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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

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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 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.

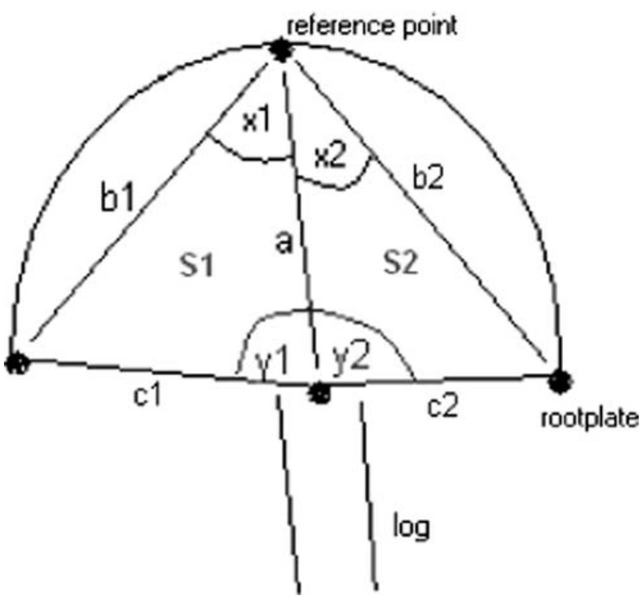


Fig. 1 Measurement of pit area. Distances *a*, *b1* and *b2*, and angles *x1* and *x2* from the reference point were recorded. Distances *c* and angles *y* can be derived using the sine and cosine theorems. Sections *S1* and *S2* were determined separately by calculating the disk sections of each and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

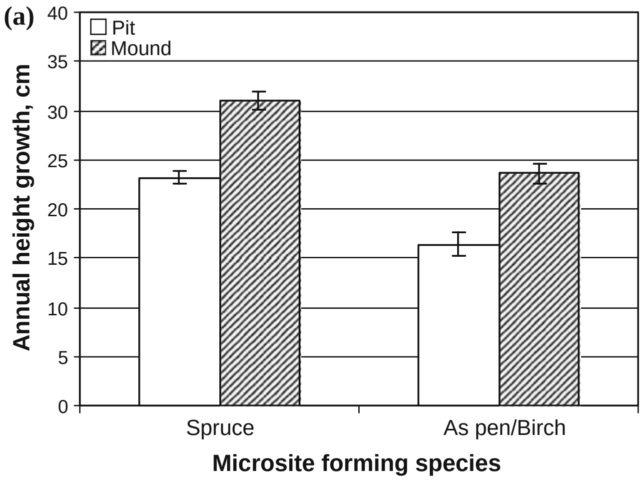
Based on the height growths of all species in all years, the most favorable microsite was a spruce mound in a heavily damaged area. Seedlings grew taller on mounds than in pits and in heavily damaged versus moderately damaged areas (Fig. 2). All factors (microsite-forming species, microsite type, and 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



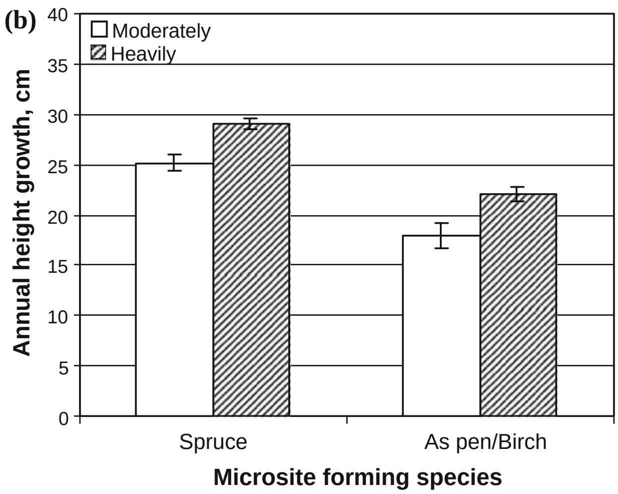


Fig. 2 The mean annual height growths of seedlings (all regenerating tree species, age classes, and observed years pooled) in microsites created by different microsite-forming species (spruce, aspen/birch) in combination with **a** microsite type (pit, mound) and **b** microsite location (moderately,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

