Natural Succession of Norway Spruce Stands in Hemiboreal Forests: Case Study in Slitere National Park, Latvia

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Abstract

The dynamics of unmanaged forest ecosystems is led by the natural disturbances, among which storms are one of the most important, especially due to occurring and predicted increase in their frequency. Mimicking of the natural disturbances is considered a part of the forest management strategy in the particular areas. However, the diversity of the possible initial stand and landscape composition leads to the various corresponding pathways of recovery after the disturbance. So far, a limited number of short term (up to 25 years after the windthrow) empirical studies have assessed them in the hemiboreal forests. In this study, the stand development 45–46 years after the stand replacing windthrow was assessed in the north-western part of Latvia, Slitere National Park. In the areas formerly dominated by Norway spruce, the post-storm tree species composition was significantly altered by the site type. Birch dominated in the overstorey; however, the dominance of spruce was found in 12 and 33% of the areas in the mesic and wet sites, respectively; the understorey and the advanced regeneration were mostly (61 and 46%, respectively) formed by spruce. In most cases, the diameter at breast height (DBH) of the overstorey spruce was similar or larger than for pioneer species (except aspen), regardless of the proportion of spruce in the stand composition. The dimensions of spruce were significantly larger in mesic than in wet sites: DBH and height was 23.8 ± 1.0 *vs*. 19.4 ± 1.5 cm and 22.5 ± 0.5 *vs*. 17.7 ± 1.0 m, respectively. Regardless of the distance from the undamaged stand, the number of the overstorey spruce was similar, indicating the sufficient seed dispersal from the windthrown trees. However, on the wet sites, the proportion of spruce from the total number of trees was significantly higher in the areas up to 50 m from spruce stand that remained after the storm. Also, the abundance of the understorey spruce had significant positive relation to the distance to the undamaged stand. The results suggest that 45 years after the stand-replacing windthrow spruce is abundant within all stand layers and might dominate the overstorey besides the pioneer species.

Key words: semi-natural dynamics, windthrow, stand replacing disturbance, post-storm regeneration.

Introduction

Norway spruce (*Picea abies* L. Karst.) is one of the most economically important tree species in boreal and nemoral regions of Europe (Spiecker 2003, Schlyter et al. 2006). It is mostly planted as intensively managed plantations (Fries et al. 1997, Uotila et al. 2002), susceptible to disturbances (Knoke et al. 2008), among which windthrows and bark beetle (*Ips typographus* L.) outbreaks are the most important (Schelhaas et al. 2003). Frequency of these disturbances is likely to increase under changing climate (Seidl et al. 2014). Hence, the economic loss might increase due to lower timber value and decreased vitality (partial damages) of surviving trees (Panayotov et al. 2011, Valinger et al. 2014). Longer vegetation period and milder winters might increase the affected area and severity of damages due to reduced tree stability on unfrozen soil (Peltola et al. 2000) and provide possibility to form more than one generation per year for spruce bark beetle (Jönsson et al. 2007). Under these circumstances, the stand replacing damages might become more frequent.

Theoretically, succession after stand replacing events is clear in simplified, long term form (Franklin et al. 2002, Angelstam and Kuuluvainen 2004). Yet, ecological processes in hemiboreal regions are less well understood than in the boreal and nemoral forests (Angelstam et al. 2013). A high number of different factors influence the stand regeneration, e.g. initial species composition, abundance of advanced regeneration, availability of seed course (e.g. Clinton and Baker 2000, Coates 2002, Kuuluvainen 2002, Zielonka 2006), providing countless combinations of possible development paths.

Forest management based on the natural disturbance dynamics receive growing interest (Toivanen and Kotiaho 2007, Koivula et al. 2014). Mimicking natural disturbances requires understanding of succession of un-managed forests (Fischer and Fischer 2012, Winter 2012). However, such hemiboreal areas are scarce due to intensive landuse (Nilsson 1997). The empirical studies of succession cover short period of time after the stand replacing windthrows – up to 25 years in boreal (Fischer and Fischer 2012), 6–7 years in hemiboreal forests (Vodde et al. 2010), providing insights only in the initial stage of stand regeneration. Still, the following stand development is unclear. The conducted studies do not provide knowledge about the role of the advanced regeneration in comparison to the emerging seedlings, as well as the time windows, during which saplings have the possibility to become canopy tree in various site types.

