the stand due to a reduction of branches and leaves, stem tilting causing stress or breakage in the root system and falling neighbouring trees causing damage to stem or roots (Allen 1992; Stathers et al. 1994). These weakened trees, in addition to healthy, but isolated single trees or groups of trees and trees making up the new storm-created forest edges, are more prone to subsequent windthrow and further disturbances (Suzuki et al. 1987; Rosenvald et al. 2008; Köster et al. 2009a; Polyachenko et al., in preparation). Furthermore, mound erosion and wood decay retard the stabilisation of microsites (Ulanova 2000; Mori et al. 2004) and dead wood hinders regeneration by its mechanical and sunblocking effects (Kurulok and Macdonald 2007).

Another potential delayed change in post-storm conditions is caused by the eventual falling of logs that were initially hanging over or leaning on other trees (Ilisson et al. 2007; Köster et al. 2009b).

The most obvious initial result of storm is the increased radiation level. In the case of extreme wind damage events, this benefits the establishment of pioneer species. In milder events, it either favours germination of shade-tolerant species, or is just enough to allow advance regeneration to grow into the canopy, maintaining or proceeding towards a shade-tolerant species composition (Suzuki et al. 1987; Ilisson et al. 2007). After canopy removal, air and soil temperatures become more extreme in the created gaps and soil moisture generally increases (Bonan and Shugart 1989). This also influences ground vegetation, mosses and lichens and thus nutrient cycling and competition for tree seedlings. Nutrient availability for regeneration may vary with different microsites. Mounds and particularly pits experience more leaching, especially on nutrient-poor podzols, soils with a less permeable layer and areas with heavier precipitation. This makes them poorer and more acidic than undisturbed ground. On the other hand, pits accumulate more humus and, due to the windthrow event, a certain part of the canopy trees will have ceased to uptake any more nutrients from the soil (Schaetzl et al. 1989; Harmon and Sexton 1995; Clinton and Baker 2000; Kramer et al. 2004). As for the CWD (coarse wood debris), available nutrient levels initially do not diverge much from pre-storm conditions, but create variable pools with the progressing decay of CWD, depending on the part and species of the tree (Krankina et al. 1999; Palviainen et al. 2010a, b).

The heterogeneity of microsites in a stand generally increases after windthrow, resulting in more elevated places and depressions (Falinksi 1978; Beatty and Stone 1986; Burney et al. 2007; Ilisson et al. 2007; Jonášová et al. 2010; Vodde et al. 2010), increased availability of establishment substrates (Siitonen 2001; Ilisson et al. 2007; Vodde et al. 2010), larger variety in nutrient levels (Beatty and Stone 1986; Krankina et al. 1999; Peterson and Pickett 2000) and reduced browsing risk for seedlings and saplings owing to the created refugia/shelters such as branches, stems and exposed root systems from windthrown trees (Peterson and Pickett 1995; Schönenberger 2002; Krueger and Peterson 2006; de Chantal and Granström 2007).

In comparison with storm, fire is generally more destructive for the understory, temporarily resulting in more extreme ground temperatures and soil moisture levels, increased levels of radiation and release of plant available nutrients (Hille and Den Ouden 2004; Lilja-Rothsten et al. 2008). Fire intensity and frequency determine the actual effects to tree survival and the vegetation seed bank and growth conditions, thus determining the direction of succession (Attiwill 1994; Kuuluvainen and Rouvinen 2000; Kurulok and MacDonald 2007; Parro et al. 2009). Fire usually contributes less to microsite variety than wind, although considerable variation in fire severity may create heterogeneous patterns of surviving and dead trees, and appearance of fire specialists (Kuuluvainen and Rouvinen 2000; Lampainen et al. 2004; Kurulok and Macdonald 2007).

Other abiotic disturbances such as frost heaving and flooding, and biotic disturbances such as grazing, insect outbreaks and pathogen infestations, proceed much more slowly through a stand and usually only act at the tree and vegetation patch (gap) level. Biotic disturbance with a chronic character (e.g. grazing or browsing) can nevertheless maintain an open landscape after a discrete event such as wind or fire (e.g. Engelmark et al. 1998). Outbreaks of spruce budworm in eastern Canada create patchy mortality, resulting in an increased microsite heterogeneity which allows coexistence of pioneers and shade-tolerant species (De Grandpré and Bergeron 1997).

Storm-induced microsite types

The types of microsites characterising a stand after storm depend largely on the modes of tree damage, with the pit-and-mound complexes as the most distinctive post-storm feature (Beatty and Stone 1986; Ilisson et al. 2005, 2007). Mounds, consisting of the upturned root-plate and attached organic soil, can have a vertical dimension of several metres (Beatty and Stone 1986) and a thickness of 0.2–7.5 m (Schaetzl et al. 1989). Pits remain where the root system and attached soil have been pulled out. Pit size depends on soil properties and the architecture of the root system, which is a function of tree species traits and soil properties. Shallow and poorly drained soils limit a tree to thin, but often laterally extensive, root-plates, resulting after windthrow in a pit area with a diameter up to 10 m (Beatty and Stone 1986; Šamonil et al. 2010). Beatty and Stone (1986) classified root-plate thickness groups (thin, plate, or ball, along with increasing thickness) and different types of treefall: hinge, where the root-plate is lifted from the pit; rotational treefall, where the root-plate ends up vertically in the pit; and incomplete treefall, where tree and root-plate are only tilted. Both thickness qualifications and treefall type have consequences for soil properties, tree position and pit-and-mound structure. Peterson and Pickett (2000) found significantly higher temperatures and radiation levels between mounds and intact soil, whereas the pits were only slightly different from vegetated intact soil in this respect. Differences in moisture conditions were not significant (Peterson and Pickett 2000), although this may depend on the season.

The presence of a pit-and-mound structure lasts for a long time: in the case of deep pits and high mounds, it may take up to a century for the vegetation composition to stabilise in the boreal zone (Gromtsev 2002) and several centuries to wipe out the structure and pedogenic composition created by a storm and get back to the pre-storm situation and processes even though the storm-created gaps may have long been closed (Lyford and MacLean 1966; Beatty and Stone 1986; Hofgaard 1993; Ulanova 2000; Gromtsev 2002; Šamonil et al. 2010).

Windthrow as well as wind breakage bring about an increase of woody debris of varying dimensions on the forest floor, adding to the range of microsites (Peterson and Pickett 2000). Logs and even low snags resulting from wind breakage may offer establishment sites for regeneration (Ishizuka et al. 1998; Nakagawa et al. 2003). The proximity of decomposing logs and root systems provide physical properties such as soft substrates facilitating root anchorage (DeLong et al. 1997) and higher nutrient concentrations for regeneration establishment and growth (Van Lear et al. 2000; Lilja-Rothsten et al. 2008). Higher disturbance frequencies reduce log size (Takahashi 1994).

The coverage of the following three main types of microsites differs according to the storm and stand characteristics. According to the published data, pits cover 1–16% of the stand area, mounds 1–36%, dead wood 7–23% and intact ground, including already existing microsites such as stones, depressions etc., 45–89% (e.g. Nakashizuka 1989; Schaetzl et al. 1989; Kuuluvainen and Juntunen 1998; Peterson and Pickett 2000; Ulanova 2000; Narukawa and Yamamoto 2003; Kuuluvainen and Kalmari 2003; Šamonil et al. 2010).

Wind-related microsites can be considered as relatively unstable in time: mineral soil erodes from mounds and the root system eventually collapses due to decay, and pits often fill with litter and mineral soil, eroding from the pit edges and partly from the mounds (Putz et al. 1983; Beatty and Stone 1986; Nakashizuka 1989; Peterson et al. 1990). Woody debris, either standing or lying, goes through different decay stages, getting literally less stable and offering variable mineral nutrients concentrations which are not always available for uptake by seedlings (Harmon et al. 1986; Narukawa and Yamamoto 2003; Zielonka 2006; Palviainen et al. 2010a, b). This also results in the previously mentioned delayed storm effects such as retarded

Table 1 Microsite characteristics with potential influence on regeneration establishment and growth, and consequences for tree species with different regeneration strategies (Beatty and Stone 1986; Carlton and Bazzaz 1998b; Clinton and Baker 2000; Harrington and Bluhm 2001; Lüscher 2002; Šamonil et al. 2010)

	Microsite characteristics				Regeneration strategies	
	Intact mineral soil	Pits	Mounds	Dead wood	Pioneer	Shade-tolerant
Bare mineral soil	−	+	+	−	+	±
Elevation (light conditions, competition)	−	−	+	+	+	±
Stability	+	±	−	−	+	+
Erosion	−	−	−		−	−
Flooding	±	+	−	−	−	−
Drought	±	+	−	−	−	−
Nutrients	+	+	−	+	+	+
pH	+	−	−	−	−	−

falling trees. Microsites that were not initially recorded as such may thus experience the indirect storm impact and eventually become part of a pit, mound or (soil covered by) log.

These and several other factors characterising storm-related microsites (Table 1) are potentially important for seedling establishment and growth, depending on the species life history strategies and the prevailing site conditions such as soil type and moisture of the area.

Salvage logging is a common policy after wind and fire disturbance. Depending on the salvage intensity and strategy, stands can become more (Lilja-Rothsten et al. 2008; Peterson and Leach 2008) or less (Ilisson et al. 2007) heterogeneous, both in the sense of the amount and structure of retention trees/logs and vegetation response. Generally, dead wood and in some cases also stumps are removed from the forest, obstructing, e.g., Norway spruce (*Picea abies* (L.) Karst.) regeneration (Svoboda et al. 2010). Knowledge of the local conditions, and their interaction with the effects of salvage logging or restoration treatments may help drive regeneration patterns in a certain direction (Peterson and Leach 2008; de Chantal et al. 2009).

Regeneration strategies

Tree functional groups, often categorised based upon the shade-tolerance of species (e.g. Barnes et al. 1998), are assumed to depend largely on radiation levels for their recruitment. This is also how most literature regards successional dynamics: light-demanding pioneer species requiring gaps of sufficient size, i.e. 150–1,000 m^2 (Nakashizuka 1989), and depend on major disturbances for their establishment. In contrast, shade-tolerant species, being able to survive under the canopy for a long time waiting for gap formation and then resume growth (Metslaid et al. 2005a, 2007; Nagel et al. 2010), will benefit from the reduced competition after single wind-thrown trees under gap-phase dynamics. In this sense, the impact of an intermediate severity disturbance regime has received relatively little attention as compared to these extremes (Papaik and Canham 2006; Hanson and Lorimer 2007), whereas Polyachenko et al. (in preparation) conclude that intermediate damage levels induce the most unstable microsite conditions considering the high chances of delayed storm effects here.

However, other factors need to be considered besides radiation. Šamonil et al. (2010) point out in their review that the proportion of the area covered by pit-and-mound complexes, and the often implicitly linked increased radiation levels, can hardly be related to the disturbance regime in terms of wind force. Many storm-induced microsites, especially dead wood (Zielonka 2006; Kathke and Bruelheide 2010), but in some cases also more stabilized pits and mounds (DeLong et al. 1997), become available for regeneration only several years to decades after formation, to some extent decoupling light availability from substrate availability (Kathke and Bruelheide 2010). The focus of most studies on gaps and light conditions, combined with the often overlooked longevity of storm-induced microsites, implies that the role of the latter in providing suitable, well-located establishment sites may have been recently underestimated (e.g. in Kathke and Bruelheide 2010). Also, several unexpected findings point in the direction of factors other than radiation, such as substrate suitability, nutrient availability, below-ground competition, and regeneration strategy (e.g. Lyford and MacLean 1966; Kuuluvainen 1994; Arevalo et al. 2000; Narukawa et al. 2003; Nagel et al. 2006; Iijima et al. 2007).

Microsite colonisation

The colonisation of a microsite—if not captured by advance regeneration or any form of sprouting, excluding colonisers—depends on its relative suitability as establishment substrate, pre-storm spatial distribution of the species in the canopy stage, tree species dispersal traits, seed amount and periodicity, seeds stored in the seed-bank and distance to potential seed sources (Asselin et al. 2001; Papaik and Canham 2006; Iijima et al. 2007) as well as species establishment traits such as seedling root systems posing specific requirements (Narukawa and Yamamoto 2003). It may take decades before storm-induced microsites offer adequately solid establishment locations, whereas the light regime meanwhile may have become less favourable (Nakagawa et al. 2003). Nevertheless, the relative proportion of regeneration found on wind-induced microsites when compared to undisturbed substrates indicates that these may be important for further successional patterns. For example, in the boreal zone of Europe, Kuuluvainen and Juntunen (1998) found that regeneration in pits and on mounds accounted for 60 and 91% of total regeneration of Scots pine (*Pinus sylvestris* L.) and silver birch (*Betula pendula* Roth) respectively, while these microsites covered only 3.4% of the area. For comparison, after fire, Scots pine has been found to regenerate best on level ground and in the surroundings of decayed wood (Lampainen et al. 2004). Norway spruce regeneration after storms performs better on mounds and dead wood than on undisturbed substrates (Hofgaard 1993; Ulanova 2000). This trend is confirmed by Kuuluvainen and Kalmari (2003), who found that Norway spruce regeneration occurred for 63% on storm-created microsites which covered 28% of the area and more recently by Svoboda et al. (2010) who found that spruce regeneration on dead wood and stumps ranged between 35 and 80%, whereas these microsites covered 4–9% of the area. In hemiboreal forests in Japan, due to undergrowth domination by dwarf bamboo, many species such as *Abies sachalinensis* (F. Schmidt) Mast., *Picea jezoensis* (Siebold & Zucc.) Carr. and *P. glehnii* F. Schmidt are often restricted to logs for their regeneration (e.g. Takahashi et al. 2000; Noguchi and Yoshida 2004; Iijima et al. 2007). Especially, the small seeds of pioneers are more favoured by elevated sites (Takahashi 1994; Lusk and Kelly 2003; Sayer 2006), such as decaying dead wood, than large-seeded species (with larger tap roots better able to establish on soil; Narukawa et al. 2003) for their establishment. Also, in eastern Canada, *Picea glauca* (Moench) Voss, *Abies balsamea* (L.) Mill. and *Thuja occidentalis* L., three conifer species ranging from light-demanding to shade-tolerant were all found to prefer establishment on highly decayed logs (Simard et al. 1998).

Logs should supply sufficient water-holding capacity (Harmon et al. 1986), stability, root penetration ease and plant available nitrogen (Arthur and Fahey 1990; Keenan et al. 1993), circumstances which are often provided in more advanced stages of decay (Takahashi et al. 2000; Iijima et al. 2007), although in some cases seedlings also germinated on fresh hard logs (Iijima and Shibuya 2010). Nevertheless, thick moss layers, increasing in height with wood decay, could be detrimental for seedling establishment (Sugita and Nagaike 2005; Iijima et al. 2007). Relatively more regeneration is found on larger diameter logs (Takahashi 1994).

Careful consideration of conditions is required, as in wet forest types mounds and logs will provide preferable establishment substrates while pits are flooded (e.g. Hörnberg et al. 1997), whereas in dry forest types pits may provide with moist mineral soils the ideal circumstances for tree colonisation. In this respect, the species of the fallen tree causing the pit-and-mound complex also matters: low mounds resulting from birch and aspen uproots provide more favourable conditions to Norway spruce regeneration, whereas birch regeneration prefers the high mounds of spruce uproots (Vodde et al. 2010). The same authors found that the shallow pits of spruce were generally preferred for regeneration establishment and growth, above the deep pits of birch and aspen windthrow.

In spite of the expectations, pioneer tree species sometimes do not establish in the larger openings, which can be attributed to various factors, such as suppression by the surviving pre-storm vegetation (Castelli et al. 1999), sprouting of snapped or uprooted trees (Peterson and Pickett 1991; Clinton and Baker 2000), rapid growth of understory plants (Castelli et al. 1999; Arevalo et al. 2000), a high proportion of surviving advance regeneration (Nagel et al. 2006), or a high proportion of pioneers killed and unable to recover (Arevalo et al. 2000). However, in some other cases, the advance regeneration is surpassed by pioneers after a couple of years, even though this may be temporary (Peterson and Pickett 1995). Also, Leemans (1991), referring to a Norway spruce forest in Sweden, states that gaps are closed by new individuals rather than by accelerated growth of advance regeneration. Thus, timing of tree establishment seems to be of crucial importance for subsequent successional development (e.g. Ishizuka et al. 1998).

Growth

Seedlings may have different requirements for growth than for establishment (Takahashi et al. 2000; Mori et al. 2004; Iijima et al. 2007). Although the small seeds of pioneers would be more favoured by elevated sites and bare mineral soils for their establishment (Sayer 2006), light availability may be more important than substrate in the proceeding stages from sapling to canopy (LePage et al. 2000; McGee 2001). In Hiura et al. (1996), periods of suppressed growth, derived from tree ring width of canopy trees, lasted for much shorter periods in pioneer species *Betula ermanii* Cham. than in shade-tolerant coniferous species, which indicates the lower shade-tolerance threshold of pioneers. This is also confirmed by Nagel et al. (2010). Thus, in the case of intermediate severity disturbance where gaps close relatively fast, pioneers depend on their growth speed and in some cases on subsequent disturbance for final recruitment/sufficient growth. The ability to reach the canopy by fast-growing sprouts, either from roots or from the remaining stump, is more pronounced in light-demanding species than in shade-tolerant species, e.g. aspen (*Populus tremula* L.) and silver birch in the boreal zone (Mochalov et al. 2005; Ruokolainen and Salo 2006; Zhul'kov et al. 2007). In windthrow areas, competition from undisturbed vegetation is higher than in burned areas, which may explain the relative unimportance of sprouting for stand development (e.g. Peterson and Pickett 1991). Nevertheless, species such as *Acer rubrum* L. and *Quercus rubra* L., which are more shade-tolerant, may also depend on sprouting for their maintenance in the canopy (Crow 1988; Cooper-Ellis et al. 1999).