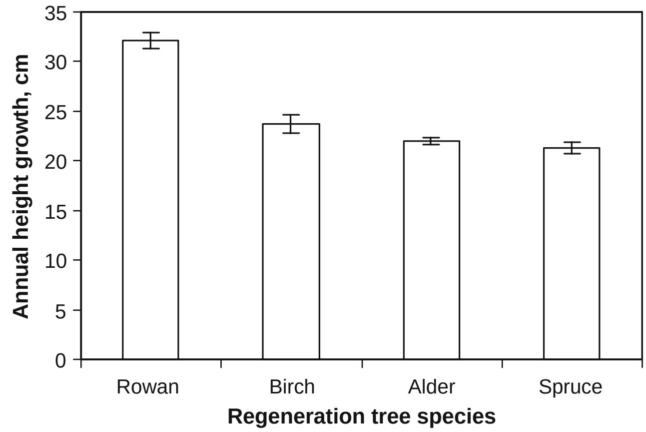


Fig. 3 The mean annual height growths of rowan, birch, alder and spruce seedlings (all microsites, age classes, and observed years pooled). *Error bars* show standard error

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

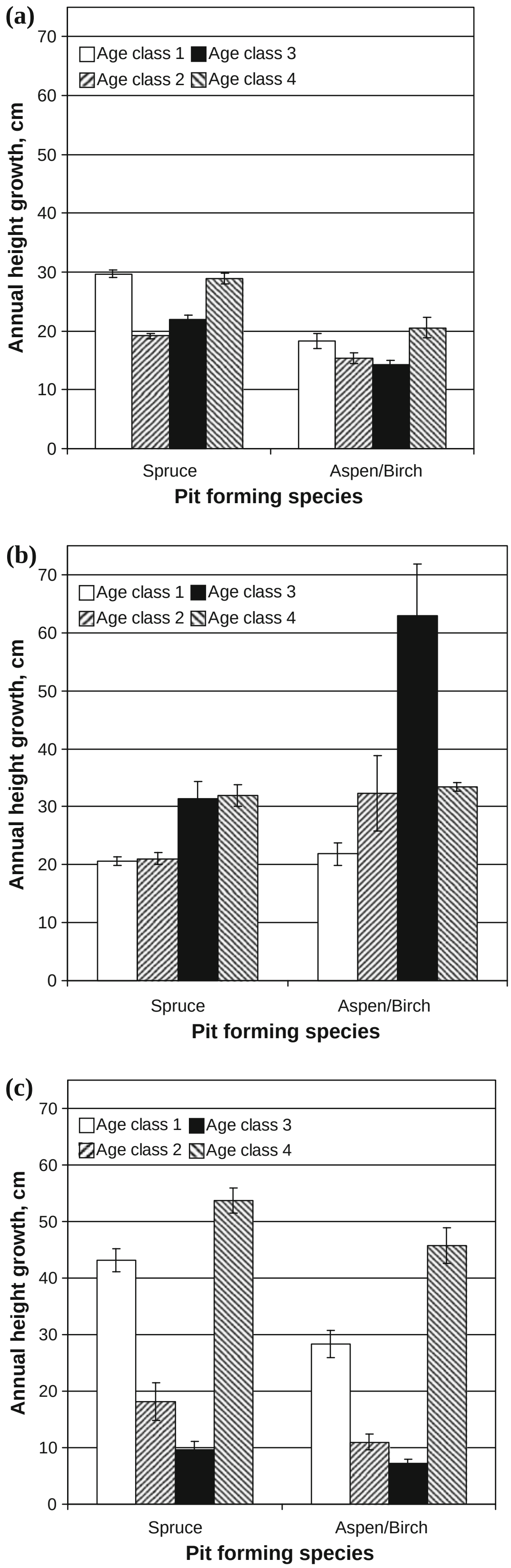


Fig. 4 The mean annual height growths of **a** birch, **b** black alder and **c** Norway spruce seedlings of different ages in pits of uprooted spruce and hardwoods (aspen/birch). *Error bars* show standard error

