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

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ABSTRACT

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

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

1. Introduction

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

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

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

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

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

2. Materials and methods

2.1. Study area

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

2.2. Field methods

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

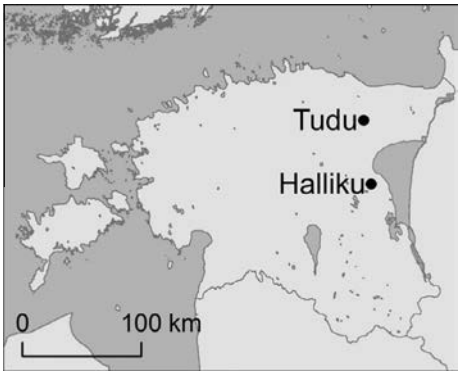

Fig. 1. Location of the study areas in Tudu and Halliku forest districts in Estonia.

Tree regeneration, which in this study includes established seedlings (height 5 cm–1.3 m), saplings (height 1.3–5 m), and understory tree regeneration (height 5 m – start of the canopy, around 70% of the average canopy tree height), 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. Systematic sampling was used to monitor regeneration on intact soil in each plot, thus covering various light conditions and potentially (e.g. salvage-logged plots) including displaced soil: ten 1×1 m quadrats were placed at regular distances (4 m) along the 40 m plot mid line. If the quadrat included logs or pit-and-mound complexes, then its position was moved to the right or left of the plot mid line. 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.

Regeneration inventories on moderately and heavily damaged plots took place annually during summer, from 2004 to 2012, except for the years 2008 and 2011, while the control plots were inventoried in 2004 and 2009, and the salvaged plots irregularly from 2004 to 2007 and in 2009. For all living regeneration, we recorded (see also Supplementary materials Table S1) 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). Tree age categories consisted of A (1–2 years old regeneration), B (3–4 years) and C (5 years and older). As silver and downy birch seedlings often are difficult to distinguish, all birch trees have been further analysed as *Betula* spp. Due to 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 analyses. Harvested and control plots therefore solely serve as a background to compare certain trends in species composition and height several years 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. In heavily damaged plots, the area covered by a total of 70 pit-and-mound complexes ranged between 10.1% and 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 individuals 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.

2.3. Data processing

The entire dataset was used for analysis of the effects of microsite, disturbance severity on density and height development by tree species. In case of mortality, regeneration was registered as such (mortality = '1') in the year after the last live height measurement. This implies data should be collected in two successive years, which was not always the case. Therefore there was not sufficient data to compare mortality for all species among all combinations of microsite types, disturbance severity levels, and at two times since disturbance. Therefore, the main data set 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. Secondly, within each of the two subsets we selected two years as far apart from each other as possible, to examine the differences in regeneration mortality at two post-disturbance stages. The microsite subset contained the regenerating tree species *Betula* spp., *P. abies* and *Sorbus aucuparia*, and the number of observations for all years (n_{all}) was 3536, including repeated monitoring of the same trees over time, while early and late stages (n_{early} and n_{late}) had 611 and 582 observations, respectively. Specific microsite-level factors and differences between the heavy and moderate damage levels were analysed only in pits in the severity-subset, with regenerating tree species *Betula* spp., *P. abies* and *A. glutinosa*. For this subset $n_{all} = 4435$, $n_{early} = 699$, and $n_{late} = 863$.

Potential factors influencing mortality are summarised in Table S1. The potentially most important storm effects for regeneration performance are increased light availability and higher levels of CWD. A storm severity index (SSI, Table S1) was calculated for all plots, based on the ratio of post-disturbance basal area (BA) of storm-damaged trees and pre-disturbance plot BA, based on the Intensity Index in Rich et al. (2007). SSI in control plots ranged from 0.06 to 0.15, in moderately damaged plots 0.24–0.63, in heavily damaged plots 0.95–1.00 and in harvested plots approximated 1.00. Post-disturbance BA of damaged trees consists of the plot sum of cross-sectional stem areas at *dbh* or at 1.3 m 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.