For both pioneers and shade-tolerant species, elevated sites such as dead wood should provide suitable conditions for assimilation (Harmon 1987) and root growth (Iijima et al. 2007). In western US, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) seedlings developed best (diameter growth) in elevated microsites with medium soil penetration (Burney et al. 2007). However, Quine et al. (1991) report that, in the UK, roots of Sitka spruce (*Picea sitchensis* (Bong.) Carrière) seedlings may not develop a uniform root system in the proximity of a stump. Nevertheless, roots of some species are able to adapt to the microsite conditions, e.g. by developing stilt roots (Canham et al. 1996; Narukawa and Yamamoto 2003; Sugita and Nagaike 2005). Other species, such as black birch (*Betula lenta* L.), are able to adapt to more shaded conditions, e.g. by increased leaf ratio (Carlton and Bazzaz 1998a).

Advance regeneration of shade-tolerant species, less dependent on bare mineral soil and elevated sites, show little diameter increase under shaded conditions. Once released, the diameter of advance regeneration increases linearly with age, at the same rate as if the conditions had been unshaded from the beginning, with height growth reacting similarly, though with some delay (Metslaid et al. 2005b; Schulze et al. 2005; Metslaid et al. 2007).

Mortality

Storm-induced microsites tend to be unstable substrates due to high erosion risk, extreme circumstances and decay (Putz et al. 1983; Beatty and Stone 1986; Nakashizuka 1989; Peterson et al. 1990; DeLong et al. 1997; Ulanova 2000; Mori et al. 2004; Ilisson et al. 2006, 2007). This means that, after the establishment and during growth, saplings on these locations still have a higher mortality risk than saplings on other substrates. Nevertheless, in a study in a red spruce (*Picea rubens* Sarg.)–balsam fir (*Abies balsamea* (Mill.) L.) forest on well-drained soils in Canada, the largest trees were found on old mounds (Lyford and MacLean 1966). Intact sites also demonstrate a shifting age pattern: due to falling dead wood and competition of understory vegetation, advance and post-storm regeneration damage or mortality can become high. Furthermore, the presence of dead wood may attract pathogenic fungi which are harmful for regeneration (Mori et al. 2004).

According to Hiura et al. (1996), there is a trade-off between seedling growth rate and mortality, implicating higher mortality under pioneer species. In northern Scandinavia, Jonsson (1999) found that Scots pine was more sensitive to site conditions (frost holes, vegetation, large stumps and logging residuals coverage) compared to Norway spruce in the establishment phase, which was translated into higher mortality and negative correlations for pine. In contrast, Norway spruce was more sensitive to site conditions than Scots pine during the early growth phase, resulting in greater height variation in spruce (Jonsson 1999). In Canada, high litter accumulation also increased winter mortality of white spruce (*Picea glauca* (Moench) Voss) on the preferred establishment sites' mineral soil and rotten logs (DeLong et al. 1997).

Microsites in the perspective of different theories on species coexistence and successional development models

The direction of succession and species coexistence have been related to disturbances. The initial composition theory, first proposed by Egler (1954), assumes that all species which come to dominate at a certain stage in succession are present right after the disturbance event, either as seed, sprouts, surviving advance regeneration or canopy trees. Succession is a combination of interactions of new trees and plant species appearing and recovery (sprouting, crown expansion, etc.) of surviving trees (Castelli et al. 1999). As we have discussed in the previous sections, much also depends on the dispersal strategies of tree species, and their ability to germinate, survive and grow on the available microsites.

Kubota and Hara (1996) propose the boundary condition hypothesis for species coexistence in the hemiboreal forest: different recruitment traits in the sapling phase (boundary conditions for adult tree growth dynamics) attributed more to the persistence of each species than did interspecific competition in the canopy phase. Ishizuka et al. (1998) add the timing of tree species: when tree seed production coincides with a significant decrease in the forest floor-covering shrub, recruitment is more likely to be a success. However, it is unclear whether this supports the initial composition theory or points more in the direction of the intermediate disturbance hypothesis (Connell 1978), where species emerge when the circumstances are right. Nevertheless, much depends on the disturbance regime. Gap dynamics caused by small perturbations continuously rejuvenate the forest, still maintaining the dominance of shade-tolerant species (Gromtsev 2002). Hereby, the species of gap-creating trees matter for the species of gap fillers: in old-growth forests mostly the same species (self-maintenance), sometimes benefiting other species (Runkle 1981). The latter result was also found in pits and on mounds after more severe storm events in Estonia (Vodde et al. 2010). In these intermediate to large storm events, where light conditions increase for a longer time period, microsites gain more importance. Those species that best survive a storm tend to show rapid growth afterwards, whereas the microsites created provide a new range of establishment sites for seedlings of different, often pioneer species. This may result in a mosaic of patches in different stages of succession (Arevalo et al. 2000), supporting species coexistence on a larger spatial scale.

Typically, those studies not mentioning or attributing only minor importance to storm-induced microsites in determining successional patterns in boreal forests focus on gap dynamics in old-growth forests, whereas studies acknowledging their significance are related to intermediate or severe events. One straightforward way to determine the impact of microsites is geo-referencing individual seedlings in order to calculate distances to microsites and other stand features (Burney et al. 2007).

Conclusions

Storm-induced microsites are mainly important for regeneration patterns in boreal forest after intermediate to catastrophic storm events. However, their importance should always be considered in relation to the storm severity, causing changes in resource levels and growth conditions, and influencing extrinsic factors such as frost heaving, erosion and browsing. Also, the dispersal traits of available tree species, including sprouting and response of surviving trees, such as canopy expansion, should be considered in evaluating microsite importance in individual cases.

In intermediate to severe windstorm events, pioneer tree species generally profit most from the additional offer in microsites, requiring bare mineral soil and elevated locations for their establishment and growth. Under gap dynamics, shade-tolerant species benefit from dead wood and elevated locations as these offer safe sites in stands with abundant understorey vegetation.

It is important to consider a stand's disturbance history and site conditions when assessing wind-induced microsite importance. Life history traits of individual species occurring in the area determine whether the species is able to wait for the right moment in the sequence of available circumstances in order to maintain itself in the stand. The timing in establishing on suitable substrates and profiting from increased light, water and nutrient levels is crucial.

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II

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Regeneration development 4–5 years after a storm in Norway spruce dominated forests, Estonia

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Abstract

The regeneration patterns in wind-damaged areas are largely influenced by damage severity and varied microrelief. Regeneration was studied in *Picea abies* dominated stands with total and partial canopy destruction and in harvested areas in *Myrtillus* and *Filipendula* site types in Estonia 4–5 years after a storm, examining particularly the influence of microsites on regeneration establishment and growth. The seedling densities of regeneration were highest in harvested plots compared to heavily and moderately damaged areas. The seedling densities were lowest on mounds and highest in pits among microsites in heavily and moderately damaged sites. The most common tree species regenerating in pits were birch (*Betula pendula* Roth., *Betula pubescens* Ehrh.) and alder (*Alnus glutinosa* (L.) J. Gaertn.). Birch and alder seedlings that survived to 2005 were taller in 2004 than those that died. Trees were also taller with lower regeneration density. Spruces (*Picea abies* (L.) Karst.) did not prefer any particular microsite, but those growing in pits were smaller than those in other microsites. The plots harvested regenerate more rapidly with hardwood species.

Keywords: Windthrow; Regeneration; Pit and mound; Wind severity; Microsite

1. Introduction

Windthrow is an important driver of gap dynamics in European temperate and boreal forest ecosystems (Ulanova, 2000). The consequences of wind disturbance can be quite varied, depending on forest structure and composition and the characteristics of each storm (Lindemann and Baker, 2001). One of these characteristics, disturbance severity, may however provide a way to organize such daunting variation among disturbances. Indeed, in at least two recent conceptual models of forest disturbance and recovery, those of Frelich (2002) and Roberts (2004), severity is one of the primary axes for differentiating disturbance effects. Disturbance severity determines which component of pre-disturbance vegetation survives or is killed. Consequently, severity can influence regeneration in two ways: (1) the physical change in light and nutrient availability; (2) the availability of seed trees, seedbanks or advance regeneration for seedling establishment.

Regeneration via seed in storm-damaged areas depends on patches suitable for germination, establishment, and survival (Ulanova, 2000; Ruel and Pineau, 2002). Environmental conditions within the gap vary greatly, and can positively or negatively influence each of these stages. Light availability, for example, increases most north of gap center (in the northern hemisphere, De Chantal et al., 2003), which could alter the community structure (Hytteborn and Packham, 1987; Dyer and Baird, 1997; Drobyshev, 2001). Uprooted trees increase environmental heterogeneity because of the creation of a pit–mound microtopography by the relocated root systems and because of the freed space on the forest floor (Greenberg and McNab, 1998; Ulanova, 2000). Pits, defined as the areas where mineral soil has become exposed; mounds, defined as the rootplates that have turned into a vertical position; intact, forest floor and decaying logs provide areas with very different microclimates and conditions (Peterson et al., 1990; Bazzaz, 1996; DeLong et al., 1997; Clinton and Baker, 2000; Peterson and Pickett, 2000; Ulanova, 2000; Ruel and Pineau, 2002), which in turn may increase biodiversity at the stand level (Lässig and Močalov, 2000; McAlister et al., 2000).

An important management question after windstorms is whether to leave or harvest the windthrown trees. General forestry practice prescribes salvage harvesting after heavy storm damage because of the fear of insect outbreaks and fire hazard. Both natural and artificial regeneration has also been

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thought to establish more efficiently on cleared sites (Karr et al., 2004; Beschta et al., 2004). However, the validity of such assumptions has recently been questioned in North America (Lindenmayer et al., 2004; Donato et al., 2006), generating much controversy.

Our objective in this study was to find out how disturbance severity and management influence recovery. The following hypotheses were formulated: (1) in accordance with the site heterogeneity, recruitment tree species diversity is greater in uncleared areas; (2) small-seeded species germinate better in exposed mineral soil (pits and mounds), large-seeded species need a more stable environment (intact soil); (3) pioneer species establish and grow better in more severely damaged areas, cleared areas, on mounds and to a certain extent in pits, while shade-tolerant species prefer uncleared, partly damaged areas and vegetated intact forest floor; (4) because of soil instability, seedlings on mounds will show the highest mortality figures; (5) in addition to soil stability, seedling survival depends on the individual's height and seedling densities.

2. Material and methods

The study areas are situated in Tudu (59°11′N, 26°52′E) and Halliku Forest Districts (58°43′N, 26°55′E) in Eastern Estonia. Thunderstorms occurred in Tudu in July 2001 and Halliku in July 2002, the amounts of dead wood reaching over 600 m^3 per hectare (Ilisson et al., 2005a). In both areas Norway spruce (*Picea abies* (L.) Karst.) dominates in mixed forests. Accompanying tree species are silver and downy birch ((*Betula pendula* Roth. and *Betula pubescens* Ehrh.), European aspen (*Populus tremula* L.) and black alder (*Alnus glutinosa* (L.) J. Gaertn.). Both Forest Districts are located in flat land and influenced by drainage. The study areas were established in the *Myrtillus* and *Filipendula* site types (Lõhmus, 2004). The *Myrtillus* site type is most commonly represented in Estonia (approximately 20% of the state forest area), while the *Filipendula* site type makes up approximately 5% of the state forest area (Lõhmus, 2004). Gley and gleyed podzolic soils occur in both Forest Districts. The age of the stands varied between 110 and 160 years. Previous publications concerning the study areas consider post-disturbance forest structure (Ilisson et al., 2005a), the decomposition dynamics of dead wood (Köster, 2005) and understorey vegetation dynamics (Ilisson et al., 2006).

Data from 12 study plots (40 m long × 20 m wide) were used, the plots being located in areas of three different disturbance severity classes—the areas with (i) partial canopy destruction (moderately damaged), (ii) total canopy destruction (heavily damaged) and (iii) areas that were logged after wind damage (harvested). The heavily and moderately damaged study plots were established in protected compartments (dead wood was left on site); and the logged plots were in the surrounding management forests of the Tudu and Halliku Forest Districts. Each "treatment" had four replicate transects. The plots were established a year after the storms.

Rubus saxatilis, *Oxalis acetosella*, *Athyrium filix-femina*, *Hepatica nobilis*, *Geum rivale* and *Vaccinium myrtillus* were most abundant herb-layer species in 2004 in moderately damaged study plots. In heavily damaged areas, *Thelypteris phegopteris*, *Oxalis acetosella*, *Epilobium montanum*, *Rubus saxatilis* and *Vaccinium myrtillus* dominated the herb layer. *Epilobium angustifolium*, *Rubus idaeus*, *Ranunculus repens* and *Epilobium montanum* dominated in harvested plots (Ilisson et al., 2006). In the moss layer, *Rhytidiadelphus triquetrus*, *Plagiomnium* spp., *Hylocomium splendens*, *Pleurozium schreberi* and *Sphagnum* spp. dominated in heavily damaged areas while in moderately damaged areas, the most common mosses were *Rhytidiadelphus triquetrus*, *Plagiochila asplenioides*, *Pleurozium schreberi*, *Hylocomium splendens* and *Sphagnum* spp. *Rhytidiadelphus triquetrus*, *Plagiomnium* spp., *Hylocomium splendens*, *Sphagnum* spp. and *Eurhynchium angustirete* were found in logged plots. The nomenclature follows the *Key-Book of Estonian Plants* (Leht, 1999).

The regeneration surveys were performed in two subsequent years (autumn 2004 and autumn 2005) in pits, on mounds and on 10 1 m^2 squares which were established on undamaged forest floor along the middle transect of each plot (Fig. 1). The species of each uprooted tree was recorded and its mound width and pit depth measured with a tape-measure. The perimeter points of pits and mounds and locations of seedlings were mapped using a surveyor's compass and electronic distance and height meter Vertex III (Haglof, Inc.) and areas of pits and mounds were calculated using the circle sector area formula to determine the density of seedlings.

The number of tree seedlings was recorded by species, and seedling height was measured. The height increment was calculated as the difference in height in successive surveys. Location (pit, mound or undamaged) and species were determined. Pre- and post-disturbance seedlings and sprouts were separated by a visual survey, and only data from seedlings established after the storm were used in statistical analyses (Tables 1 and 2). Seedling density was found by dividing the number of trees by the area of the microsite, the result being categorized into three density classes (I class <5 seedlings; II class <10 seedlings; III class ≥10 seedlings per m^2). The pre-disturbance regeneration comprised approximately 7% of all regeneration trees in moderately and heavily damaged areas in 2004. When only regeneration trees on intact forest floor were considered, the given proportion was 27%.

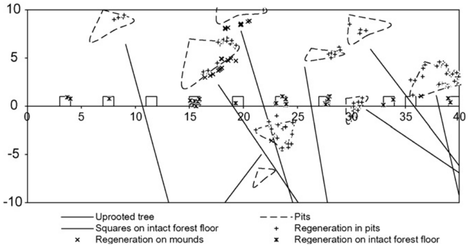

Fig. 1. An example of a study plot in a heavily damaged area. The uprooted trees, pits, intact forest floor squares and regeneration trees have been mapped using the *x*, *y* coordinate system.

Table 1
Status of tree recruitment in 2004 (numbers refer to individuals that survived to 2005, categorized by species)

	Pit		Mound		Intact		Harvested	
	Surviving	Dead	Surviving	Dead	Surviving	Dead	Surviving	Dead
Aspen	5	13	1	–	5	8	26	12
Birch	94	130	5	3	17	7	77	93
Spruce	26	15	27	2	33	2	6	–
Alder	65	135	–	–	6	2	–	–
Rowan	12	15	51	34	37	21	9	1

The data of trees in pit, mound and intact microareas comes from moderately and heavily damaged plots.

Kruskal–Wallis ANOVA was performed first to find the effect of disturbance severity and microsite on seedling density. The Mann–Whitney *U* test was then performed on seedling densities among microsites to test for pairwise species microsite preference.

The increment of recruitment trees was logarithmically transformed and nested ANOVA was used to determine the influence of study plot, soil type (gley or gleyed podzolic), storm year (2001 in Halliku Forest District and 2002 in Tudu Forest District), damage severity (heavily or moderately damaged), microsite (pit, mound or intact forest floor) and recruitment tree species (birch, spruce, black alder, aspen, rowan) on increment. One-way ANOVA was used to examine the influence of microsite, pooled seedling density classes on microsite and density classes of particular species being studied. The Tukey test was used to find differences within the factor groups.

Logistic regression was used to examine factors that influence the mortality of tree seedlings. The 2004 heights of seedlings that lived to 2005 and those that died by 2005 were compared. The probability of surviving was tested as a logistic function of tree height and the following characteristics: (i) recruitment tree species, (ii) microsite, (iii) damage severity, (iv) soil type, (v) year of storm, (vi) pooled seedling density on microsite and (vii) density of a particular species on microsite. Analyses were also performed with recruitment tree species separately.

The program Statistica 6 (StatSoft, Inc.) was used for data analysis.

3. Results

Species composition of seedlings differed in areas with different damage severity and among microsites (Table 3). The Shannon diversity was highest in areas with moderate damage, followed by heavily damaged areas. The least diversity and eveness were found in harvested plots, where birch strongly dominated (Fig. 2). Pits showed the highest diversity among microsites. Species were also more evenly distributed in pits.

The damage severity had significant influence on pooled total seedling density and densities of aspen, birch, spruce, alder and rowan (Kruskal–Wallis tests, $p < 0.001$ in all cases). The pooled total seedling density and density of aspen seedlings were higher in harvested plots than heavily damaged and moderately damaged plots. The density of birch was highest in harvested plots and lowest in moderately damaged plots. Spruce was least abundant in harvested areas. Rowan

Table 2
Mean tree heights (in cm) and standard errors (S.E.) of tree recruitment in 2004

	Pit		Mound		Intact		Harvested	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Aspen								
Surviving	115	33.05	40	–	86	13.36	61.7	4.98
Dead	22.3	7.55	–	-	80.6	13.9	55.4	10.54
Birch								
Surviving	21.3	2.08	32.8	11.9	39	8.26	28.4	2.53
Dead	9.71	0.6	8.33	3.33	45	20.35	18.4	1.66
Spruce								
Surviving	18.2	1.69	34.81	4.4	62	7.56	29.2	7.12
Dead	26.06	4.33	18	7	20	5	–	–
Alder								
Surviving	6.9	0.36	–	–	226.7	59.1	–	–
Dead	5.3	0.2	–	–	32.5	2.5	–	–
Rowan								
Surviving	85.6	12.73	72.3	6.16	116.9	13.56	76.7	17.02
Dead	39.9	8.17	70.5	9.45	46.7	15.45	10	–

The data on trees in pit, mound and intact microsites comes from moderately and heavily damaged plots.