The aim of the study was to assess stand development 45–46 years after stand replacing windthrow and factors affecting it. We hypothesized that after stand replacing windthrow (1) the shade tolerant Norway spruce appears relatively late and forms the understorey in the stands dominated by pioneer species and (2) the distance from the seed source, i.e. undamaged stand, has no influence on the post-storm abundance of spruce regeneration.

Materials and Methods

Study site

The study site is located in the north-western part of Latvia, Slitere National Park (57°38'N, 22°17'E). The study was carried out in the oldest part of it, where no silvicultural measures were done since the 1921. Currently, the forested landscape of this part of the national park consists of the hemiboreal coniferous, broadleaved and mixed forest (ca. 82%), bogs and mires (ca.16%) and other land (ca. 2%), with the area of 1100 ha. According to the inventory data of the 1963 (pre-storm), the forests were dominated by Norway spruce (*Picea abies* L. Karst.) and Scots pine (*Pinus sylvestris* L.), 44 and 31%, respectively. The most abundant broadleaved species were birch (pooled *Betula pendula* Roth and *B. pubescens* Ehrh.), black alder (*Alnus glutinosa* L. Gaertn) and European ash (*Fraxinus excelsior* L.) that dominated 13, 7 and 4% of the stands, respectively. The stand-replacing windthrow occurred on November 2, 1969. The windthrown area was 187 ha, among which ca. 81% were spruce stands. No salvage logging or other silvicultural measures were carried out after the storm.

Study data

Data were collected in the stands located on the fertile mineral soil with normal moisture regime (forest types according to Bušs (1976): *Hylocomiosa*, *Oxalidosa* and *Dryopteriosa*) further in the study classified as the site type "mesic" and on the wet mineral soil (*Vaccinioso-sphagnosa*, *Myrtilloso-sphagnosa*, *Myrtilloso-polytrichosa* and *Dryopteriosa*) classified as the site type "wet". The areas of more than 40 years old spruce dominated stands (based on the forest inventory data of 1963, the proportion of spruces ≥80% of the standing volume) with more than 90% of the canopy area loss during the storm (the analysis of the satellite images: Bāders et al., 2014) were selected for the study. To cover all such areas in the selected landscape, data from two non-overlapping series of measurements were performed:

1) In autumn 2013, sample plots (28 and 47 on the mesic and wet sites, respectively) were measured. In each of the selected stand, four circular sample plots (each representing 100 m^2) were placed on the longest diagonal of compartment: first at the distance of 20 m from the undamaged stand and 25-m distance between the centres of the following plots.

2) In autumn 2015, the measurements of additional sample plots (151 and 15 on the mesic and wet sites, respectively) were done. The plots were distributed on the grid by 55×55 m between their centres, each of the plot represented 100 m^2. The grid was located at least 20 m from the undamaged stand, as well as at least 55 m from the plots of the first series.

Within each plot in the both types of the measurement series, forest type was identified. The number of trees was accounted according to the species and stand layer, i.e. overstorey, understorey or advanced regeneration. Based on the proportion of number of spruces, the plots were divided into four groups: less than 1%, from 1 to 39%, from 40 to 69% and more than 70% (spruce as the dominant species). Within each of the stand layer, the diameter at breast height (DBH) and height was measured for one to three (circumstantial to their proportion) trees of each species. Trees smaller than DBH 2.1 cm were accounted as advanced regeneration. The assessment of the abundance of trees that survived in the windthrow was done visually, based either on the sharp variation of the distance between the branch whorls (presumably occurring due to the release of growth after the storm) or on the tree dimensions. The distance from each sample plot to the undamaged spruce stand older than 40 years (potential seed source) was measured using proximity toolbox in ArcGIS software (ESRI, Inc. Redlands, CA). According to the distance from the undamaged stand, plots were divided into four groups: closer than 25.0 m, from 25.1 to 50.0 m, from 50.1 to 75.0 m and farther than 75.1 m.