Competition indices for regeneration are generally based on position relative to competing trees (Hegyi, 1974; adapted for saplings in Metslaid et al., 2005a), in some cases adjusted for direction relative to the sun (shading, Kuuluvainen and Kalmari, 2003), individual and competing tree heights (Hegyi, 1974; Kuuluvainen and Kalmari, 2003) or basal diameter (Collet and Le Moguedec, 2007). The maximum distance at which to include competing trees varies with tree size (Collet and Le Moguedec, 2007; Sims et al., 2009). Because in this study regeneration was in clearly distinguishable microsites, we used regeneration in a single microsite to estimate competition experienced by a regenerating tree. Competition from surrounding mature trees was incorporated in the disturbance severity of a plot. Height (not diameter) of regeneration trees was measured; therefore height and density of competing regeneration was the basis for calculation of competition indices *CI*1 and *CI*2, as a combination of previous competition indices (Hegyi, 1974; Kuuluvainen and Kalmari, 2003; Collet and Le Moguedec, 2007):

$$CI_i1 = \frac{\overline{h}_j}{h_i} * D_j \quad (1)$$

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

where CI_i is the competition index of regenerating tree i, $\overline{h}_j$ 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 likely more suppressed than its neighbours and *vice versa* for negative values. 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 2–6 year period before year n (H_{2n}, H_{3n}, etc., Table S1).

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 browsed in the current or previous years were not used in the analysis of regeneration 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.

2.4. Statistical analysis and modelling

The probability of mortality for regenerating trees (p_i) in the first decade since disturbance was analysed for the previously defined microsite and severity subsets. 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 S1):

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

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 were 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 were 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 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).

3. Results

3.1. Occupation of microsites in storm areas

Throughout the years, regeneration densities differed significantly (bold values) between microsites and species (Table 1 and Fig. 2). 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}, Fig. 3). These values can be compared to the mean regeneration density on intact soil on harvested sites (4.29 m^{-2}) and control sites (0.81 m^{-2}, Fig. 4). 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 (Fig. 3). Birch regeneration dominated pits in heavily damaged areas and black alder and birch were the most common species in pits of moderately damaged areas. 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 with 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.

3.2. Factors affecting regeneration mortality

Regeneration mortality was lowest for spruce regeneration ($p < 0.001$). On mounds, mortality was significantly higher in moderately damaged areas than in heavily damaged areas. No overall trend over time since disturbance in mortality for all species pooled was observed. Taking all microsites together, birch and rowan mortality was initially slightly lower in plots with 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 mortality later increased in plots with higher disturbance severity including high dead wood levels, whereas black alder and spruce mortality was initially low in areas of higher amounts of dead wood. For all years together, black alder (analysed in pits only) had higher mortality probability with higher storm severity (Table 2).

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 2). 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.

Table 1
Significance of storm damage level and microsite type on regeneration density. ANOVA *P*-values for main effects and interaction (SSQ type 3). Significance levels $P < 0.005$ are bold. Function anova() in *R*'s package lmerTest, Satterthwaite for approximation of degrees of freedom.

	All species			*Betula* spp.			*P. abies*		
	Sev.	Micr.	Sev* Micr	Sev.	Micr.	Sev* Micr	Sev.	Micr.	Sev* Micr
All yrs	0.700	**<0.001**	0.467	0.291	**<0.001**	**0.004**	0.529	**<0.001**	**<0.001**
2004	0.781	**<0.001**	0.186	0.419	0.177	0.191	0.603	**0.002**	**0.012**
2005	0.563	**0.034**	0.709	0.293	0.258	0.461	0.695	**0.006**	0.073
2006	0.692	0.260	0.765	0.553	0.265	0.550	0.645	**0.024**	0.137
2007	0.604	**0.004**	0.747	0.349	0.235	0.591	0.817	**0.001**	0.050
2009	0.914	**0.008**	0.906	0.425	0.205	0.420	0.957	**0.003**	0.079
2010	0.398	0.055	0.152	0.683	0.072	0.366	0.251	**0.017**	0.275