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

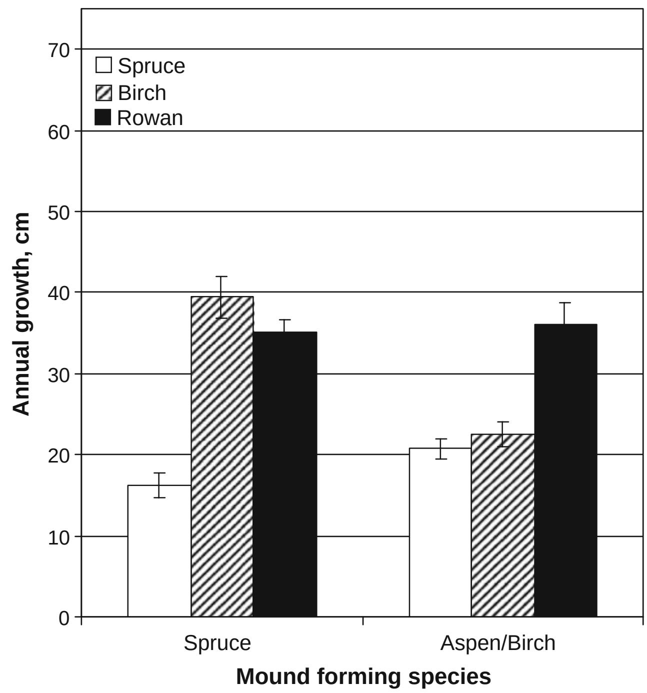


Fig. 5 The mean annual height growths of spruce, birch and rowan seedlings on mounds of uprooted spruce and hardwoods (aspen/birch). *Error bars* show standard error

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

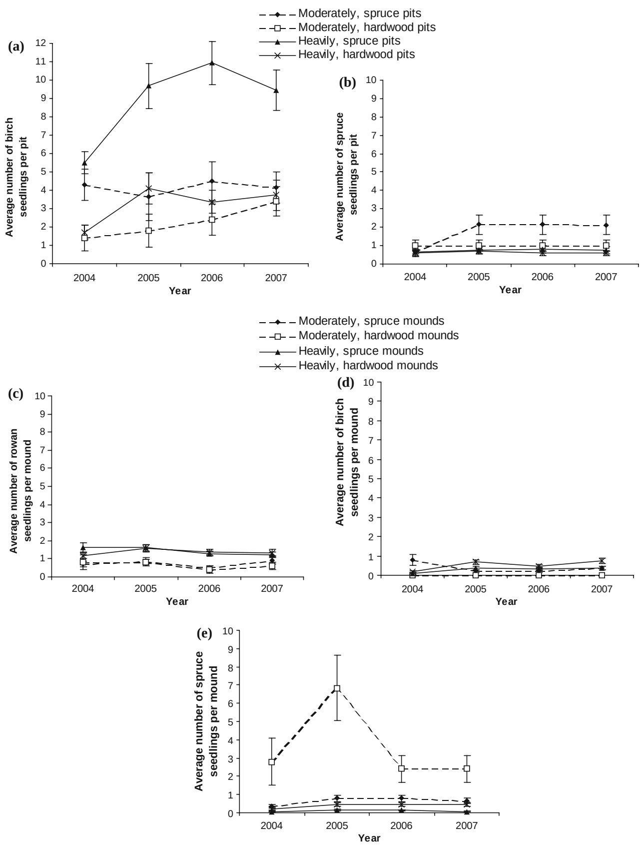


Fig. 6a–e Average number of birch and spruce seedlings per pit (**a**, **b**), and rowan, birch and spruce seedlings per mound (**c**–**e**), respectively, by microsite type and species of uprooted tree in different years. *Error bars* show standard error

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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