Table 3
Shannon diversity (H') and evenness (E_h) of five recruitment tree species (based on seedling densities)

	H'	E_h
Damage severity		
Harvested	0.741404	0.53481
Heavy	1.1358	0.705712
Moderate	1.169148	0.726433
Microsite		
Pit	0.81853	0.508581
Intact	0.595424	0.369958
Mound	0.545539	0.393523

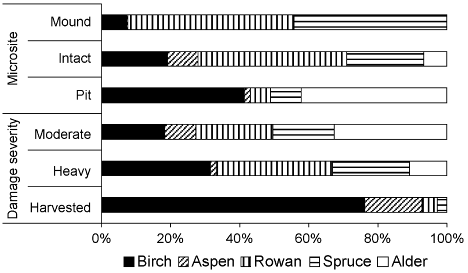

Fig. 2. Composition of seedlings (based on seedling density) in three different microsites (pit, mound, intact) and areas with different damage severity (heavy, moderate, harvested) in 2004.

densities were highest in heavily damaged areas and alder on moderately damaged areas (Fig. 3).

Microsite significantly affected pooled total densities (Kruskal–Wallis tests, $p = 0.0055$), as well as the densities of birch ($p < 0.001$) and alder ($p < 0.001$) (Fig. 4). The pooled total seedling density was the lowest on mounds compared to pits and intact area. Birch had highest seedling densities in pits. Alder was mostly in pits as well, only 8 trees being found on intact ground. Seedlings of other species did not show any preferences among microsites.

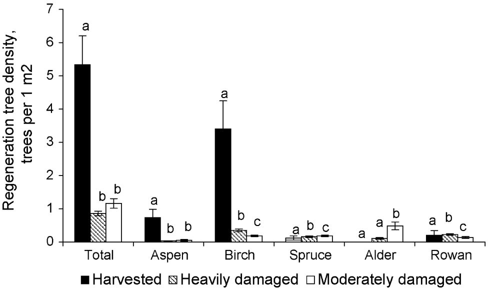

Fig. 3. Mean regeneration tree densities in areas with different damage severity in 2004. Standard errors of means are given as error bars. Letters above bars show the interspecific difference between areas with differential damage.

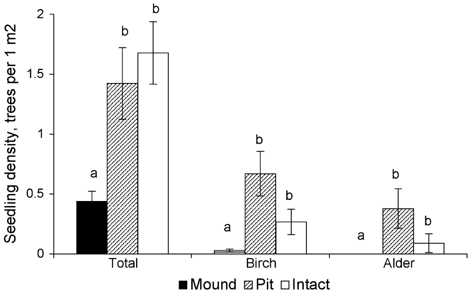

Fig. 4. Mean regeneration tree densities in three different microsites in moderately and heavily damaged areas in 2004. Standard errors of means are given as error bars. Letters above bars show the interspecific difference between microsites.

There was no significant influence of transect, damage severity, soil type or storm year on recruitment tree growth, but microsite and tree species showed significant influence (nested ANOVA, see Table 4**).** The incremental growth of birch and rowan was significantly greater with lower seedling density. Birch was most dense on mounds as against intact areas and pits, while rowan was least dense on intact areas (one-way ANOVA, see Table 5).

Survival of recruitment trees was influenced by seedling height and seedling species (logistic regression, $p < 0.001$ in both cases). Birches surviving to 2005 were significantly taller in 2004 than those that died by 2005 ($p < 0.001$). Surviving birches were also taller on gleyed podzolic soils ($p = 0.0187$) and on areas where birch seedling abundance was lower ($p = 0.0354$).

Survival of spruce did not depend on tree height, but the height differed among microsites ($p = 0.0024$). The tallest spruces were found on intact microsites and the shortest were in pits. Spruces were also taller in heavily damaged areas than those moderately damaged ($p = 0.0406$).

Surviving alders were taller in heavily damaged areas ($p < 0.001$), on gleyed soils ($p < 0.001$), with lower total seedling abundance ($p < 0.001$) and with lower alder seedling abundance ($p < 0.001$). Rowans and aspens surviving to 2005 were only significantly influenced by tree height ($p = 0.0081$ and $p < 0.001$ respectively). Those that were taller in 2004 had more chance of surviving to 2005.

Pit depth and mound thickness differed among uprooted species (Kruskal–Wallis tests, $p < 0.001$ in both cases). Uprooting of Norway spruce created the shallowest pits and thinnest root plates (Fig. 5). No significant differences in the numbers of seedlings on different uprooted tree species were found, although a slight trend for hardwood mounds to have more seedlings than spruce can be observed. In general, seedling abundance was relatively low on mounds.

4. Discussion

The recovery of a stand in the uncleared areas may be influenced by the very heterogeneous microtopography. The

Table 4
Summary of nested ANOVA on seedling increment

No. of analysis	Random effects	Sums of squares	Degree of freedom	Mean squares	Den. syn. error d.f.	Den. syn. error MS	*F*	*p*
I	Transect	29.219	7	4.17	15.05	2.5540	1.63	0.2004
	Microsite (Transect)	42.310	15	2.82	43.00	1.2249	2.30	0.0166
	Species (Transect × Microsite)	49.263	35	1.41	297.00	0.5598	2.51	0.0001
II	Severity	2.926	1	2.93	4.43	3.6917	0.79	0.4191
	Microsite (Severity)	18.759	4	4.69	21.33	2.4467	1.92	0.1445
	Species (Severity × Microsite)	68.747	17	4.04	332.00	0.5726	7.06	0.0001
III	Soil	0.070	1	0.07	4.40	4.1571	0.02	0.9026
	Microsite (Soil)	18.977	4	4.74	22.71	2.9205	1.62	0.2025
	Species (Soil × Microsite)	107.224	18	5.96	331.00	0.5704	10.44	0.0001
IV	Storm year	0.611	1	0.61	4.08	4.5568	0.13	0.7325
	Microsite (Storm year)	19.207	4	4.80	22.73	2.7383	1.75	0.1731
	Species (Storm year × Microsite)	90.313	18	5.02	331.00	0.5882	8.53	0.0001

pits, mounds and intact forest floor can vary greatly in nutrient level, soil moisture, light and temperature (Peterson et al., 1990; Bazzaz, 1996; DeLong et al., 1997; Carlton and Bazzaz, 1998; Clinton and Baker, 2000; Peterson and Pickett, 2000; Ulanova, 2000; Ruel and Pineau, 2002), which implies greater species diversity in uncleared areas, as confirmed in our study.

The harvested plots exhibit the highest degree of disturbance. Harvesting machines seriously damage the ground and forest vegetation after windthrow (Lüscher, 2002; Small and McCarthy, 2002) including advanced regeneration (Močalov and Lässig, 2002). When not damaged, advance regeneration can potentially dominate recovery of windthrow areas (Hytteborn and Packham, 1987; Dyer and Baird, 1997; Peterson, 2000; Ulanova, 2000; Drobyshev, 2001; Schönenberger, 2002; Wohlgemuth et al., 2002; Rammig et al., 2006). Thus harvesting is likely to alter species composition for many decades by increasing the representation of pioneer species such as aspen and birch in our study. This trend is also confirmed by several other studies (Schönenberger, 2002; Močalov et al., 2003).

The seedling densities were greater in harvested plots than in heavily and moderately damaged areas. Schönenberger (2002) and Wohlgemuth et al. (2002), who also compared uncleared and harvested plots, achieved similar results. Schönenberger (2002) suggested that fallen logs in uncleared areas may be an obstacle to seedling establishment during the first decades. Such negative effects could occur through influences on germination, establishment or growth. Surprisingly, there were no differences between moderately and heavily damaged stands in species diversity and seedling densities, increment growth and height. The amount of light reaching the ground should be considerably less in moderately damaged areas because of the remaining partial canopy, which should reduce the growth rates of regenerating seedlings (Harrington and Bluhm, 2001). One explanation of the apparent similarity between the two damage classes may be that the extremely large number of fallen trunks and coarse debris in heavily damaged areas provides shade (Ilisson et al., 2005a). If this is so, a faster growth rate is to be expected in heavily damaged areas when regeneration exceeds the height of the fallen trunks.

Table 5
Summary of one-way ANOVA on seedling increment

Fixed factor	Sums of squares	Degree of freedom	Mean squares	*F*	*p*
Birch					
Microsite	3.3051	2	1.6525	3.785	0.0256
Density classes	4.5850	2	2.2925	5.391	0.0058
Rowan					
Microsite	22.7817	2	11.3908	16.789	0.0001
Density classes	11.5071	2	5.7536	4.8392	0.0099

Crushed vegetation and eliminated moss carpet due to windthrow can efficiently contribute to the establishment of seeds (DeLong et al., 1997; Wohlgemuth et al., 2002). As pits are the areas in the forest floor where mineral soil is exposed, they provide good opportunities for the germination and establishment of small-seeded species like birch and alder in our study (see also Peterson et al., 1990; Bazzaz, 1996; Kuuluvainen and Juntunen, 1998; Peterson and Pickett, 2000; Ulanova, 2000), whereas spruce (intermediate-sized seeds) and rowan (large-seeded) showed indifference to microsite.

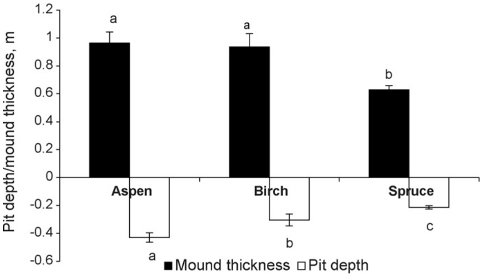

Fig. 5. Pit depth and mound thickness depending on the tree species of the uprooted tree. Letters above bars show the significant differences between species.

However, the environmental conditions of pits are quite unfavorable for seedlings. Clinton and Baker (2000) suggested that tree-fall pits have excessive soil moisture content and risk of seasonal flooding. During spring or after a large precipitation event, seedlings in pits can suffer because of overflow (Harrington and Bluhm, 2001). Lüscher (2002) reported that the water content also increases because of the lack of interception by canopy trees. At the same time, the temperatures increase near the soil surface. Thus pits can have very wet or very dry phases, depending on the weather conditions, a possible reason for the low density of some species in pits.

Survival of seedlings in tree-fall pits can be also problematic because of greater accumulation of litter and burial under soil slides falling from mounds during heavy rains (Bazzaz, 1996; Ulanova, 2000; Harrington and Bluhm, 2001). Peterson et al. (1990) point out that the pits accumulate litter differentially from part to part. For example, in our study the accumulation during the third year after the storm decreased in the middle and outer edge of pit, but the erosion from the mound increased. Harrington and Bluhm (2001) noted that every seedling not located near the periphery of the windthrow pit was buried sooner or later. The success of seedlings that germinate in pits may depend on individual growth rate, since taller trees may survive partial burial. Moreover, the competition within and between tree species is significant.

Norway spruce is one of the few natural tree species in Northern Europe that is able to establish itself in shade and grow into overstory. Spruce density certainly increased with decreasing disturbance severity. Although in our study they were smallest and lowest in density in pits compared to other microsites where birch and alder showed no marked difference, spruce seedlings had the lowest mortality figure of all species in pits. A reason for small seedlings and low densities of spruce in pits could be the later time of establishment because of difficult environmental conditions rather than the lower light availability in pits as suggested by Clinton and Baker (2000).

While the light availability and temperature are highest on mounds (Clinton and Baker, 2000), the regeneration densities were lowest there. This is probably due to soil instability and dryness (DeLong et al., 1997), although this is difficult to establish. In our study, spruce tree-fall mounds were significantly thinner than aspen and birch mounds, which may lead to more rapid erosion. However, seedling density on mounds was too low overall for significant results. In general, some time lapse is probably needed for mound collapse and successful seedling establishment on a more stable surface. The location above the forest floor on mounds might give seedlings a great advantage in ascending to the canopy (Bazzaz, 1996), but this potential microsite benefit has not yet been rigorously demonstrated.

Natural regeneration in uncleared areas is a long-term process (Hytteborn and Packham, 1987; Schönenberger, 2002) and future seedling establishment may increase as fallen logs decompose sufficiently to become good seedbeds (Hytteborn and Packham, 1985; Hofgaard, 1993; Grey and Spies, 1997; Cornett et al., 2001; Wohlgemuth et al., 2002). Observations by Wohlgemuth et al. (2002) suggest that fallen logs provide recruitment opportunities for *Picea abies* seedlings seven years after the storm. Because only 3–4 years have passed since the storm events in our study areas, there was no regeneration found on logs – the fourth microsite in our study – as yet. Future research in these areas, with such a great amount of dead wood, should determine whether logs play an important role as seedbeds. In that case, we expect that the importance of spruce regeneration in uncleared areas will increase over several decades, producing a mixed, uneven-aged stand.

Two other functions of storm-felled trees iare to protect seedlings against animal browsing (Long et al., 1998; Schönenberger, 2002; Krueger and Peterson, 2006; De Chantal and Granström, 2007) and possibly to alter nutrient dynamics. Some of the nutrients from the dead wood leaches into the forest soil (Hyvönen et al., 2000) and can be taken up by regenerating seedlings (Bormann and Likens, 1994; Krankina et al., 1999). Because the decomposition rate is found to be negatively correlated with size of dead wood (Harmon et al., 1986; Harmon and Sexton, 1996; Mackensen et al., 2003), uncleared areas with abundant dead wood may offer nutrient input from leaching for a longer period. Our intention is to examine the soil and dead wood nutrient content in the future to document this process.

5. Conclusions

The recovery of windthrow areas may be strongly influenced by the cumulative severity of natural and anthropogenic disturbances. This study has shown that extent of canopy destruction and logging activities influence regeneration patterns. Such findings agree with the predictions of recent conceptual models (Frelich, 2002; Roberts, 2004) that high severity is likely to produce major changes in species composition. Post-windthrow harvesting increases disturbance severity, and the results reported here demonstrate how small-seeded pioneer species benefit from soil disruption and open areas by rapid establishment, resulting in less seedling species diversity than unharvested windthrow areas.

An important influence on regeneration in uncleared areas is the physical and environmental heterogeneity created by pit and mound microrelief and the large amount of dead wood. While pits are found to be the most suitable establishment locations for small-seeded tree species like birch and alder, the seedling survival is quite poor because of flooding and erosion. The competition between and within species plays an important role. Seed establishment on mounds is less frequent than on other microsites, perhaps because of the instability of the substrate. Establishment is more likely on mounds of uprooted hardwood species that have a thicker root plate than spruce. The variation in species preferences and survival opportunity in different microsites means that the heterogeneity of unharvested post-disturbance stand structure contributes to greater species diversity. Large-seeded and shade tolerant species do not show a particular preference for microsites for germination and growth. The findings of this study do not support the suggestion by Schönenberger (2002) that fallen logs left in situ are detrimental to regeneration by mature-forest species such as spruce.

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SPECIAL FEATURE: ORIGINAL ARTICLE **Feasibility of Silviculture for Complex Stand Structures**

Regeneration in windthrow areas in hemiboreal forests: the influence of microsite on the height growths of different tree species

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Abstract Natural regeneration of windthrow areas is an important issue when planning forestry measures after forest disturbances. Seedling recruitment was investigated in storm-damaged hemiboreal mixed forests in eastern Estonia. The establishment and growth of seedlings from natural regeneration was registered for tree species in soil pits and in mounds of uprooted trees in stands that were either heavily or moderately damaged. Seedling growth is expected to be better in large but shallow soil pits created by uprooted Norway spruce [*Picea abies* (L.) Karst.] and poorer in small but deep pits created by the hardwoods in the area, silver birch (*Betula pendula* Roth.) and European aspen (*Populus tremula* L.). The most abundant regenerating species was birch. Pits hosted larger seedling numbers than mounds, due to soil instability in mounds. Rowan (*Sorbus aucuparia* L.) showed significantly faster growth than the other seedling species. Norway spruce pits were preferred to pits of other species by both birch and spruce seedlings. Black alder [*Alnus glutinosa* (L.) J. Gaertn.] did not show a preference for pits of a certain species of uprooted tree. Both spruce and rowan preferred hardwood mounds over spruce mounds. Storm severity also affected species composition: birch predominantly occurred on pits and mounds in heavily disturbed areas, while spruce was more abundant in the moderately damaged areas. The effects of advance regeneration and surrounding stands on seedling microsite preferences should be considered in future research and subsequent management recommendations.

Keywords Microsite · Norway spruce · Regeneration · Silver birch · Wind disturbance

Introduction

Natural disturbances generate an altered, often more favorable, availability of resources for forest regeneration. The option to rely on natural regeneration following disturbance and the planning of additional management operations in severely damaged forests demand careful analysis to anticipate and respond to complex changes in environmental conditions (Stanturf et al. 2007; Lilja-Rothsten et al. 2008; Peterson and Leach 2008). Wind storms, a frequent disturbance in boreal mixed forests (e.g., Schelhaas et al. 2003; Schlyter et al. 2006), can cause tree failure due to breakage of the main stem, reduction or loss of the crown, or windthrow, which causes the tree to fall to the ground (Everham and Brokaw 1996; Ennos 1997; Ilisson et al. 2005). Storms generally induce increased light levels at ground level and enhanced nutrient and water availability through the removal of biomass from the canopy and understory.