	A. glutinosa			*S. aucuparia*		
	Sev.	Micr.	Sev* Micr	Sev.	Micr.	Sev* Micr
All yrs	0.137	**<0.001**	**<0.001**	0.053	**<0.001**	**0.028**
2004	0.795	**0.015**	**0.041**	0.146	**<0.001**	0.708
2005	0.518	0.154	0.050	0.145	**<0.001**	0.763
2006	0.387	0.055	0.317	0.190	**0.013**	0.557
2007	0.500	**0.039**	**0.010**	0.213	**<0.001**	0.762
2009	0.055	**<0.001**	**<0.001**	0.140	**0.003**	0.518
2010	0.211	**<0.001**	**<0.001**	0.168	**0.029**	0.241

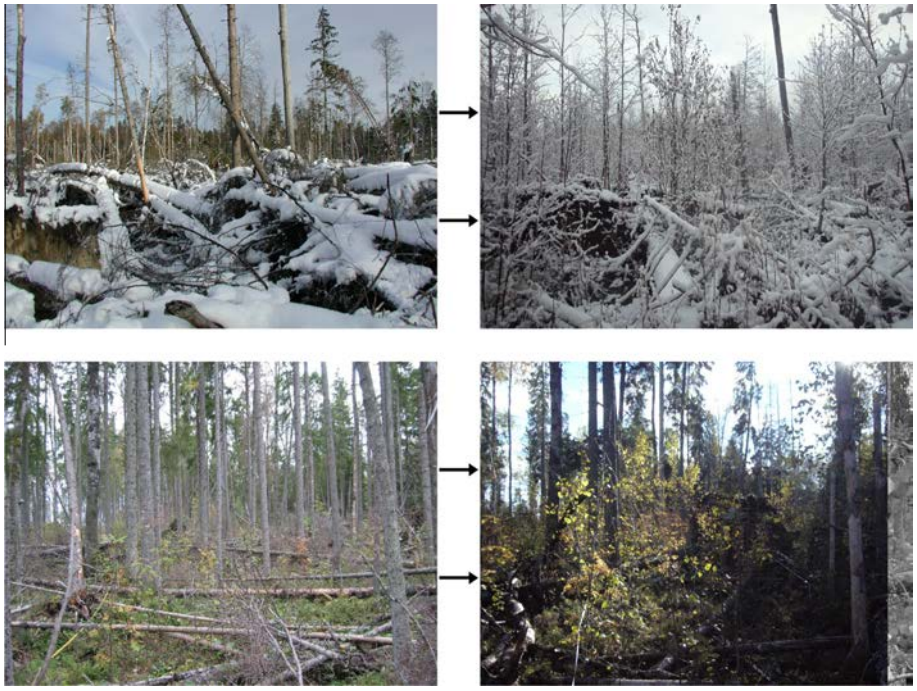

Fig. 2. Structural development in a 'heavily damaged' plot (above, 2002 and 2012) and a 'moderately damaged' plot (below, 2003 and 2013).

Deeper pits seemed to be safer for birch (not shown, because only significant in models that were not selected) and less so for spruce (Table 2), 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 mortality was generally negatively correlated to 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 2).

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 (severity-subset), over all years black alder had higher mortality probabilities than birch and spruce (Table 2). 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 (Fig. 5 and Table 2) or had grown faster in the past, although in some cases initial fast growth increased mortality risk (Table 2). Higher levels of competition increased mortality probability as time since disturbance increased. Rowan was the only species on all microsites that initially had high mortality linked to higher competition. In pits the difference between the stages was remarkable: initially, higher competition implied better conditions for germination,