Data analysis

The one way analysis of variance (ANOVA) was used to assess the effect of the site type and stand layer on the stand density, DBH and height of the species, the effect of the incidence of pre-storm advanced regeneration on the number of trees, abundance of the current advanced regeneration and DBH of the overstorey spruce, as well as the effect of the distance to the undamaged stand to the number of the overstorey species. The Chi-squared test was used to assess the distribution of the number and proportion of spruces, the distribution of species composition and the distribution of the groups of proportion of spruce within the stand layers between the site types. The GLM multivariate was used to assess the influence of the distance from the undamaged stand on the proportion of spruce between and within the site types. All calculations were done in R 3.0.2. (R Core Team 2013).

Results

Overall, 5,644 trees of 14 species were sampled during the measurements. The stand density of the mesic and wet sites was similar (ANOVA; $p > 0.05$) within all stand layers (Figure 1). However, the distribution of number of spruce within the overstorey and understorey differed significantly between the site types (χ^2 test; $p < 0.01$). Small but significant (χ^2 test; $p < 0.05$) differences were found in the species composition between the site types, as well as among the stand layers. However, the proportion of the spruce was similar (χ^2test; $p > 0.05$) at the both site types. In the overstorey, the most abundant tree species were birch (40%) and spruce (26%). As expected, the understorey was mostly formed by spruce (61%). The advanced regeneration was rarely found, only in 12% of the plots. It was mostly dominated by spruce (46%), still high proportion (39%) of the species classified as "others" was found, mostly *Tilia cordata* Mill., *Fraxinus excelsior* L. and *Quercus robur* L.

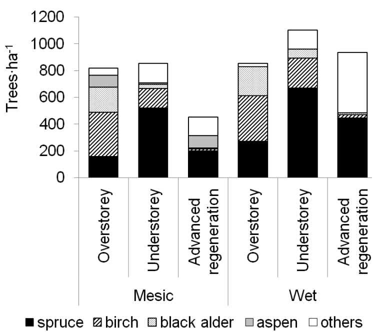

Figure 1. The number of trees per hectare according to the species, site type and stand layers. O – overstorey, U – understorey and A – advanced regeneration

Spruce was found in all stand layers: in 48, 79 and 57% of the plots in the overstorey, understorey and as advanced regeneration, respectively. However, spruce was the dominant overstorey species in 12 and 33% of plots in the mesic and wet sites, respectively (Figure 2). The distribution of spruce in distinguished layers was similar (χ^2 test; $p > 0.05$) in both site types.

In the overstorey, the dimensions of spruce at the mesic sites significantly (ANOVA; $p < 0.01$) exceeded these on the wet sites. The DBH and height was 23.8 ± 1.0 *vs*. 19.4 ± 1.5 cm and 22.5 ± 0.5 *vs*. 17.7 ± 1.0 m, respectively. Spruce was thicker than birch and black alder (Figure 3). However, this trend was significant ($p < 0.01$) only within the plots with proportion of spruce from 1 to 39%. Yet, the DBH of these broadleaved species and the DBH and height of the spruce was similar (all $p > 0.05$), regardless of the abundance of

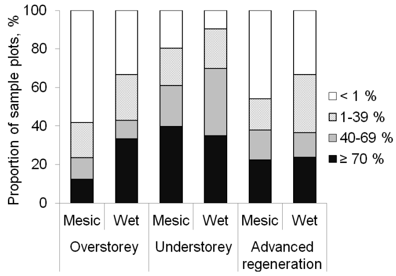

Figure 2. The proportion of sample plots according to the proportion of spruce within plot, site type and stand layer