A secondary effect of wind disturbance is the amount of ground disturbance that results from the uprooting of

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windthrown trees. Microsite types created by windthrow mainly consist of pits created by the uprooting of the root plates of windthrown trees, and mounds created by the soil of the upturned root plates. According to Ulanova (2000), the fraction of the total area covered by pits and mounds is 7–12% and can even rise up to 15–25% in large-scale storm-damaged areas. Boles, stumps and fallen branches make up only a minor, unstable share of the regeneration substrates, and their influence decreases over time, so they are therefore often ignored in regeneration studies. However, in poorly drained soils, the elevated portion of the stem may be important for species that can regenerate on organic material, such as birch, and Norway spruce may also utilize this substrate in the later stages of decay (Ulanova 2000; Kuuluvainen and Kalmari 2003). The increased heterogeneity of microsites also increases the regeneration potential in terms of the extended range of conditions available for both the establishment and growth of seedling species (Carlton and Bazzaz 1998; Elliott et al. 2002; Ilisson et al. 2007; Peterson and Leach 2008).

The physical properties of pits and mounds have been addressed in many studies (Beatty and Stone 1986; Ulanova 2000; Peterson and Pickett 1990; Peterson 2004). Removal of biomass in pits allows seed to fall onto exposed mineral soil, initially encountering little competition for light, water and nutrients. Dormant seeds in the usually untouched seed bank also benefit from such a situation, although most of the seed bank in boreal coniferous forest consists of seeds of herbaceous plants (Zobel et al. 2007). The competing vegetation encounters the same factors influencing habitat formation, and, depending on when they appear and species traits, this results in either enhanced or diminished chances of seedling survival. Elevated establishment areas such as mounds have a decreased browsing risk. Additional safe sites for regeneration may be created by the fallen crown material (Krueger and Peterson 2006), whether from stem breakage or windthrow. The tangle of branches may protect seedlings from herbivores (de Chantal and Granström 2007; Ilisson et al. 2007). Hazards for seedlings, once established in pits and on mounds, include soil erosion, the instability of the substrate, the temporary nature of favorable conditions, and standing water in pits in poorly drained soils.

Another factor that influences regeneration in windthrow-related microsites is the vicinity of the surrounding vegetation—neighboring forest stands, single surviving trees, advance regeneration and herbaceous plants—which depends on both disturbance size and severity. The scale of the disturbance to the canopy determines the size of the opening created; smaller openings will result in gap-phase regeneration, while larger openings may respond more like a clearfelling (Boose et al. 1994; Canham et al. 2001). The size of the opening may increase for several years after the wind disturbance as trees around the opening fail. The disturbance severity is defined as the actual damage done to a forest in terms of biomass loss, downed trees, etc., by a storm of a certain intensity for example. Species, stem size, and rooting as a function of soil texture and drainage all affect whether stems decline by breaking or toppling (Nicoll et al. 2006). The severity determines the nature and distribution of newly formed microsites, and is thus directly related to the area suitable for seedling establishment and growth. Severity affects the openness of the area, hence influencing the composition of and competition between regenerating species. Elliott et al. (2002), for example, found a higher species diversity in a moderately disturbed forest than in adjacent undisturbed stands. Studies have demonstrated the rapid establishment of hardwoods in severely disturbed and salvage-harvested areas (Ilisson et al. 2007), but studies on the combined impact of microsite and disturbance severity on seedling establishment and growth are rare.

This study deals with an empirical analysis of microsite characteristics and their influence on seedling establishment and growth under different windthrow disturbance severities. The aim of the current study is to compare regeneration patterns over 6–7 years in stable and unstable microsites resulting from moderate-to-heavy storm gusts. We hypothesized that the more stable microsites, such as large shallow pits and low mounds, provide better growth and survival prospects for regenerating tree species than unstable small deep pits and high mounds. We expect that, due to the different microsite circumstances resulting from the range of disturbance severities, pits and mounds with comparable specific characteristics have a differential effect on seedling survival and growth and species composition.

Materials and methods

The study plots are situated in two storm-damaged forest districts in eastern Estonia. Thunderstorms occurred in the Tudu Forest District (59°11′N, 26°52′E) in July 2001 and in the Halliku Forest District (58°43′N, 26°55′E) in July 2002. The amount of dead wood reached over 600 m^3 per hectare (Table 1). Both areas are characterized by mixed forests of Norway spruce, silver birch and downy birch (*Betula pubescens* Ehrh.), European aspen and black alder. The forest districts are located in flatland and influenced by regional artificial drainage. The study areas were established in sites of type *Myrtillus* and *Filipendula* (Lõhmus 2004), which have rich and humid soils and are widespread in Estonia. Gley and gleyed podzolic soils occur in both forest districts. The ages of the stands varied between 110 and 160 years. Uprooting, when compared to stem breakage,

Table 1 Description of the study plots after the windstorms in the Tudu and Halliku study areas: both the *Myrtillus* and *Filipendula* site types are characterized by rich soils with medium and high moisture levels, respectively

Location	Plot number	Damage	Site type	Composition	Year of origin	Volume standing (m^3/ha)	Volume downed (m^3/ha)	Mound/pit complex number
Tudu	1	Heavy	*Myrtillus*	45Sp 43As 12Bi	1865	~0	616	17
Tudu	5	Heavy	*Filipendula*	76Sp 12Bi 6Al 6As	1865	~0	397	25
Tudu	7	Moderate	*Myrtillus*	57Sp 27As 13Bi 3Al	1845	271	238	2
Tudu	9	Heavy	*Myrtillus*	71As 26Sp 2Bi 1Al	1845	~0	651	14
Halliku	3	Moderate	*Myrtillus*	53Sp 30Al 13Bi 2Ac 2As	1873	217	138	9
Halliku	4	Moderate	*Filipendula*	62Bi 32Sp 3Al 2Pi 1Ac	1873	186	71	3
Halliku	6	Moderate	*Myrtillus*	76Sp 16As 6Bi 1As 1Ac	1893	105	225	5
Halliku	8	Heavy	*Myrtillus*	82Sp 17Bi 1As	1893	~0	231	8

"Composition" is based on % of volume per species. "Volume" describes the volume of standing and downed wood

Ac, common alder (*Alnus incana* (L.) Moench); *Ah*, ash; *Al*, black alder; *As*, European aspen; *Bi*, birch; *Pi*, Scots pine (*Pinus sylvestris* L.); *Sp*, Norway spruce

was prevalent in both areas for the larger diameter classes of Norway spruce, birch and European aspen (Ilisson et al. 2005).

We monitored permanent sample plots in order to follow the height growth dynamics. The permanent plots selected were located in forests with different damage severities, including control and salvage-harvested stands. Ten plots were established in Tudu and eight in the Halliku Forest District. The size of a plot was 20 × 40 m. In heavily and moderately damaged plots (where practically all and half of the canopy is destroyed, respectively), all of the treefall pits and mounds were described and the regeneration dynamics were examined (Ilisson et al. 2007). In this study, we used regeneration data from treefall pits and mounds in the heavily and moderately disturbed stands, accounting for eight plots (Table 1).

The first measurements were carried out in 2004; after that, the regeneration was remeasured in 2005, 2006 and 2007. For each seedling, we recorded the species, measured its height, mapped it so that we could locate the seedling in subsequent years, and registered whether it was positioned in a pit or on a mound. The number of seedlings was recorded. Consecutive measurements produced height growth observations (difference in height between successive surveys) and establishment and mortality data. For height growth analysis, the seedlings were assigned to an age class of 1, 2, or 3, depending on their year of establishment. Age class 1 describes the one-year-old seedlings established after 2004 but before the inventories of 2005, 2006 or 2007 (up to one-year-old seedlings). Age class 2 corresponds to two-year-old seedlings where the height growth was measured for the second year in either 2006 or 2007 (up to two-year-old seedlings). Age class 3 refers to three-year-old seedlings measured for the third time in 2007 (up to three-year-old seedlings). We did not measure the post-disturbance regeneration that was established before 2005 because we did not know the exact ages of the seedlings. An exception was data on seedlings recorded during the first measurements in 2004 for which height growth was registered in 2007; these seedlings are more than three years old and represent an "old regeneration" group that we named age class 4.

Pit and mound characteristics were measured each year from 2004, with the 2004 measurement used as the baseline. Pit depth was measured at several points, including the far end of the pit (opposite the root plate), both sides, and in the center of the pit. As the central point was found to be the deepest, this parameter was used for further analysis. Pit area can be calculated in many different ways, resulting in divergent values. We considered the surface area estimated as a plane at ground level to be the best estimate of the pit area. We established a baseline coincident with the stem base through the root plate (Fig. 1) and visualized two circular sections. We calculated the area of each section using the sine and cosine theorems. When we refer to "windthrow mounds," we mean the mineral soil and humus layer that was pulled up with the root plate during the storm. These are important potential establishment locations for regeneration. Mound width and height were measured directly after windthrow as the distance between the projection of the points where the mound's horizontal cross-section parallel to the stem direction was thickest (usually at the stem base), and as the highest point measured from the undamaged ground level, respectively. The generally wider and lower hardwood mounds are considered more stable microsites than the narrow and high spruce mounds.

We used the software package MLwiN to fit a multilevel random coefficient model with annual seedling height growth as the response variable, respecting the four-level hierarchy of the observations: district, plot, pit and seedling. District was set as a fixed effect and the other three levels as random effects. Other fixed effects were damage level, pit area and pit depth. The species of the uprooted trees and seedlings as well as seedling age and year of observation were set as dummy variables.

Of the levels, only pit and seedling exerted a significant influence. Damage level and species of uprooted tree had a significant effect on seedling growth, whereas pit area and pit depth did not. A linear model incorporating diameter at breast height of the uprooted tree showed a direct relationship between pit area and species of uprooted tree. In the same way, pit depth and mound width were found to be significantly correlated to tree species (*t* test, $P < 0.05$ for all cases). Windthrown spruce produced significantly larger and shallower pits and higher mounds than the hardwoods, as represented by birch and aspen (Table 2). Mound height may be more vulnerable to changes such as erosion, since differences between tree species were not significant just two years after the storm. Therefore, in the subsequent analysis, we decided to relate seedling height growth to the uprooted tree species instead of these separate factors, together with seedling age and observation year.

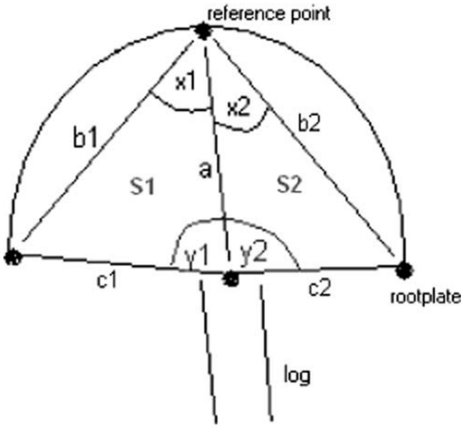

Fig. 1 Measurement of pit area. Distances *a*, *b1* and *b2*, and angles *x1* and *x2* from the reference point were recorded. Distances *c* and angles *y* can be derived using the sine and cosine theorems. Sections *S1* and *S2* were determined separately by calculating the disk sections of each and taking the average of *c1* and *a* as the radius of section *S1* and the average of *c2* and *a* as the radius of section *S2*

The principal analyses were carried out with the SAS (release 9.1) procedure *Mixed*. This procedure performs general linear mixed variance analysis (SAS Institute Inc. 1999), which in the present case allows us to test whether and how stand location, type of wood that formed the microsite, regenerating seedling species, microsite, age of seedling, year and other factors determine the seedling height growth. Study site (Tudu and Halliku) was taken into account as a random factor. Multiple ANOVA (Statgraphics Centurion XV, StatPoint Inc.) was used to analyze the regeneration height growth dynamics exhibited by species in treefall pits. Treefall pits and mounds were separated by species, and the effects of the type of wood (Norway spruce or hardwood, i.e., aspen and birch) were determined.

Results

The most abundant species among the post-disturbance seedlings was birch (both silver and downy birch). Overall, there were 442 seedlings present in the pits and mounds in 2007. Black alder and rowan had 181 and 116 seedlings, respectively. Among coniferous species, Norway spruce was the most abundant in 2007, with 125 seedlings. European aspen and common ash (*Fraxinus excelsior* L.) also regenerated, but because of their low numbers of seedlings we did not analyze their height growth rates.

Based on the height growths of all species in all years, the most favorable microsite was a spruce mound in a heavily damaged area. Seedlings grew taller on mounds than in pits and in heavily damaged versus moderately damaged areas (Fig. 2). All factors (microsite-forming species, microsite type, and damage severity) were significant, but their interactions were not (Table 3).

Annual height growth of seedlings followed the order rowan > birch > alder > spruce (Fig. 3). The annual height growth of rowan was significantly different from the other species, which were not significantly different in

Table 2 Pit and mound characteristics associated with spruce uproots and hardwood (birch and European aspen) uproots

Species that formed the microsite	Number of pits/mounds formed in 2001/2002 storms with damage level		Average pit area (m^2)	Average central pit depth (m)	Average mound height (m)	Average mound width (m)
	Heavy	Moderate				
Spruce	41	14	5.39 (4.02)	0.21 (0.09)	2.07 (0.79)	0.63 (0.21)
Hardwood	23	5	3.70 (2.72)	0.38 (0.15)	1.82 (0.61)	0.95 (0.31)

Standard deviations are denoted in parentheses

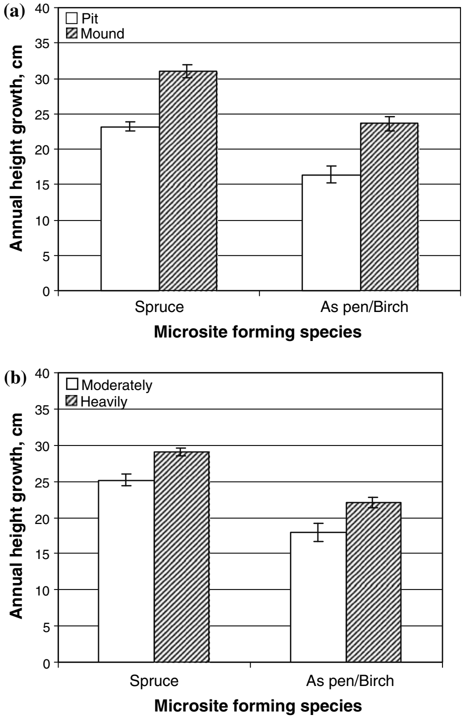

Fig. 2 The mean annual height growths of seedlings (all regenerating tree species, age classes, and observed years pooled) in microsites created by different microsite-forming species (spruce, aspen/birch) in combination with **a** microsite type (pit, mound) and **b** microsite location (moderately, heavily damaged situation). *Error bars* show standard error

Table 3 The effects of damage level (moderate/heavy), microsite forming species (spruce/hardwood), and microsite type (pit/mound) on the annual height growth of seedlings (multiple ANOVA results)

Source of variation	*df*	Sum of squares	*F* value	*P* value
Damage level (a)	1	2178.79	5.15	0.0233
Microsite-forming species (b)	1	6698.04	15.85	0.0001
Microsite type (c)	1	7880.52	18.64	<0.0001
Interactions				
ab	1	18.28	0.04	0.8375
ac	1	64.54	0.15	0.7002
bc	1	1.81	0.00	0.9486
Error	1524	644170.35		
Corrected total	1530	664557.91		

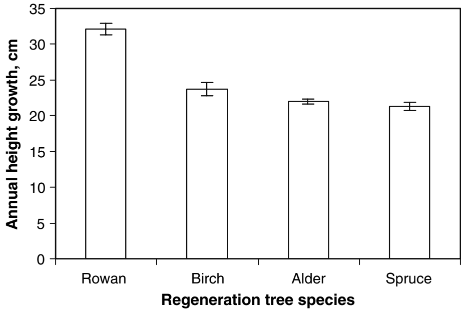

Fig. 3 The mean annual height growths of rowan, birch, alder and spruce seedlings (all microsites, age classes, and observed years pooled). *Error bars* show standard error

Table 4 The effects of storm severity, microsite-forming species, seedling species, microsite type, observed year, and age of seedlings on the annual height growths of birch and alder in treefall pits (ANOVA type 3 results)

Source of variation	NDF	DDF	*F* value	*P* value
District (R)	1		16.38	
Severity	1	1291	17.86	<0.001
Microsite-forming species	1	1291	23.38	<0.001
Seedling species	1	1291	0.00	0.9728
Microsite type	1	1291	13.96	0.0002
Observation year	2	1291	15.18	<0.001
Seedling age	3	1291	7.74	<0.001

NDF, degrees of freedom of the numerator for the *F* test; *DDF*, degrees of freedom of the denominator; *R*, random effect; *F*, value of the *F* statistic; *P* value tests the null hypothesis “factor or contrast has no effect on height growth”

terms of their height growths. The study site (Tudu or Halliku) did not significantly affect the height growth of seedlings. Moreover, the regenerating species was not a significant factor within the species group of birch and black alder (Table 4).

Height growth of birch was different in pits created by uprooting of spruce as compared to hardwood pits (Fig. 4a). Height growth of birch seedlings was greater in pits created by fallen spruce. The significance of the microsite-forming species is reported in Table 5. Age was significant if included as a factor in multiple ANOVA: one-year-old seedlings grew better than two- and three-year-old seedlings. Seedlings older than four years appeared to be accelerating in their height growth. The growth year also had a significant influence; measurements from 2005 demonstrate greater height growth than in other years.