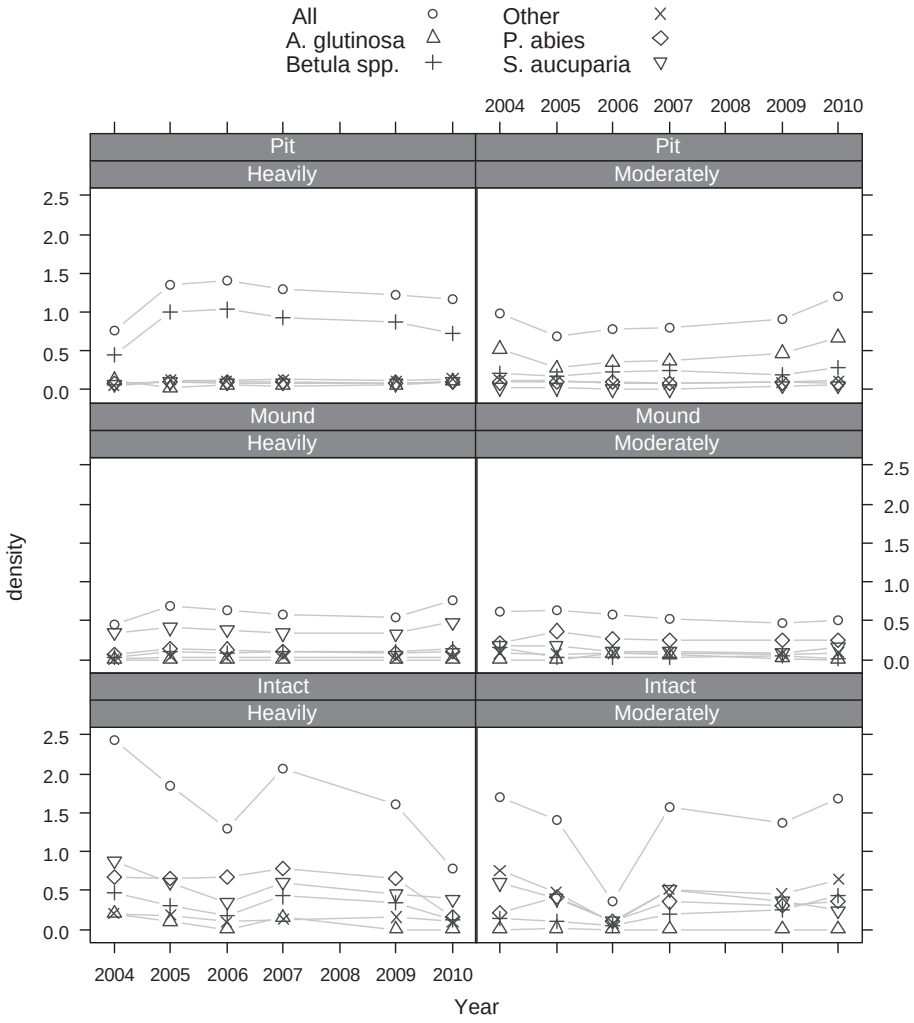

Fig. 3. Density development of regenerating trees per species (#m^{-2}), arranged by damage severity level and regeneration microsite.

establishment and survival of many seedlings, whereas in later years, high competition levels increased regeneration mortality (Table 2).

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 2).

3.3. Regeneration height development

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, Fig. 6). Regarding individual species, *P. abies*, *Betula* spp. and *A. glutinosa* initially were all in the lower ranges of height, whereas together with *S. 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 regeneration in moderately damaged areas was 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 (HSD test, Fig. 6).

4. Discussion

We analysed regeneration densities and heights one decade post-disturbance under different circumstances and whether factors affecting regeneration mortality vary with time since wind disturbance. In the latter, division of the main database into smaller subsets led to significant insights. Birch was a good example: in the microsite-subset survival was higher with increased disturbance severity early and with more dead wood later after disturbance, whereas in the severity-subset, with only pits included, disturbance severity seemed to promote mortality later on. One possible explanation could be interception of light by