Black alder had a different growth pattern (Fig. 4b). Although the height growth values were surprisingly higher

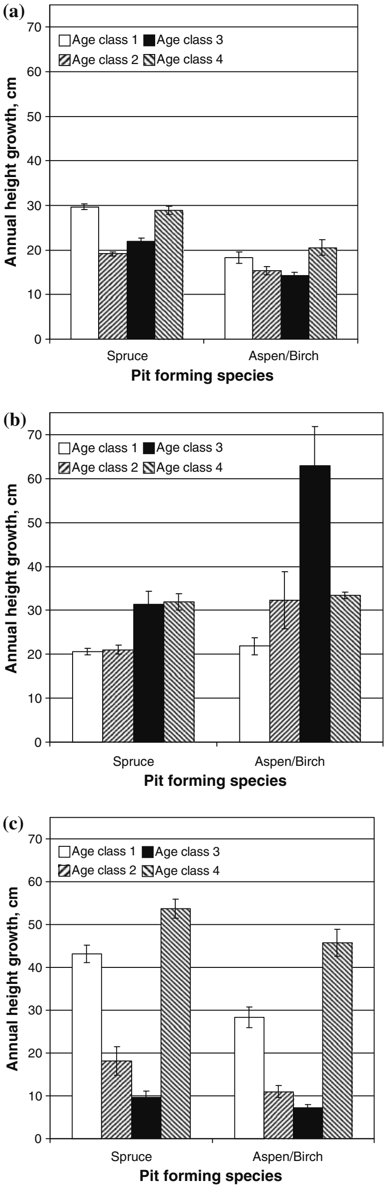

Fig. 4 The mean annual height growths of **a** birch, **b** black alder and **c** Norway spruce seedlings of different ages in pits of uprooted spruce and hardwoods (aspen/birch). *Error bars* show standard error

Table 5 The effects of seedling age and microsite-forming species on the annual height growths of birch, black alder and Norway spruce seedlings (multiple ANOVA results, *P* values of individual factors and interactions)

Source of variation	Birch	Black alder	Norway spruce
Microsite-forming species	<0.0001	0.0978	0.0682
Seedling age	0.0009	<0.0001	0.0009
Interactions	0.2800	0.8500	0.3810
D.F. corrected total	986	130	257

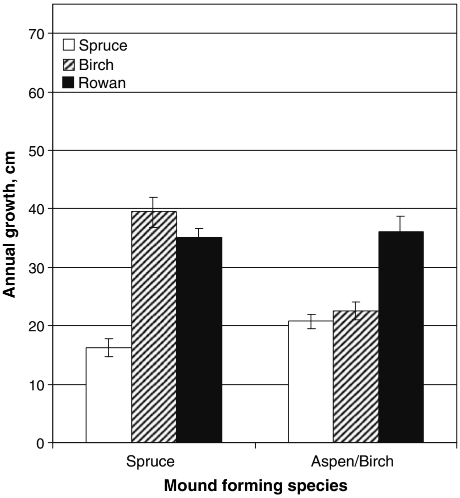

Fig. 5 The mean annual height growths of spruce, birch and rowan seedlings on mounds of uprooted spruce and hardwoods (aspen/birch). *Error bars* show standard error

in hardwood pits, which were deeper and thus had more extreme circumstances, the influence of the pit-forming species was not significant. Height growth increased with age in spruce pits, but the number of observations from hardwood pits was low, with only one three-year-old seedling demonstrating great height growth (Fig. 4b). Year of measurement did not affect alder growth (Table 5).

The annual height growth of Norway spruce showed a similar trend to birch growth (Table 5). One-year-old seedlings demonstrated fast growth (Fig. 4c), as did the oldest seedlings (age class 4), suggesting accelerated growth.

The growths of seedlings on pits and mounds were significantly different (e.g., for birch and black alder see Table 4), and so the height growths of Norway spruce, birch and rowan as the main species on mounds were

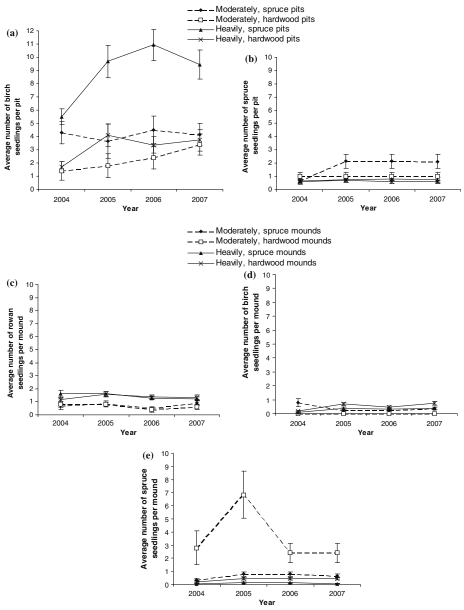

Fig. 6a–e Average number of birch and spruce seedlings per pit (**a**, **b**), and rowan, birch and spruce seedlings per mound (**c**–**e**), respectively, by microsite type and species of uprooted tree in different years. *Error bars* show standard error

analyzed separately. The height growth of seedlings established on mounds was not related to the mound-forming species or to seedling species (Fig. 5). There were significant differences between species in height growth, with spruce exhibiting the poorest height growth. Surprisingly, seedlings seemed to grow best on on spruce mounds, despite the fact that spruce mounds were flatter and relatively less stable than hardwood mounds.

In terms of abundance, birch seedlings clearly preferred pits resulting from spruce uprooting in heavily damaged areas, while spruce seedlings were most abundant in pits formed by spruce in moderately damaged areas (Fig. 6a, b). On mounds, spruce also performed better in moderately damaged areas on hardwood uproots. Birch seedlings initially did not show a clear difference, but eventually, like rowan, they became more abundant in the heavily damaged areas (Fig. 6c–e). For birch and rowan there were no obvious preferences with regard to the species of the tree that caused the mound. Although not significant, seedling numbers tended to decrease over time on mounds, while their numbers were stable or slightly increased in pits (Table 6).

Table 6 Number of newly established and dead seedlings per pit or mound by species in each year of investigation after 2004

	2005	2006	2007
Heavily damaged/pit			
Newly established			
Birch	18.40 (15.52)	6.92 (9.38)	3.58 (4.25)
Norway spruce	24.66 (16.45)	3.44 (3.61)	5.05 (4.42)
Rowan	12.91 (11.28)	8.82 (10.37)	3.05 (4.31)
Dead			
Birch	11.96 (12.41)	3.89 (2.85)	5.68 (5.15)
Norway spruce	7.40 (3.76)	4.26 (2.98)	5.85 (4.29)
Rowan	13.50 (14.24)	3.78 (2.89)	5.31 (5.20)
Heavily damaged/mound			
Newly established			
Birch	11.31 (10.41)	5.02 (10.08)	2.44 (3.57)
Norway spruce	12.37 (11.32)	1.20 (2.59)	2.35 (3.40)
Rowan	9.12 (9.08)	4.75 (9.89)	1.82 (3.03)
Dead			
Birch	9.10 (12.08)	3.08 (2.84)	2.87 (3.62)
Norway spruce	4.22 (4.50)	2.55 (2.65)	2.44 (3.25)
Rowan	8.28 (12.02)	2.56 (2.56)	2.61 (3.51)
Moderately damaged/pit			
Newly established			
Birch	13.31 (10.36)	9.12 (8.02)	6.22 (9.91)
Norway spruce	14.38 (10.01)	9.36 (8.08)	5.79 (10.02)
Rowan	14.58 (10.33)	10.14 (7.91)	6.00 (10.26)
Dead			
Birch	24.25 (18.47)	7.86 (8.08)	8.47 (9.72)
Norway spruce	24.78 (18.29)	8.47 (8.08)	9.13 (9.78)
Rowan	10.26 (18.62)	8.69 (8.19)	9.82 (9.79)
Moderately damaged/mound			
Newly established			
Birch	8.49 (7.62)	1.61 (2.37)	6.41 (8.57)
Norway spruce	8.64 (7.24)	1.48 (2.31)	5.80 (8.42)
Rowan	7.70 (8.11)	2.83 (3.29)	4.87 (9.37)
Died			
Birch	6.23 (6.93)	5.03 (4.26)	1.18 (2.68)
Norway spruce	5.71 (6.86)	4.60 (4.32)	1.08 (2.59)
Rowan	6.32 (3.24)	2.92 (3.24)	1.93 (3.54)

Standard deviations are denoted in parentheses

Discussion

The importance of disturbed microsites after a windstorm and dead wood in the advanced stages of decay has been clearly demonstrated for Norway spruce regeneration (Wohlgemuth et al. 2002; Kuuluvainen and Kalmari 2003) and the regeneration of other conifers (Noguchi and Yoshida 2004), and even more so for small-seeded and light-demanding species such as birch (Carlton and Bazzaz 1998; Kuuluvainen and Juntunen 1998; Ulanova 2000).

The nature and distribution of these microsites will vary depending on the severity of the disturbance and the vulnerability of the stand to breakage or windthrow. In the current study, uprooting by windthrow was dominant over stem breakage (Ilisson et al. 2005). The canopy remaining after a disturbance can provide better conditions for germination (restricted desiccation) but limited light levels in subsequent years. Nevertheless, shade-tolerant species can benefit by establishing under these conditions (Calogeropoulos et al. 2004).

The impact of severity level on species composition and seedling density was analyzed in the study areas (Ilisson et al. 2007), and the highest birch and rowan numbers were found in the most severely disturbed areas, which was not surprising given their light-demanding pioneer characteristics. No clear difference in seedling density between severity levels was found for Norway spruce. In the current study, with the additional inventory years and by combining the severity factor with microsite (pit or mound) and species of uprooted tree, Norway spruce showed a preference for the moderately damaged areas.

Severity also determines the legacy of the storm in terms of residual vegetation and woody debris, which both influence post-disturbance regeneration response. Residual vegetation coverage and height can significantly decrease seedling establishment potential (Harrington and Bluhm 2001; Bell et al. 2000; Wohlgemuth et al. 2002; Sugita and Nagaike 2005). The vegetation in the plots of this study was investigated by Ilisson et al. (2006), who found no significant difference between the heavily and moderately disturbed areas, although only the vegetation on undisturbed soil was studied. The coverage of the bush layer in general was low.

The pool of buried seeds and advance regeneration are important factors in vegetation changes and the regeneration of the tree layer. When abundant, advance regeneration outcompetes new seedlings in pits (Harrington and Bluhm 2001). Advance regeneration generally results from an earlier disturbance and is often waiting in the understory for gaps; it has species-specific waiting patterns (Kubota et al. 1994). Repeated disturbance events may produce a complex pattern of regeneration, including multiple releases of advance regeneration, resulting in several cohorts, also depending upon the time at which coarse woody debris is created (Foster 1988; Kubota 1995; Kuuluvainen and Kalmari 2003). In this study, only regeneration within the borders of pits and mounds was monitored. Although our first intention was to include regeneration on intact ground and harvested plots, due to insufficient data we were unable to carry out a statistically adequate analysis. Advance regeneration was therefore not considered either, apart from a small number in the periphery of pits and mounds that were accidentally included as post-disturbance regeneration. In the overall severity level analysis, we assumed that more advance regeneration remained in the moderately disturbed plots, similar to the canopy layer, than in the heavily disturbed plots. Nevertheless, future LAI measurements and inventories of the conditions surrounding microsites should determine the actual impact of advance regeneration.

The previous study (Ilisson et al. 2007) did not detect significant differences in seedling densities, diameter increment or height between moderately and heavily damaged areas, which was attributed to the large amount of downed woody debris. After two additional years of investigation, seedlings in the present study that exceeded the fallen trunks in height were expected to grow faster in the heavily damaged plots. Indeed, in this study, birch and Norway spruce exhibited accelerated growth after the third year since establishment.

Relative to mounds, the diversity of tree species and the seedling densities increase in microsites of treefall pits that are available for regeneration (Peterson and Pickett 1990, Kuuluvainen 1994). Pits with initially highly favorable conditions and high seedling densities, however, may turn into flooded or eroded areas covered with downwashed soil and mud within a couple of years. Moderately damaged areas may provide the additional bit of shelter necessary to generate a few strong survivors that are better armed to compete with the surrounding vegetation. Mixed forests can form after the natural regeneration of storm-damaged areas (Peterson and Leach 2008). This was also found, at least in the seedling phase of regeneration development, in this study. In general, depending on the light requirements of the regenerating species, the shallower pits of spruce uproots and the higher and usually less-shaded mounds of hardwood uproots are the most favorable for both severity types. The regenerations of both Norway spruce and birch showed faster height growths in pits of uprooted spruce trees than in uproot pits created by other tree species. For black alder there was no preference concerning uproot species; a possible reason for this could be its greater tolerance for the wetter conditions in the aspen and birch pits. Fast seedling height growth on spruce mounds could be due to the moisture-saturated soils inherent to these soil types, thus resulting in more favorable growth conditions in mounds than pits.

Mortality can be caused by intrinsic factors (competition, nutrient and water cycling within the plant, etc.) as well as by extrinsic factors such as frost heaving, flooding, burial by soil and litter, or browsing (Carlton and Bazzaz 1998; Nilson et al. 1999). Although browsing was observed in this study, it did not occur very often; therefore, browsing was not studied further with regard to seedling mortality.

Ilisson et al. (2007) found in earlier studies that dying seedlings had a considerably poorer height growth and reached a lower height prior to dying compared to surviving seedlings during the same period. That suggests that competition is a driving factor in mortality, although the relation with seedling densities was not significant. Maher and Germino (2006) observed the greatest mortality rates in seedlings that had just emerged from seed and were in their first year of growth, and in seedlings that had the least amount of cover provided by trees or other landscape features that block exposure to the sky. In this study, fast height growth during the first year may be a result of confounding caused by excluding the mortality of seedlings that died before the end of the vegetative period. We saw many first-year birch seedlings that died before measurement, and these were not taken into consideration for height growth analysis. Certainly, seedling establishment and height growth patterns vary with species traits, their requirements, and their adaptive capacities. Our first measurements in 2004 may be a reflection of the fittest individuals surviving after establishment, whereas regeneration in the fourth year of measurements in 2007 may be more affected by competition. Measurement year conditions also may influence growth; 2005 was a favorable year for plant growth and many first-year seedlings emerged in this year (Table 6).

Salvage logging is another type of disturbance that affects the number and distribution of microsites (Lindenmayer et al. 2004; Nelson et al. 2008; Peterson and Leach 2008). This management action rearranges and removes material, causes ground disturbances, and may reduce the overstory. In our study area, salvage logging took place in neighboring plots following severe windstorm damage, and the impact of this on vegetation composition and post-disturbance regeneration was reported by Ilisson et al. (2006, 2007). Adapted thinning and extended rotations can influence the species composition of vegetation and natural regeneration in disturbed stands (Kangur et al. 2005; Kohv and Liira 2005; Moora et al. 2007). Moreover, management decisions taken after a disturbance, such as salvage logging, relying on natural regeneration, and landscape level issues also have an effect on the regenerating species and the resistance of the stand to future disturbances (Stanturf et al. 2007). These considerations are especially important in the light of a changing climate, which may increase storm events and intensities (Schelhaas et al. 2003; Blennow and Olofsson 2008).

We conclude that tree species have different microsite preferences in the initial stages for establishment and early growth. Birch seedlings have the tendency to perform better in spruce pits and mounds, whereas spruce seedlings seem to prefer spruce pits and aspen mounds. If we take into account the storm severity too, these findings contribute towards explaining why birch is the main regenerating species in heavily storm-damaged spruce forests, and why spruce dominates after storms in hardwood forests and after lower-intensity storms in spruce forests. Moreover, in hardwood-dominated forests, stem breakage is more likely than uprooting (Ilisson et al. 2005), thus providing better chances for non-pioneers like spruce. Due to the increased microsite heterogeneity after windthrow, mixed stands are expected to develop from natural regeneration. Observing regeneration over a seven-year period after a windstorm allows us to draw some conclusions based on empirical evidence. However, an extended investigation is needed with more precise characterization of the physical conditions in order to determine the importance of other microsites, such as intact ground, including potentially present vegetation and advance regeneration, dead wood and changing microsites due to delayed storm effects such as falling logs and leaning dead wood, and to develop management guidelines based on this.

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IV

Vodde, F., Jõgiste, K., Engelhart, J., Frelich, L.E., Moser, W.K., Sims, A., Metslaid, M.

DOES POSITION MATTER IN WIND-INDUCED MICROSITES FOR TREE SEEDLING ESTABLISHMENT, GROWTH AND SURVIVAL?

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Does position matter in wind-induced microsites for tree seedling establishment, growth and survival?

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Abstract

Questions: Storm events increase heterogeneity in the range of potential tree establishment sites. This heterogeneity does not, however, guarantee survival. Many studies on post-disturbance stand development are limited to only the first few years after disturbance: 1) Which factors affect tree regeneration survival and performance during the first post-storm decade? and 2) How do these effects change in time: are establishment, growth and mortality initially directed by endogenous factors, generating a degree of spatial partitioning within a microsite, whereas gradually species' life-history traits and competition take over?

Location: Hemiboreal mixed spruce-hardwood forests in north-east Estonia.

Methods: Regeneration height and mortality 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. Comparison of logistic mixed effect models identified the most important factors for mortality probability and performance 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.) at different stages since disturbance.

Results: 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 *P. abies* initially benefitted and later suffered from increased levels of coarse woody debris. Initially only for *Betula* and subsequently for all species, height and height increment in previous years were more clearly negatively related to mortality probability and competition levels in previous years increased chance of death.

Conclusions: Although regeneration height and mortality levels were not considerably different between and within microsites, each site was dominated by a different species community. This study indicates that it is important to distinguish disturbance severities and timing of a study when evaluating post-storm impact on forest succession.

Keywords: Mortality; Competition; Establishment sites; Regeneration dynamics; Windthrow

Running head: Regeneration dynamics after windthrow

Introduction

Storm events can contribute to microsite heterogeneity in a forest stand by increasing the amount of coarse woody debris (CWD) and adding root mounds and pits of wind thrown trees. This, in its turn, may increase stand diversity in terms of regenerating tree species composition and stand vertical and horizontal structure (Peterson & Pickett 1990; Kuuluvainen 1994; De Grandpré & Bergeron 1997; Ilisson et al. 2007). Most studies of post-storm stand development focus on the first few years of regeneration development after disturbance events (Caquet et al. 2010; Vodde et al. 2011; Fischer & Fischer 2012), a period when mortality is often high (Peet & Christensen 1987) and highly variable (Nakashizuka 2001; Queenborough et al. 2007). Nevertheless, early mortality is regarded as a key process in forest development (Lutz & Halpern 2006). In combination with other differences, such as the spatial extent of the study scale level 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 & Peet 2011).