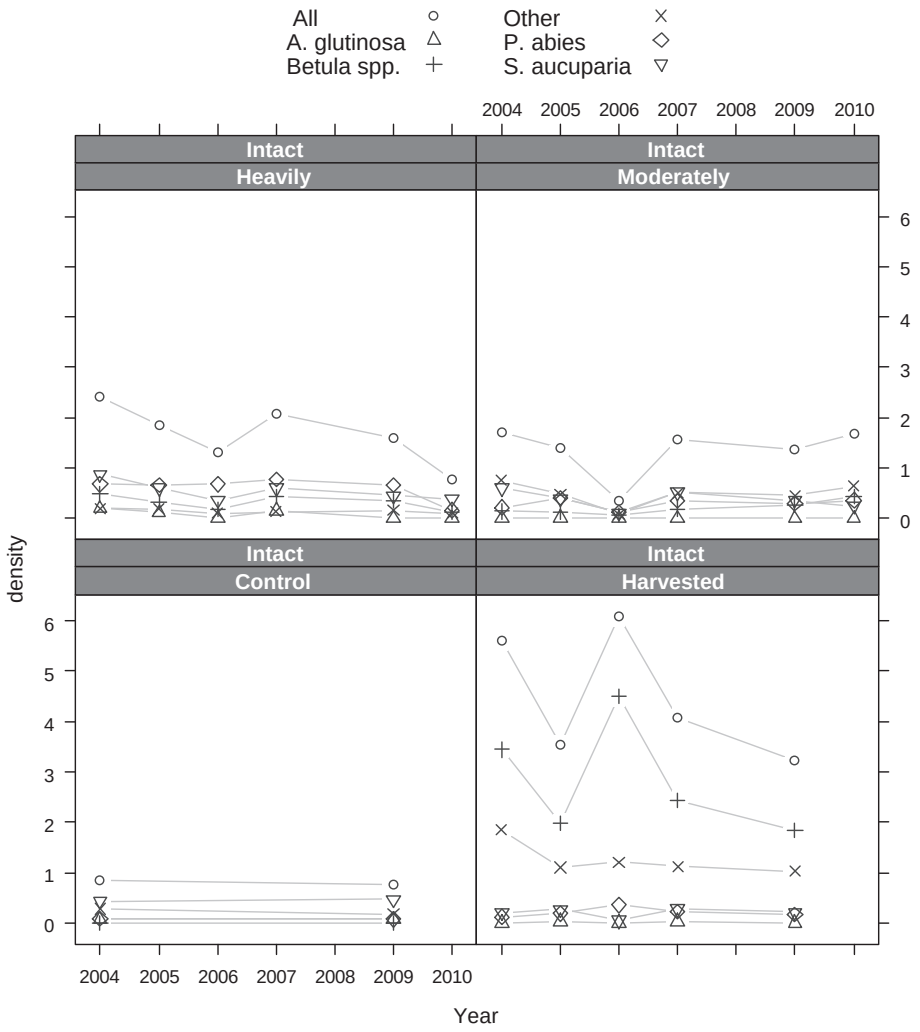

Fig. 4. Regeneration densities on the additional control and harvested severity 'treatments' on intact soil.

concentrations of coarse woody debris that affect birch in pits at relatively low locations more than elsewhere, despite the overall non-significance of CWD in the models. Norway spruce mortality was not significantly influenced by storm severity, in agreement with Löf et al. (2007), who found that Norway spruce seedling survival was very high even under the most dense canopy conditions. We analysed total plot CWD effects on mortality probability, assuming that represented the average effect of sun-blocking or nutrient supply. However, the spatial distribution of regeneration in relation to CWD can also be important. Although the more advanced stages of decay in CWD are 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 and Peterson, 2006; de Chantal and Granström, 2007), was partly confirmed in this study. We acknowledge that past browsing (e.g. Eichhorn et al., 2010) and insect infestations (Nordlander et al., 2011) have affected population dynamics. Although signs of browsing were recorded, 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.

Our results showed that mortality risk for regeneration on storm-induced microsites was in general no higher than elsewhere, but that certain circumstances within these microsites may interact with species to raise or lower mortality. Differences within microsite pits become clear when examining gradients. For Norway spruce deeper pits increased risk of mortality. Increased survival was experienced by birch and black alder regeneration in larger (also shallower) pits, and by black alder at greater distances from pit centres (i.e. deepest points in pits). These and other physical conditions apparently affected regeneration mortality in pits more shortly after disturbance while disturbance severity started to influence mortality probabilities later on. Taking all microsites together, 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 individual years. Furthermore, the increasing impact of height and competition in later years confirms our expectation that competition gradually becomes more important. Apparently, regeneration initially benefits from competition, or in this case facilitating individuals that likely reduce extreme circumstances, stabilise soil and improve moisture and nutrient conditions (Callaway and Walker, 1997).