In the first decade after windthrow, storm-surviving mature trees struggle with radical changes in environmental circumstances, among which increased exposure to radiation, wind, fungus outbreaks and insect infestations. Simultaneously, several groups of regeneration will compete for a place in the future canopy: 1) storm-surviving advance regeneration, 2) new sprouts and basal shoots from downed, broken or buried tree stems or root systems, and 3) new, post-disturbance established seed-germinated regeneration. Vitality of surviving individuals, their size and spatial distribution depend on the pre-storm status and the storm characteristics (e.g. Kuuluvainen 1994; Collet et al. 2007). Seed source availability, tree species' traits and the size of disturbance gaps determine the potential share of newly regenerating trees in the canopy. Branches and logs of fallen trees may safeguard new and advance regeneration from ungulate browsing (Krueger & Peterson 2006; de Chantal & Granström 2007). Furthermore, there is the aftermath of the disturbance which may influence stand development: survivors that eventually die, delayed falling of dead wood and persistently blocked sunlight as a result of the accumulated log load or surviving vegetation (Castelli et al. 1999; Kurulok & 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 & Eriksson 1997; Leishman et al. 2001). The somewhat more favourable germination conditions notwithstanding, natural tree regeneration at wind-induced sites is generally found to suffer 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 & Kalmari 2003), especially for small-seeded and light-demanding tree species, whereas flat sites are more stable. However, also on the latter substrates, new regeneration 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 & Stone 1986). On wet sites, regeneration may, soon after colonising the pit centres, suffer mortality due to inundation by pooling water, whereas on dry sites, it may be the only place to survive summer droughts. Therefore, microsite location, regeneration location within the microsite, competition from other seedlings 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 & Bruelheide 2010) and early seedling mortality (Maher & Germino 2006) all may influence post-storm stand development.

To better predict seedling survival in wind-impacted microsites, it is important to understand how seedlings perform in different areas of a single microsite and between different microsite types. We analyse 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 adequate performance in these microsites after the first post-storm decade. Furthermore, we compare final tree height and abundance, and relate this to microsite availability to illustrate the importance of wind-induced microsites after a decade since the event. 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.

Methodology

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 (Figure 1). 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 in order to maintain the mature to old-growth forest and provide habitat for several protected animal species, including the flying squirrel (*Pteromys volans*). The passive management strategy was continued after the 2001 storm event, 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 110-158 years. The storm was so locally destructive that no specific tree species was impacted more or less than any other. Trees on gleyed podzolic soils showed significantly more stem breakage than tree uprooting, whereas for trees on the gley soil type the difference was negligible (Ilisson et al. 2005). More details on storm damage and vegetation community changes can be found in Ilisson et al. (2005) and Ilisson et al. (2006), respectively. Study plots were initially selected to represent all three damage severity levels, heavy, moderate and control (i.e. scarcely damaged). In surrounding areas with comparable stand characteristics, where harvesting of completely downed stands took place, the impact of this superimposed anthropogenic disturbance on stand development was considered.

Field methods

In 2002 (Tudu) and 2003 (Halliku), permanent sample plots were established, followed by an investigation of damage severity by mapping canopy tree locations, position and vitality conditions. Plots were established in the centre of each patch of a certain storm severity in order to minimise potential border effects. In the 15 selected 20x40m study plots, four in each 'treatment' and three control areas, regeneration inventories started in 2004, three and two years after the storm events, respectively.

Tree regeneration, which we defined as established seedlings (height 5 cm - 1.3 m), saplings (height 1.3 m - 6 m), and understory tree regeneration (height >6m), was inventoried in all wind-induced microsites. Cluster sampling was used to monitor the pit-and-mound complexes: all were sampled within each plot in the wind-disturbed areas. Additionally systematic sampling was used to monitor regeneration on intact soil in each treatment: ten 1 x 1 m squares were placed at regular distance (4m) along the 40 m plot middle line. If the square included logs or pit-and-mound complexes, the square was placed on the other side of the middle line of each plot under each treatment, or 1 m left or right of the middle line until it covered only ‘intact soil’. Intact soil in this study thus means the forest floor excluding the before mentioned wind-induced microsites, under various light conditions and, on salvage logged plots, potentially including displaced soil. The experimental design could be described as a block design, with ‘plot’ and ‘microsite’ as the random effects and the treatments ‘storm severity’ and ‘microsite type’ as the fixed effects. However, out of the total of eight plots, four have experienced severe storm damage and four moderate storm damage. In all plots, all types of microsites were studied and within all microsites, tree regeneration occurrence and development was recorded. Inventories took place annually during summer, from 2004 to 2012, except for the years 2008 and 2011. For all living regeneration, we recorded the species, height, incidence of physical damage (generally caused by browsing and insects), mortality, microsite and position, either relative to the middle line (intact microsites) or from a fixed measuring point at the pit edge opposite to the root plate (wind-induced microsites). As silver and downy birch seedlings often are difficult to distinguish, all birch trees have been further analysed as *Betula* spp. Due to a relatively low frequency of data collection in the harvested and control plots, only the successive years of monitoring in moderately and heavily damaged plots provided data to determine mortality and consider the impact of factors in further analysis. Harvested and control plots therefore solely serve as a background to compare certain trends in species composition and height at one decade post storm.

Characteristics of the wind-induced microsites, i.e. position, size and species of the uprooted tree, pit depth, mound height and width, were assessed in 2004. Earlier publications (Ilisson et al. 2007; Vodde et al. 2010) showed that spruce, with its flat but extensive root system, caused significantly larger and shallower pits, and correspondingly higher and thinner mounds than the broadleaved species. Additionally, there is a positive trend between uprooted tree species *dbh* (diameter at breast height, 1.3 m) and microsite dimensions (Vodde et al. 2010). Nevertheless, as we intended to find the best model fit, all characteristics (e.g. uprooted tree species as well as uprooted tree dimensions and pit dimensions) are included.

In heavily damaged plots, the area covered by a total of 70 pit-and-mound complexes ranged between 10.1-21.0% of the total plot area for pits and 3.2-8.8% for mounds, whereas in moderately damaged plots the figures for 25 pit-and-mound pairs were 3.0-11.5% and 1.4-2.9% respectively. Even though in some cases coarse woody debris (CWD) covered a considerable share of the plot, it had not decayed to a stage conducive to tree establishment during the study and therefore we found very low numbers of new regeneration on this substrate. Of 6936 observations up to 2010, including seedlings that were measured several times throughout the years, 4.3% and 1.0% were registered as advance regeneration and sprouts from a stump or stem, respectively. Among the sprouting regeneration, European rowan and birch were most abundant and within advance regeneration, Norway spruce and European rowan were most abundant. During the first years of data collection the research focus was predominantly on the wind-induced pit and mound microsites: practically all were monitored, whereas the samples on intact soil only covered up to 2% of the total microsite area available within a plot. In order to enlarge the share of intact soil monitored, in 2011 regeneration was investigated in twelve additional 10x10m subplots in or close to the heavily damaged plots, and in 2012 in twelve 5x5m subplots in moderately damaged plots. Measurements of species composition and height of regeneration on the different microsites, taken from these squares 10 years after disturbance, served to validate our findings on height and density development from previous years.

Data processing

When a regenerating tree died, it was registered as such (mortality = ‘1’) in the year after the last height measurement. In order to have sufficient data to compare mortality and test effects among microsites, among damage types, among regenerating tree species and between two stages since disturbance, the main dataset was divided into nested subsets. Firstly, we delineated two partially overlapping data subsets, one used for evaluating differences among microsites (microsite-subset), including only the data from regeneration in heavily damaged areas, and one used to test for differences among damage levels (severity-subset), including only the data from regeneration in pits. The separation into these subsets was necessary for the analysis of the four predominant regeneration species: black alder was generally occurring in pits only, whereas rowan preferred mounds. When including pits only, sufficient data was available for three species covering all severity levels, whereas when including all microsites, only on the heavily damaged areas all species except black alder had a satisfactory representation. Secondly, after testing overall effects on the entire dataset, we selected, within both subsets, two years as far apart from each other as possible, to illustrate the difference in effects of these stages since disturbance on regeneration mortality. Finally, we separated the three most common tree species within each data subset. In the microsite-subset, containing the regenerating tree species *Betula* spp., *Picea abies* and *Sorbus aucuparia*, for all years together the number of observations (n_{all}) is 3536, although this figure includes cases of repeated monitoring of the same trees throughout the years. When analysing the different stages separately, n_{early} = 611 and n_{late} = 582. Specific microsite-level factors and differences between the damage levels heavy and moderate, analysed only in pits in the severity-subset, were tested for the regenerating tree species *Betula* spp., *Picea abies* and *Alnus glutinosa*. For this subset all years together gave n_{all} = 4435, and separate stages n_{early} = 699 and n_{late} = 863.

Potential factors influencing mortality were categorised according to their presumed correlation (Table 1). The potentially most important storm effects for regeneration performance are increased light availability and higher levels of CWD. The impact of wind disturbance, storm severity, is often used as an approximation of the physical force of the storm, i.e. storm intensity. A storm severity index was calculated for all plots, based on the ratio of post-disturbance basal area (BA) of storm-damaged trees and pre-disturbance plot BA (Table 2). This approach, although not applied for individual tree species, was based on the Intensity Index presented by Rich et al. (2007). Post-disturbance BA of damaged trees consists of the plot sum of cross-sectional stem areas at *dbh* or at 1.3m from the stem base for all dead trees, consisting of standing and hanging trees and snags of decay stage I, as well as stumps and downed trees or parts of trees of decay stages I and II of which the roots, in an upright position, would be located within the study plot. Pre-disturbance BA consists of the sum of BA of storm-damaged trees and surviving trees. Trees in more advanced stages of decay were not considered in the severity index calculation, because they were assumed dead before the storm. Decay stages were assigned at the initial storm inventory. Stages I-V vary from fresh stems without a sign of decay to stems which are almost entirely decomposed (e.g. Palviainen et al. 2008). Pit area was estimated as the sum of the areas of two circle sections (described in Vodde et al. 2010). Mound area was approximated as the vertical projection of a rectangle with mound width and diameter as its sides.

We derived a competition index for regeneration based on previously developed indices. These used the position relative to competing trees (Hegyi 1974; adapted for saplings in Metslaid et al. 2005), in some cases adjusted for direction relative to the sun (shading, Kuuluvainen & Kalmari 2003), individual and competing tree heights (Hegyi 1974; Metslaid et al. 2005; Kuuluvainen & Kalmari 2003) or basal diameter (Collet & Moguedec 2007). The surrounding area considered, or the maximum distance at which to take into account competing trees vary with tree size (Collet & Moguedec 2007; Sims et al. 2009). As we study regeneration in clearly distinguishable microsites with very specific conditions, we decided to use regeneration density and average height in a single microsite as measures to estimate competition experienced by a regenerating tree at a particular height. Potential competition from surrounding mature trees is incorporated in the disturbance severity of a plot. Only tree height (not diameter) was measured of regeneration trees, therefore height and density were the basis for the calculation of competition indices *CI1* and *CI2*, as a combination of previous competition indices (Hegyi 1974; Kuuluvainen & Kalmari 2003; Collet & Moguedec 2007):

$$CI_i1 = \frac{\bar{h}_j}{h_i} * D_j \qquad (1)$$

$$CI_i2 = \ln\left(\frac{\bar{h}_j}{h_i}\right) * D_j \qquad (2)$$

where CI_i is the competition index of regenerating tree i, $\bar{h}_j$ represents average tree height in microsite j, h_i is the height of tree i and D_j is regeneration density in microsite j. The latter equation gives a better expression of the competition experienced by a single regenerating tree: positive values indicate that the tree is probably more suppressed than it creates suppression and *vice versa.* Effects of past height (H), height increment (HI) and competition on mortality of individual regeneration stems were tested separately for year n-1 up to n-6 (denoted as H_{n1}, H_{n2}, …, HI_{n3}, HI_{n4}, …, $CI1_{n5}$, $CI2_{n6}$, *etc.*) and, for height, as the average over a 2 to 6 year period before year n (H_{2n}, H_{3n}, *etc.)*.

Less than 3% of the observations had reported browsing or insect damage in the past, where Norway spruce (5.3%) and rowan (4.7%) were more susceptible than birch (1.2%) and black alder (1.0%). Browsed regeneration was included in competition index calculations of other regeneration and browsing as a factor in mortality analysis, but records of regeneration, which was browsed in the current year or in previous years, were not used in the analysis of seedling performance. Though tree fall direction is important for the degree of shading by the root mound experienced by the regeneration in the pit, in our study most trees fell to the north-east making it an irrelevant factor to consider here. As a surrogate variable for substrate humidity in pits, we included distance of regeneration to the lowest point of the pit, generally at one fourth of the distance from the root plate to the other side of the pit.

Statistical analysis and modelling

The probability of mortality for regenerating trees (p_i) in the first decade since disturbance was analysed for the defined microsite-subset and severity-subset, holding the regeneration data from the wind-disturbed areas. As the response variable is binary, we used a logistic regression model, where the logistic transformation of p_i is expressed as a linear function composed of the explanatory variables (Table 1):

$$\operatorname{logit}(p_i) = \ln\left(\frac{p_i}{1-p_i}\right) = \beta \cdot X_{ijk} \qquad (3)$$

where β is a matrix representing $m + 1$ grouped regression coefficients of the explanatory variables at the regenerating tree level (i), the microsite level (j) and the plot level (k), grouped in matrix X_{ijk}. Pairs of variables with presumed correlation are employed in separate model runs. Although we were looking for trends across all species throughout the years, individual species were analysed as well to determine the explanatory power of individual variables for each regenerating species. Additionally, as we expect factors influencing different stages since disturbance to change over time, we evaluated the years 2006 and 2009/2010 separately using the linear mixed effects R function lmer from the package lme4 (Bates et al. 2011). All years together are analysed with the SAS procedure GLIMMIX (Schabenberger 2005), which can handle a response variable with binomial distribution, as well as the hierarchic structure and the longitudinal character of the database, recognising repetitively recorded individuals of the same regenerating tree as dependent samples. Selection of the two to four best models per data-subset was based on Akaike's Information Criterion (AIC) in combination with the number of observations and the significance of factors.

Mixed models (lmer in R's lme4 package) were used to analyse the effects of damage severity, microsite type and regenerating tree species on density and height development of individual regeneration. The package 'lmerTest ' produced ANOVA (type III sum of squares) tables with Satterthwaite approximation for degrees of freedom and HSD comparison tests. Height data were log-transformed to better approach normality. All further analyses and figures were accomplished using R (R Core Team 2012).

Results

Occupation of microsites in storm areas

Throughout the years, regeneration densities differed significantly between microsites and species (Table 3). On storm-disturbed sites, densities were highest on intact soil (1.63 m^{-2}), average in pits (1.09 trees m^{-2}) and lowest on mounds (0.63 trees m^{-2}, Figure 2). These values can be compared to the mean regeneration density on intact soil on harvested sites of 4.29 m^{-2} and on control sites of 0.81 m^{-2} (Figure 3). Furthermore, heavily damaged areas and moderately damaged areas hosted a comparable amount of regeneration (1.08 and 1.04 trees m^{-2}, respectively). Regenerating species were more equally distributed on intact soil than on wind-induced microsites where species dominance differed between treatments and microsites (Figure 2). Birch regeneration dominated pits in heavily damaged areas and black alder and birch were the most common species in pits of moderately damaged areas (individual regenerating trees denoted as symbols in Figure 4). Either spruce or rowan was dominant on mounds in moderately damaged areas, whereas rowan was prevalent on mounds in heavily damaged areas. Although differences between years were not statistically significant, both for all regenerating tree species pooled and for individual species except black alder, the overall trend was that densities decreased in time. The share of newly establishing regeneration was higher on storm-induced microsites, compared to intact soil (data not shown). Establishment rates decreased in time since disturbance, although the variation between years was considerable. Norway spruce generally showed the least new establishment of the four main species ($p=0.003$) and black alder occurred in pits more than other microsites. Likewise, regeneration mortality was lowest for spruce seedlings ($p<0.001$). On mounds, mortality was significantly higher in moderately damaged areas than in heavily damaged areas. No overall trend in mortality was observed.

Factors affecting regeneration mortality

For each regeneration tree species or species group in a specific year or group of years, terms were added to or removed from the logistic regression model (Table 1). Although true comparison of models requires datasets of equal observation size, some variables are measured in different years and do not overlap. A lot of information is lost if only the records with data for all variables would be included. We therefore did not abandon any of the variables and chose to select a set of two to four 'best' models (Table 4), depending on Akaike's Information Criterion (AIC) in addition to the number of observations. Besides the model explaining factors, significances of p-values of individual terms were also obtained (data not shown).

Taking all microsites together, birch and rowan initially benefited slightly from higher disturbance severity; in later stages, birch survival was positively related to the amount of dead wood. In contrast, spruce incurred more mortality later on by higher amounts of dead wood. However, when pits were analysed separately, birch later suffered from higher disturbance severity including high dead wood levels, whereas black alder and spruce seemed to profit initially from higher amounts of dead wood. For all years together, black alder had higher mortality probability in pits with higher storm severity (Table 4).

The regeneration microsite did not clearly influence regeneration mortality. In two of the models for the later stages, the storm-induced microsites displayed greater survival, especially for birch, than did intact ground (Table 4). Spruce generally had a greater probability of mortality in pits when microsite was evaluated as the sole factor.

Survival probability was higher in the larger pits (based on significance of individual effect, data not shown) for black alder throughout the years and for birch during the later years. Deeper pits seemed to be safer for birch (not shown) and less so for spruce (Table 4), but spruce as the uprooted tree species, creating shallower pits with a larger area than the hardwood species involved (Ilisson et al. 2007), enhanced survival probability of birch and spruce regeneration. Black alder generally profited from the presence of higher, wider and larger mounds as single model terms. The distance of a regenerating tree to the pit centre (i.e. deepest point) may also influence regeneration mortality. Nevertheless mortality probability was only significantly higher closer to the pit centre for black alder (Table 4).

Birch (followed by rowan) was the most vulnerable regeneration species, when analysing all microsites together, especially at a later stage since disturbance. In pits only, black alder had higher mortality probabilities than birch and spruce (Table 4). Recruitment registered as advance regeneration, mainly present on mounds and intact soil, generally had higher survival chances, except, initially, birch advance regeneration (data not shown).

Initially only birch was significantly related to height and height increment in the previous year, later on all species had higher survival chances when they were taller (Figure 5, Table 4) or had grown faster in the past, although in some cases initial fast growth increased mortality risk (Table 4). Higher levels of competition increased mortality probability as time since disturbance increased. Rowan was the only species on all microsites that initially suffered from higher competition. In pits the difference between the stages was remarkable: initially, higher competition implied better conditions for germination, establishment and survival of many seedlings, whereas in later years, high competition levels increased mortality (Table 4).

Beyond the storm impact on subsequent stand development, browsing by ungulates such as moose and roe deer can impact seedlings. Generally browsing in the past increased the probability of mortality, although with increasing number of years since being browsed probability of mortality decreased for regenerating rowan trees. With time since the storm, recruitment mortality risk increased for most species, except black alder and rowan. On the other hand, in pits chance of mortality decreased with regeneration age, where with all microsites together the middle age class was most vulnerable (Table 4).

Regeneration performance

Comparison of models analysing effects on regeneration height (log-transformed) indicated a 'best-fit' of a two-level (plot and microsite) block model based on disturbance severity (damage level) and regeneration tree species. Throughout the monitoring period, regeneration in heavily damaged areas was significantly taller than regeneration in moderately damaged areas for the species birch ($p=0.002$) and alder ($p<0.001$), and the pooled other species ($p<0.001$, lmerTest, Figure 6). Regarding individual species, *Picea abies*, *Betula* spp. and *Alnus glutinosa* initially were all in the lower ranges of height, whereas together with *Sorbus aucuparia* (significantly highest, with *Fraxinus excelsior*), these species had (and still have a decade after the storm) the highest densities. HSD (post-hoc) tests identified black alder initially as the shortest species, while at later stages it caught up with the other species. In heavily disturbed areas, the few individuals monitored were the tallest trees. At a later stage since disturbance, birch seedlings in moderately damaged areas were significantly shorter than spruce. Height differences between microsites for all species showed no clear relationship with time. However, differences between the intact ground (higher) and wind disturbed microsites in annually measured regeneration was initially significant and later on became insignificant in the moderately damaged areas and opposite in the heavily damaged areas. When also considering the additional subplots in 2012, regeneration on intact ground in moderately damaged areas was still significantly highest (HSD test, Figure 6). Furthermore, closer to the pit centre, there was more variation in tree heights than further away, (Figure 4).

Discussion

In this study we analysed whether factors affecting regeneration mortality vary at different stages since wind disturbance. Besides testing for overall effects, the anticipated benefits of the division of the main database into smaller subsets clearly paid off. Birch was a good example: in the microsites dataset survival prospects were higher with increased disturbance severity early and with levels of dead wood later after disturbance, whereas in the severities dataset, with only pits included, disturbance severity seemed to promote mortality later on. Although there was no significance with CWD levels, one explanation could be that for birch in pits, which are generally at lower locations relative to their surroundings, concentrations of dead wood, responsible for light interception, have more impact than elsewhere. Norway spruce mortality probability was not significantly influenced by the storm severity, which is in accordance with Löf et al. (2007), who found that Norway spruce seedling survival rate was very high even under the most dense canopy conditions. We examined the impact of total CWD volume in a plot, assuming that the amount represented the average effect of sun-blocking or nutrient supply. The spatial distribution of regeneration in relation to the presence of CWD should however also be taken into account. Although the more advanced stages of decay in CWD are found more suitable for regeneration (e.g. Zielonka 2006), stumps can be suitable earlier than logs (Bace et al. 2011). Moreover, the vicinity of CWD has proved favourable for birch (De Chantal et al. 2009; Grenfell et al. 2011) and Norway spruce regeneration (Motta et al. 2006; De Chantal et al. 2009). The protective function of dead wood in the early stages, against browsing (e.g. Krueger & Peterson 2006; de Chantal & Granström 2007), was partly confirmed in this study. We acknowledge that past browsing (e.g. Eichorn et al. 2010) and insect infestations (Nordlander et al. 2011) are affecting population dynamics. However, although signs of browsing were registered on a structural basis, it was not always possible to determine the year in which the damage was done nor the exact agent. For this reason we excluded browsed individuals from height analysis. The true impact of browsing should be investigated in an experimental design, using exclosures.

According to our results regeneration in storm-induced microsites has no increased mortality risk and may rather even increase survival probability in some cases. Focusing on within-microsite development also entails taking into account the surrounding circumstances. However, by the modelling we have tried to identify the generalities about tree survival under different circumstances in storm-induced microsites. The differences within the microsite pit only become clear when distinguishing the different gradients, e.g. for Norway spruce deeper pits increased risk of mortality. Other pit-related characteristics such as larger pit area and thus shallower pits (birch and black alder regeneration) and distance to what was considered the deepest point at the pit centre (black alder regeneration) increase survival probabilities. Both these and other physical conditions apparently affected regeneration mortality in pits more in the beginning of the inventories, whereas disturbance severity started to influence mortality probabilities at a later stage. Taking all microsites together, at least CWD volume only started to affect mortality at later stages since disturbance.

Regeneration species had more impact on mortality probability when analysing all years together, rather than in the separate years. Furthermore, the increasing impact of height and competition later after disturbance confirms our expectation that competition gradually becomes more important. Apparently, initially regeneration even benefits from competition, or in this case facilitating individuals, potentially due to the effect of reducing extreme circumstances, soil stabilisation and improving moisture and nutrient conditions (Callaway & Walker 1997).

At the SAS procedure GLIMMIX, residual analyses indicated that there was no homogeneity of residuals, which may be a sign that some explanatory factor is missing. Other causes of regeneration mortality are post-disturbance tree-fall due to delayed tree death in our study area (Köster et al. 2009) and falling of decaying hanging logs may occasionally cause regeneration mortality. Also meteorological fluctuations, e.g. extreme drought during the growing season (Allan et al. 2010), or soil freezing in early spring or in cold winters with little snow (Sakai & Larcher 1987) can be detrimental. In our case, annual weather data relevant to the subsequent growing seasons show that March 2005 was exceptionally cold, July 2007 was dry and August 2008 was very wet (Tudu and Tiirikoja meteo-stations). Generally, the weather was not so extreme during the period of the inventories (2004-2012) and did not visibly affect the regeneration during the subsequent growing season. Moreover, as the years selected for the mortality study did not coincide with the growing seasons following to the mentioned harsher weather conditions, we have not considered weather in our analyses.

In this study advance (pre-disturbance) and new (post-disturbance) regeneration were analysed as one group. At the start of regeneration inventories in 2004, an attempt was made to distinguish between the new, advance and sprouting regeneration types. However, subsequent observations indicate that more seedlings and saplings established before the storm than previously assumed (Engelhart et al., unpubl.). This illustrates the complexity of determining the type of regeneration even only a few years after disturbance. Due to a lack of continuity in data collection on control and harvested plots, we had to exclude them from the analyses of processes such as height increment and mortality, which require data from successive years. Control data would have provided a better baseline of the pre-disturbance forest, especially regarding the presence and performance of advance regeneration. Furthermore, a new study area, established immediately after a storm in 2010 in northern Estonia, points at the tremendous demographic changes that may take place directly after disturbance (Engelhart et al., unpubl.). As a consequence, comparison between the two regeneration types in our study areas was ruled out at this stage. Nevertheless, we can assume that in tree-fall pits, advance regeneration is much less represented than in the other, more vegetated microsites. In this respect, it is interesting to note that regeneration height in pits has clearly caught up with the regeneration height in other microsites. However, in the additional subplots, where an increased area of intact ground was investigated, regeneration on intact ground in moderately damaged areas was still significantly higher, which may be due to the higher starting position and the assumption that more advance regeneration has survived in less severely damaged areas.

Height and height development in the current study eventually correspond with the theory of life history traits. At first sight, it seems that regeneration strategy does not yet apply in the early stages after windthrow, as birch average height was lower than spruce average height whereas birch surpasses spruce at a later stage since disturbance. However, the response of birch can be explained by the highly significant negative relationship of mortality probability with regeneration height for birch as the only species experiencing this in the earlier inventories, in combination with the fact that birch has the highest seedling densities. The tallest individuals survived and have thus increased the average height. The current study analysed density dependent mortality indirectly through competition indices. There are signals that, at certain spatial scales, intraspecific competition may be stronger than interspecific competition, hence favouring species coexistence (Queenborough et al. 2007; Clark 2010; Metz et al. 2010). This also demonstrates the need to take individual seedling performance and individual species densities into account when analysing seedling mortality. Although we miss the details of pre-disturbance stand characteristics, plots were selected based on comparability regarding canopy tree species composition and stand development stage. Therefore we had an idea of which species were indeed present in the seed bank and this matched also with the dominant species in the regeneration. Regeneration densities were more related to microsite type and less to disturbance severity, nevertheless resulting in clear preferences of species for a certain microsite, which was found in Grenfell et al. (2011) as well. These differences in regeneration species' preferences, in combination with the fine-scale spatial distribution of microsites also pointed at higher species diversity at the stand scale (rather than the microsite scale) in wind-disturbed areas when compared to salvage logged or undamaged forests. In contrast, despite the increased heterogeneity in species, the cohort-like way of regeneration after stand-replacing disturbances may contribute to instability in future stands (Mitchell 2013).

The current study consisted of only two research areas, encompassing two storm events. The low number of repetitions increased the risk of pseudo-replication and of having Type I errors (incorrectly rejecting a true null hypothesis). However, the stochastic character of wind disturbance often does not leave much choice. On top of that, the Estonian Forest Act requires salvage logging in areas with more than 70% damage, which in fact even demonstrates our privileged position of having two areas with comparable forest site types in which the heavily damaged areas are left untouched.

Given the limited number of sample areas in our study, we nevertheless found some clear indications that microsite type, disturbance severity and timing of the study relative to the disturbance year have considerable impact on regeneration mortality probability. It is therefore recommended to be careful with extrapolating the results of a short term study on post-disturbance stand development. A decade of post-storm regeneration inventories implies that due to the heterogeneity of establishment sites, the inherent growth conditions and variation in survival probabilities, the position of a seedling is indeed crucial. More than after clear-cut or other types of natural disturbance, it is likely that in 'left-alone storm sites' the heterogeneity will be reflected in species composition and stand structure. When aiming at disturbance-emulating management, relying on natural regeneration provides a wide range of opportunities. The clear differences in preference of species for wind-induced microsites offer an indication of the future stand composition, with the possibility to both control the proportion of pre- and post-disturbance regeneration (e.g. Seymour & Hunter 1999) and increase disturbance severity, impacting regeneration performance.

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Table 1. Potential mortality factors and hierarchical structure: factors under the same heading are assumed to have a correlation between them and were thus not entered together in the same model test. In both subsets factors were tested for three regeneration tree species separately as well as for all three species together. Bp - *Betula spp.*, Pa - *Picea abies*, Sa - *Sorbus aucuparia* and Ag - *Alnus glutinosa*. Most factors were enclosed in models for the inventory years together as well as in an early stage (2006) after disturbance and a later stage (2009 in microsites subset / 2010 in severities subset), indicated as 'All'. Year was included as a model term in all inventory years together ('O').

Model term	*Description, values, units*	*Level*	Microsites-dataset				Severities-dataset			
			All3	Bp	Pa	Sa	All3	Bp	Pa	Ag
Response variable	Regeneration tree mortality - binary	*ijk*	All	All	All	All	All	All	All	All
Explanatory variables (candidates)		*ijk*								
Storm severity	Plot level	*k*								
Storm severity level	Moderately (contrast), Heavily						All	All	All	All
Storm severity index	0-100 (no damage - all trees dead)		All	All	All	All	All	All	All	All
CWD volume	In m^3ha^{-2}		All	All	All	All	All	All	All	All
CWD basal area	In m^2ha^{-1}		All	All	All	All	All	All	All	All
Microsite	Microsite level	*jk*								
Microsite type	Intact soil (contrast), mound or pit	*jk*	All	All	All	All				
Pit characteristics	Microsite level	*jk*								
Species uprooted tree	Hardwood (contrast) or Norway spruce	*jk*					All	All	All	All
Uprooted tree dbh	In cm						All	All	All	All
Pit area	Two circular sections, in m^2	*jk*					All	All	All	All
Pit depth	At former stem base, in m	*jk*					All	All	All	All
Mound area	In m^2						All	All	All	All
Mound height	From ground level at stem base, in m	*jk*					All	All	All	All
Mound width	At stem base, in m	*jk*					All	All	All	All
Regeneration	Regeneration level									
Regeneration species	Birch (contrast) versus rest	*ijk*	All				All			
Regeneration age	Regeneration level									
Age category	Age cat A (contrast) – C	*ijk*	All	All	All	All	All	All	All	All
Regeneration height	Regeneration level									
Hn1-Hn6	Height in year-1 - year-6	*ijk*	All	All	All	All	All	All	All	All
H2n-H6n	Average height over 2-6 years	*ijk*	All	All	All	All	All	All	All	All
Regeneration height growth	Regeneration level									
HIn1-HIn4	Annual height increment in year-1 to year-4	*ijk*	All	All	All	All	All	All	All	All
Competition	Regeneration level									
CI1n1-CI1n6	Competition index 1 in year-1 to year-5	*ijk*	All	All	All	All	All	All	All	All
CI2n1-CI2n6	Competition index 2 in year-1 to year-5	*ijk*	All	All	All	All	All	All	All	All
Browsing	Regeneration level									
Browsing in past	Binary	*ijk*	All	All	All	All	All	All	All	All
No. of years browsed	In number of years	*ijk*	All	All	All	All	All	All	All	All
Time since disturbance										
Inventory year	Longitudinal aspect of the dataset	*l*	O	O	O	O	O	O	O	O

Table 2. Storm severity index.

Plot	Severity class	BA (m^2/ha) of storm-damaged downed trees	BA (m^2/ha) of storm-damaged standing trees	post-storm BA (m^2/ha) - undamaged standing trees	pre-storm BA (m^2/ha)	Disturbance severity index
H5	Control	1.01	2.41	34.42	37.84	0.090
T2	Control	0	6.82	37.11	43.93	0.155
T8	Control	1.31	1.00	36.47	38.78	0.059
H3	Moderately	4.99	1.83	21.90	28.72	0.237
H4	Moderately	2.81	6.29	17.51	26.61	0.342
H6	Moderately	7.94	9.55	10.47	27.96	0.626
T7	Moderately	2.59	9.58	27.65	39.82	0.306
H8	Heavily	10.74	0.07	0.59	11.41	0.948
T1	Heavily	19.59	10.44	0	30.03	1.000
T5	Heavily	14.56	10.84	0	25.40	1.000
T9	Heavily	21.66	24.62	1.31	47.58	0.973
H1	Harvested	3.42	27.67	0	31.09	1.000
H2	Harvested	2.10	32.38	0.08	34.56	0.998
T6	Harvested	6.76	28.24	0	35.00	1.000
T10	Harvested	4.23	33.37	0	37.60	1.000

Table 3. Pr(>F) of ANOVA type III F-test SS effects of heavy and moderate damage and regeneration microsite on regeneration densities (R-package lmerTest). P-values are *italic* where the interaction between severity and microsite was significant. In the years 2011 and 2012 two additional sets of subplots were monitored in heavily and moderately damaged areas, respectively.

	All species		B. spp.		P. abies		A. glutinosa		S. aucuparia	
	Sev.	Micr.	Sev.	Micr.	Sev.	Micr.	Sev.	Micr.	Sev.	Micr.
All yrs	0.700	**<0.001**	*0.291*	***<0.001***	*0.529*	***<0.001***	*0.137*	***<0.001***	*0.053*	***<0.001***
2004	0.781	**<0.001**	0.419	0.177	*0.603*	***0.002***	*0.795*	***0.015***	0.146	**<0.001**
2005	0.563	0.034	0.293	0.258	0.695	**0.006**	0.518	0.154	0.145	**<0.001**
2006	0.692	0.260	0.553	0.265	0.645	**0.024**	0.387	0.055	0.190	**0.013**
2007	0.604	**0.004**	0.349	0.235	0.817	**0.001**	*0.500*	***0.039***	0.213	**<0.001**
2009	0.914	**0.008**	0.425	0.205	0.957	**0.003**	*0.055*	***<0.001***	0.140	**0.003**
2010	0.398	0.055	0.683	0.072	0.251	**0.017**	*0.211*	***<0.001***	0.168	**0.029**
2011S	Heav	0.139	Heav	0.213	Heav	0.110	Heav		Heav	**0.006**
2012S	Mod	**0.006**	Mod	0.158	Mod	0.265	Mod	**0.012**	Mod	**0.047**
2012	0.953	**0.015**	0.505	0.054	0.892	0.166	*0.083*	***<0.001***	0.144	**0.002**

Table 4. Linear mixed effects logit regression of regeneration. Asterisks represent the level of significance of single terms' effects Pr(>|z| = 0.1 . 0.05 * 0.01 ** 0.001 ***) for the best 2-4 models per column. Parameter estimate signs are in parentheses. M - no significant effect in the model, but required for good model fit. Bp - *Betula spp.*, Pa - *Picea abies*, Sa - *Sorbus aucuparia*, Ag - *Alnus glutinosa*.