We did not measure all factors contributing to mortality, and there was substantial unexplained variability in the models. Other causes of regeneration mortality in our study area are post-disturbance tree-fall due to delayed tree death (Köster et al.,

Table 2
Linear mixed effects logit regression of regeneration mortality probability. 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; + indicates higher mortality probability with increasing model term. M – no significant effect in the model, but required for good model fit. C: contrast. Bp – *Betula* spp., Pa – *Picea abies*, Sa – *Sorbus aucuparia*, Ag – *Alnus glutinosa*. Please refer to Table S1 for variable description, values and units, and to Table S2 for fitted models.

Model term	All years together (GLIMMIX)				2006 (lmer)				2009 (lmer)			
	All3	Bp	Pa	Sa	All3	Bp	Pa	Sa	All3	Bp	Pa	Sa
Microsite-subset												
Storm severity index					***(−)	***(−)	M	**(−)				
CWD volume									*(−)	**(−)	*(+)	M
CWD basal area							M			*(−)	*(+)	M
Inventory year	***(+)	***(+)	**(+)	·(−)								
Mound (c: Intact soil)								M	*(−)	*(−)		
Pit (c: Intact soil)								M	M	*(−)		
Reg. species Pa (c:Bp)	***(−)				M							
Reg. species Sa (c:Bp)	**(−)				·(+)							
H_{n1}	***(−)	***(−)	*(−)	***(−)	***(−)	**(−)		·(−)				
H_{n2}									**(−)	***(−)	·(−)	*(−)
H_{n3}												*(−)
H_{n4}									***(−)	**(−)	**(−)	*(−)
H_{2n}										***(−)		
H_{3n}			*(−)						**(−)			
H_{4n}												
HI_{n1}					**(−)	**(−)	M	M				
HI_{n2}											*(+)	
HI_{n3}												
HI_{n4}									**(−)	***(−)		
$CI1_{n1}$												
$CI1_{n2}$												
$CI1_{n3}$												
$CI1_{n4}$												
$CI2_{n1}$	M	M	M	·(+)	M			*(+)				
$CI2_{n2}$					M			M	M			
$CI2_{n3}$												
$CI2_{n4}$												
Browsing in past	*(+)								**(+)	**(+)		M
No. of years browsed	*(−)		M	*(−)	M			M				
Age category B (c:A)	***(+)				*(+)			M				
Age category C (c:A)	***(−)				M			M				

Model term	All years together (GLIMMIX)				2006 (lmer)				2010 (lmer)			
	All3	Bp	Pa	Ag	All3	Bp	Pa	Ag	All3	Bp	Pa	Ag
Severity-subset												
Storm severity level										**(+)	M	
Storm severity index				**(+)					·(+)	**(+)	M	
CWD volume							M					
CWD basal area			M		M		M					
Inventory year		**(+)		***(−)								
Pit area						M						
Pit depth						*(−)	·(+)			M		
Mound area												
Mound height												
Upr tree Pa (c:hw sp)[a]										M	M	
Upr tree dbh					*(+)							
Reg. species Pa (c:Bp)	***(−)				M				M			
Reg. species Ag (c:Bp)	***(+)				***(+)				M			
Distance to pit centre					*(−)			*(−)				M
H_{n1}	***(−)	***(−)	M	***(−)		**(−)			***(−)	***(−)	*(−)	
H_{n2}												
H_{n3}									**(−)			
H_{n4}												
H_{3n}												
H_{4n}												
HI_{n1}					*(−)	**(−)						
HI_{n3}												
HI_{n4}												
$CI1_{n1}$			·(−)	M		M			**(+)	**(+)	·(−)	*(+)
$CI1_{n2}$								M				
$CI1_{n3}$												
$CI1_{n4}$												
$CI2_{n1}$			·(−)									*(+)
$CI2_{n2}$					**(−)	*(−)		*(−)				
$CI2_{n3}$												
$CI2_{n4}$												

(*continued on next page*)

Table 2 (*continued*)

Model term	All years together (GLIMMIX)				2006 (lmer)				2009 (lmer)			
	All3	Bp	Pa	Sa	All3	Bp	Pa	Sa	All3	Bp	Pa	Sa
Browsing in past												*(+)
No. of years browsed			M									
Age category B (c:A)	**(−)			***(−)								***(−)
Age category C (c:A)	***(−)			***(−)								*(−)

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

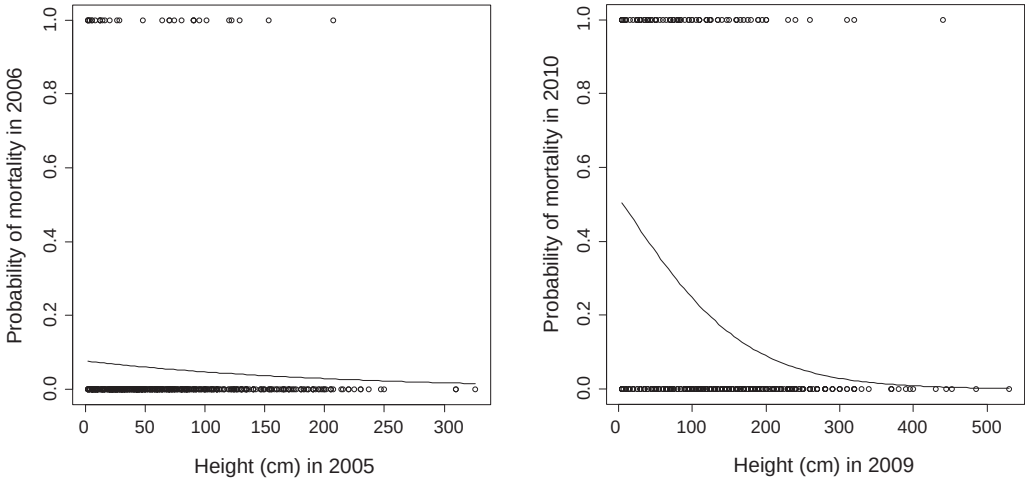

Fig. 5. Mortality probability in year n as a function of regeneration tree height in year $n-1$ at different stages since disturbance, for all regeneration tree species pooled.

2009) and falling of decaying hanging logs. Meteorological fluctuations can be detrimental to regeneration, including extreme drought during the growing season (Allan et al., 2010), or soil freezing in early spring or in cold winters with little snow (Sakai and Larcher, 1987). Weather data for post-disturbance growing seasons show that March 2005 was exceptionally cold, July 2007 was dry and August 2008 was very wet (Tudu and Tiirikoja meteo-stations). However, in general the weather was not extreme during the inventory period (2004–2010) and did not visibly affect the regeneration.

Furthermore, what could have been measured from the beginning, are site conditions, e.g. air humidity, soil moisture, microclimate, soil chemical composition and texture, incoming PAR, etc. in the different microsites and between the severity levels. We have tried to overcome this deficiency by proxies such as distance to the pit centre (negatively correlated to soil moisture), abundance of CWD in the plot and storm severity index (reflecting light conditions), and supportive literature e.g. (Beatty, 1984; Beatty and Stone, 1986; Callaway and Walker, 1997) for soil chemical and physical conditions after the storm. 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) were included.

In this study advance (pre-disturbance) and new (post-disturbance) regeneration were analysed together. 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.). It is hard to judge from tree growth form whether it is pre- or post-storm 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 these 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, showed that tremendous demographic changes 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 tree-fall pits have little advance regeneration compared to 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. Details with respect to the recovery capacity of advance regeneration and the impact on newly establishing regeneration remain relatively obscure (Metslaid et al., 2005b).

Height and height development in the current study correspond with the theory of life history traits. Shortly after disturbance the average height of early-successional, shade-intolerant birch was shorter than late-successional, shade-tolerant spruce, whereas birch height surpasses spruce later on. However, this differential response is not due solely to the expected faster height growth of birch; the response of birch can be explained by the highly significant negative relationship of mortality probability with