Microsite-dataset

	All years together (GLIMMIX)				**2006 (lmer)**				**2009 (lmer)**			
Model term	**All3**	**Bp**	**Pa**	**Sa**	**All3**	**Bp**	**Pa**	**Sa**	**All3**	**Bp**	**Pa**	**Sa**
Storm severity index					***(-)	***(-)	M	**(-)				
Volume CWD									*(-)	**(-)	*(+)	
Basal area CWD							M		*(-)	*(-)	*(+)	
Year	***(+)	***(+)	**(+)	.(-)								
Mound (c: Intact soil)									*(-)	*(-)		
Pit (c: Intact soil)									M	*(-)		
Reg. species Pa (c:Bp)	***(-)											
Reg. species Sa (c:Bp)	**(-)											
Hn1	***(-)	***(-)	*(-)	***(-)	***(-)	**(-)	M	.(-)				
Hn2									**(-)	***(-)	.(-)	*(-)
Hn3			**(-)								*(-)	*(-)
Hn4									***(-)	**(-)	**(-)	*(-)
H2n										***(-)		
H3n			*(-)						**(-)			
H4n												
Hln1					**(-)	**(-)	M	M				
Hln2											*(+)	
Hln3												
Hln4									**(-)	***(-)		
Cl1n1												
Cl1n2												
Cl1n3												
Cl1n4												
Cl2n1	M	M	M	.(-)				*(+)				
Cl2n2					.(-)							
Cl2n3												
Cl2n4												
Past browsing	*(+)								**(+)	**(+)		M
Number of brws years	*(-)		M	*(-)								
Age category B (c:A)	***(+)				*(+)			M				
Age category C (c:A)	***(-)											

Severities-dataset

	All years together (GLIMMIX)				**2006 (lmer)**				**2010 (lmer)**			
Model term	**All3**	**Bp**	**Pa**	**Ag**	**All3**	**Bp**	**Pa**	Ag	**All3**	**Bp**	**Pa**	Ag
Damage level										**(+)	M	
Storm severity index				**(+)					.(+)	**(+)	M	
Volume CWD							M					
Basal area CWD					M		M					
Year		**(+)		***(-)								
Pit area						M						
Pit depth						M	*(+)			M		
Mound area												
Mound height												
Upr tree Pa (c:hw sp)[1]										M	M	
Tree dbh												
Reg. species Pa (c:Bp)	***(-)								M			
Reg. species Ag (c:Bp)	***(+)				M							
Distance to pit centre					M			**(-)				M

Hn1	***(-)	***(-)		***(-)		**(-)		***(-)	***(-)	*(-)	
Hn2											
Hn3								***(-)		.(-)	
Hn4											
H3n											
H4n											
Hln1					*(-)	**(-)					
Hln3											
Hln4											
Cl1n1			.(-)					***(+)	***(+)		*(+)
Cl1n2							M				
Cl1n3											
Cl1n4											
Cl2n1			.(-)					***(+)			*(+)
Cl2n2						*(-)	*(-)				
Cl2n3											
Cl2n4											
Past browsing											*(+)
Number of brws years											
Age category B (c:A)	**(-)			***(-)							M
Age category C (c:A)	***(-)			***(-)							M

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[1] Uprooted tree species: *Picea abies*; contrast: uprooted trees of hardwood species

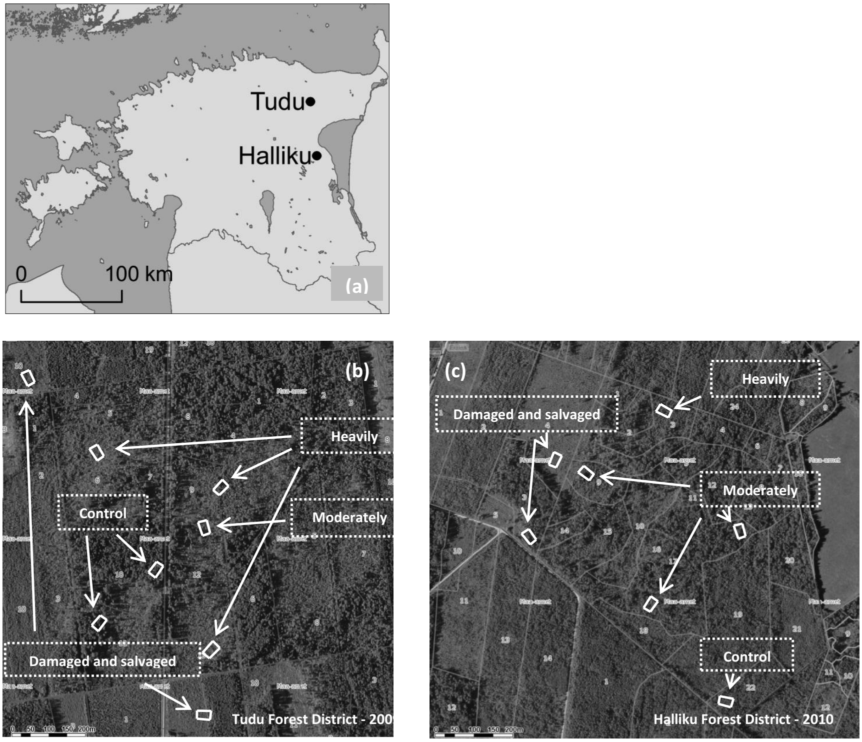

Figure 1. Location of the study areas in Tudu and Halliku forest districts in Estonia (a). Location of the plots in Tudu (b) and Halliku (c). Source aerial photographs: Maa-amet & Metsaregister.

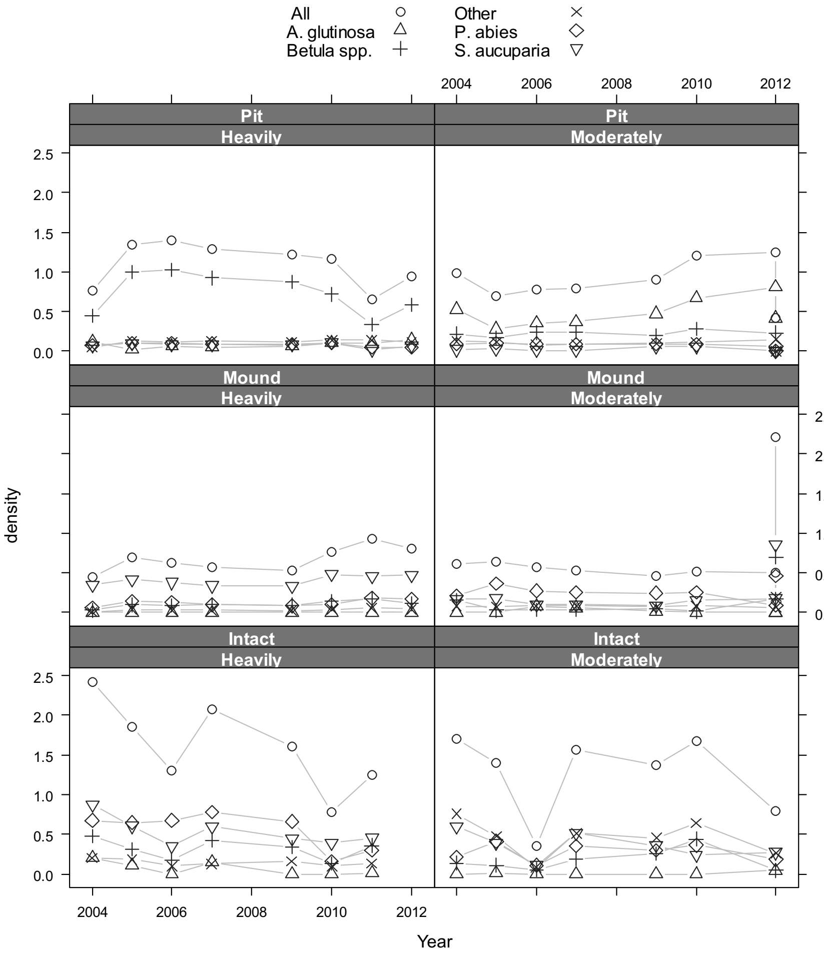

Figure 2. Density development of regenerating trees per species (# m^{-2}), arranged by damage severity level and regeneration microsite.

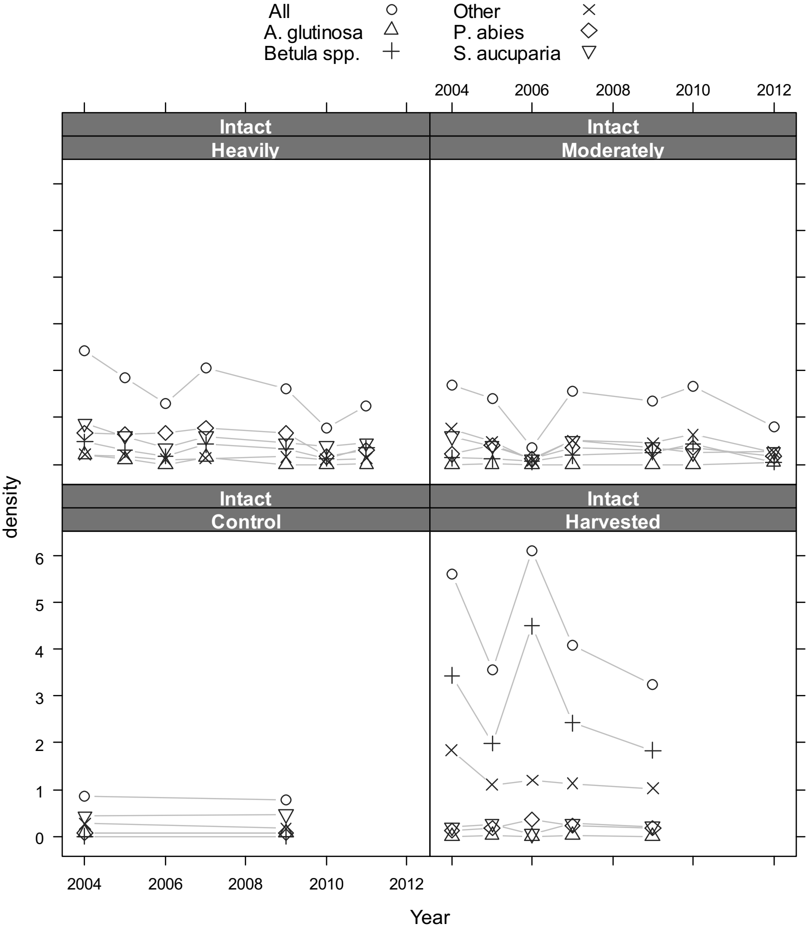

Figure 3. Regeneration densities on the additional control and harvested severity 'treatments' on intact soil.

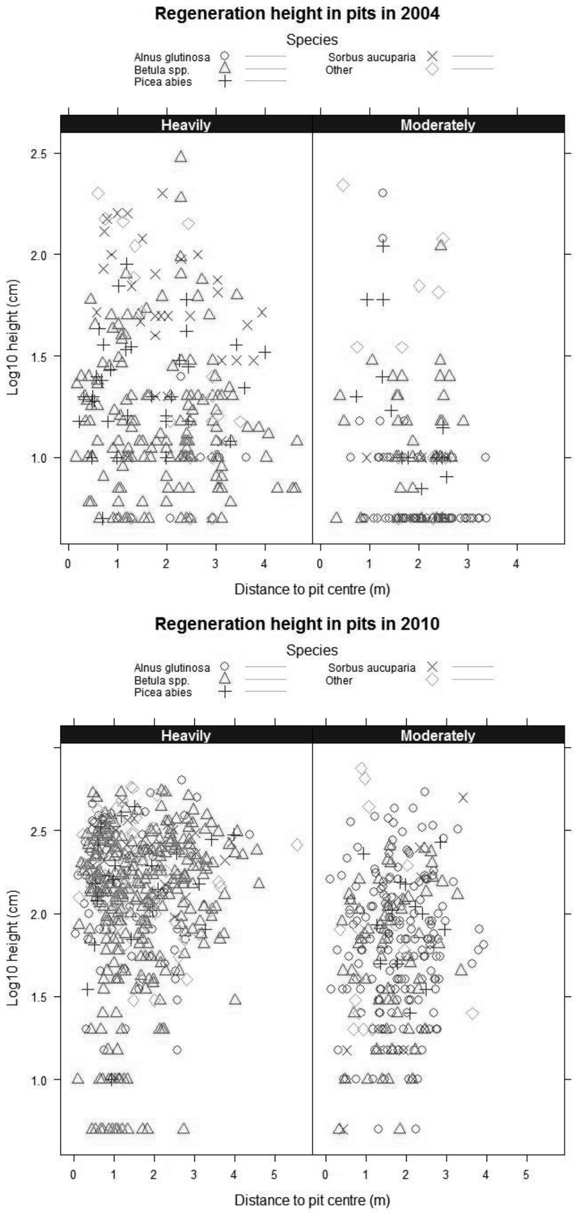

Figure 4. Regeneration (log-transformed) height in relation to distance to the pit centre at different stages since disturbance [can be redone in black and white]

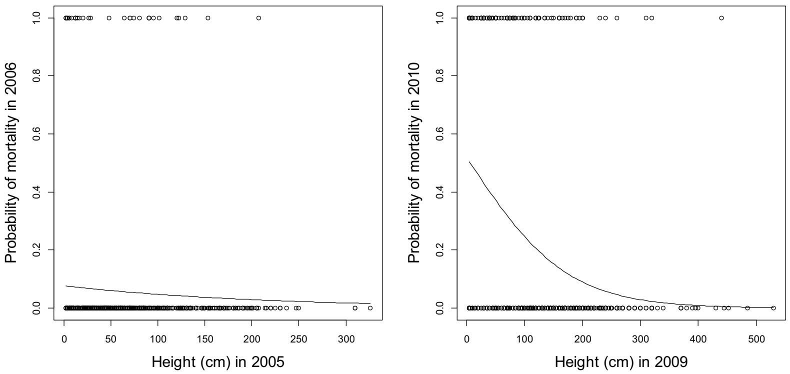

Figure 5. Mortality probability in year *n* as a function of regeneration tree height in year *n*-1 at different stages since disturbance

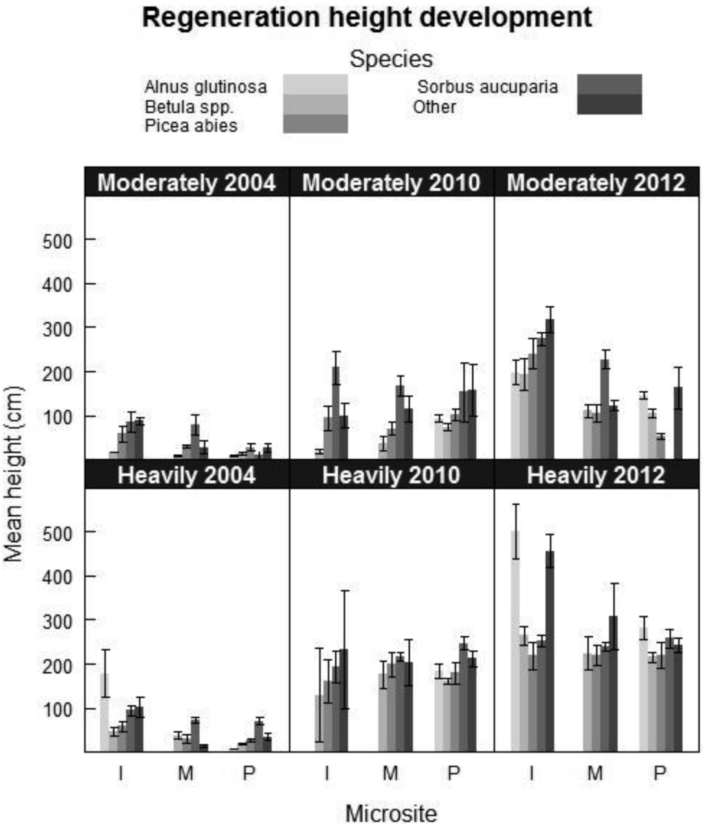

Figure 6. Regeneration height development by species under varying growth circumstances. The 2012 measurements include the additional subplot data, which particularly enlarged the sample area of intact soil. Error bars represent standard error. I – intact soil, M – mound, P – pit.

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2011	PhD winter school "Forest Disturbance Ecology" (Estonia)
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Awards:

2008	Prince Bernhard Cultural Fund Grant for Young Artists and Scholars to Study Abroad

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2008–2013	Target financed project SF0170014s08: "The effect of changing climate on forest disturbance regimes in temperate and boreal zone". Investigator
2011-2012	Baseline financed project 8-2/T9002MIMI: "Forest design studies". Investigator
2010–2012	Estonian Science Foundation grant No. 8496: "Microsites and other ecological factors influencing natural regeneration in disturbance areas". Investigator
2009–2010	Environmental Investment Centre project 8-2/ T9030MIMI: "Economic and ecological estimation of forest windthrow and fire". Principal investigator
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2002–2006	EU COST Action E27 – Protected Forest Areas in Europe – Analysis and Harmonisation

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2008	Doktorikursus "Ecology, silviculture and economics of multi-functional forestry" (Eesti)
2006	Doktorikursus "Restoration in boreal and broadleaved (temperate) forest zones" (Soome, Eesti, Rootsi, Taani)

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2008	Prints Bernhardi Kultuurifondi stipendium noortele kunstnikele ja teadlastele välismaal õppimiseks

Projektid:

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2010–2012	ETF grant nr 8496: "Mikroreljeefi ja ökoloogiliste faktorite mõju puurinde looduslikule uuendusele häiringualadel". Täitja
2009–2010	Baasfinantseeritav teema nr 8-2/T9030MIMI: "Tormikahjustuste ja metsapõlengute majanduslik ja ökoloogiline hindamine"
2007	EFORWOOD Work Package 2.4 – Risk Assessment
2002–2006	EU COST Action E27 – Protected Forest Areas in Europe – Analysis and Harmonisation

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VIIS VIIMAST KAITSMIST

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(*Byturus tomentosus* De Geer)
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Professor **Jüri Olt**
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(*Malus domestica* Borkh.) POOKEALUSEST JA KALTSIUMIGA VÄETAMISEST
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