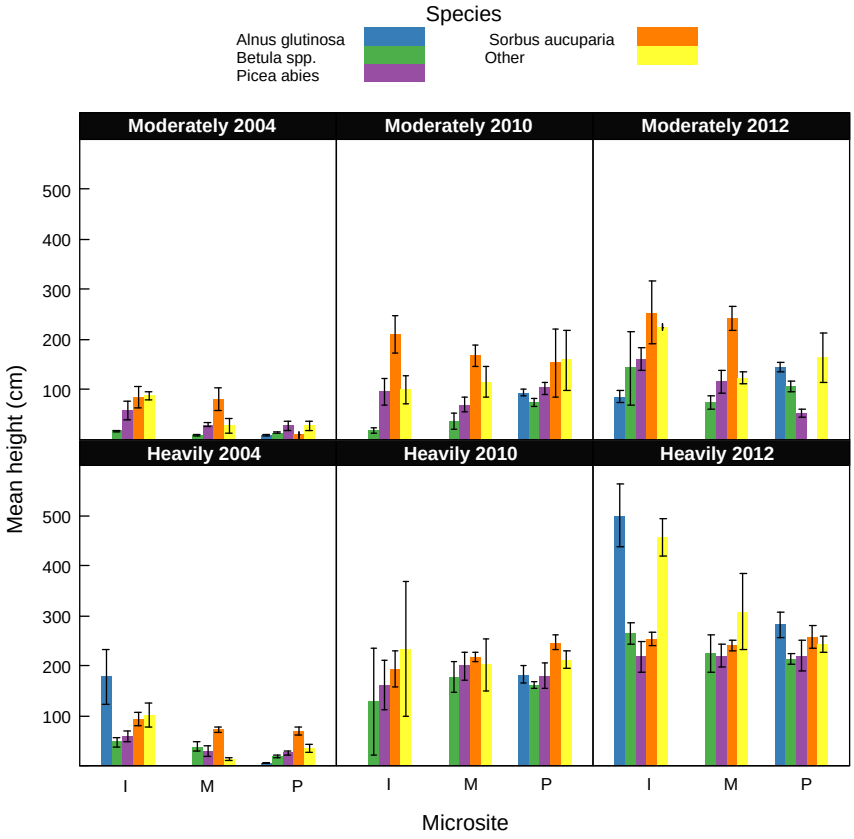

Fig. 6. Regeneration height development by species, microsite and disturbance severity level during the first post-disturbance decade. Error bars represent standard error. I – intact soil, M – mound, P – pit.

regeneration height for birch as the only species experiencing this in the earlier inventories, in combination with the fact that birch has the highest regeneration densities. The tallest individuals survived and have thus increased the average height. Thus, height and density are closely linked to the overall response of post-disturbance regeneration.

The current study analysed density dependent mortality indirectly through competition indices. Previous studies hinted 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). In this study, regeneration densities were more related to microsite type and less to disturbance severity, resulting in clear preferences of species for a certain microsite, a result also found by Grenfell et al. (2011). Remarkable is that, even though merely a trend, in only one case did the dominant species of regeneration in the wind-induced microsites coincide with the co-dominant or dominant species on intact soil (Fig. 2). In the light of climate change the results may also offer perspectives for adapting stand species composition, including species which are currently regarded as sub-optimal. The differences in regeneration species' preferences, in combination with the fine-scale spatial distribution of microsites apparently lead to higher species diversity at the stand scale (rather than the microsite scale) in wind-disturbed areas as compared to salvage-logged or undamaged forests, resulting in complex 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, and convincing the government to leave two areas with comparable forest site types in which the heavily damaged areas are left untouched demonstrates our privileged position.

5. Conclusions

Although the number of available study areas was limited, we nevertheless found some clear indications that microsite type, disturbance severity and time since disturbance have considerable impact on regeneration mortality. Regeneration mortality and species composition are initially directed by exogenous factors linked to storm severity and microsite heterogeneity, generating a degree of spatial partitioning within a microsite, whereas gradually species' life-history traits and competition take over. As this process may take several years post-disturbance to become apparent, we recommend taking great care when extrapolating the results of short term studies on post-disturbance stand development. A decade of post-storm regeneration inventories implies that, due to the inherent heterogeneity of establishment sites, growth conditions, and resulting 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 for sites left-alone after major wind disturbance, this 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 and Hunter, 1999) and increase disturbance severity, impacting regeneration performance.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2015.03.052.

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