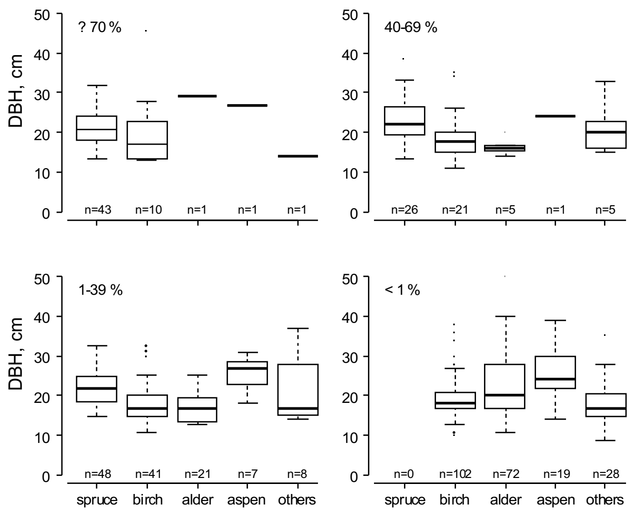

Figure 3. The mean diameter at breast height (DBH) of the overstorey tree species according to the proportion of spruce in the plot

spruce in the plots. The height of spruce was 20.7 ± 0.7, birch 21.6 ± 0.5, black alder 21.5 ± 0.7, aspen 27.3 ± 1.5 m, but for others (mostly *Tilia cordata* and *Fraxinus excelsior*) 19.2 ± 1.0 m. Significant differences between the height of spruce and birch ($p = 0.03$), aspen ($p < 0.01$) and others ($p = 0.01$) were detected.

In the understorey, the site type had significant ($p < 0.05$) effect on the height of spruce, while the DBH was similar (p = 0.97). The height was 11.18 ± 0.58 *vs.* 9.10 ± 0.57 m and DBH was 8.3 ± 0.7 *vs.* 8.3 ± 0.9 cm on the mesic and wet types, respectively. The DBH of spruce significantly exceeded DBH of birch ($p < 0.01$) and other ($p < 0.01$) tree species. However, spruce was significantly ($p < 0.01$ between all pairs) lower than all other species. The height of spruce was 10.6 ± 0.5, birch 13.4 ± 0.5, black alder 14.0 ± 0.9, aspen 16.6 ± 1.2 m, and for others 12.4 ± 0.6 m.

Overall, 91 trees from the pre-storm generation were identified, mostly spruce (55%) and black alder (35%). Such trees were found within the 30% of the plots, distributed similarly (χ^2 tests $p > 0.05$) between the site types. The incidence of the identified trees of the pre-storm generation had significant ($p < 0.01$) positive effect on the frequency of the advanced regeneration. Almost half (42% of the plots) of the incidence of the advanced regeneration were found in the plots where spruce of the pre-storm generation was presented. In contrast, the overstorey density was lower, if the trees of the pre-storm generation were present: 777 ± 247 in comparison to 848 ± 71 trees ha^{-1}. However, these differences were not significant ($p > 0.05$). In such plots, the significantly ($p < 0.01$) larger DBH of the overstorey spruce were found.

Similarly, the overstorey spruce had significantly ($p < 0.05$) larger DBH closer to the undamaged stand. The distance to the undamaged stand had significant ($p < 0.01$) positive effect on the number of the overstorey species. The number of the overstorey, as well as the advanced regeneration spruce was similar (ANOVA; $p > 0.05$), regardless of the distance from the undamaged stand within both site types (Figure 4). Yet, the significantly ($p < 0.01$) higher proportion of the spruce dominated stands were found closer than 50 m from the undamaged stand, in comparison to farther located plots (Figure 5). Similarly, the trend ($p > 0.05$) of the higher proportion of the spruce dominated stands closer than 25 m form the undamaged stand was found in overstory of the mesic sites. In the understorey, the distance had significant positive effect on the density ($p < 0.01$) and proportion ($p < 0.01$) of spruce at both site types. In contrast, the number and proportion of the advanced regeneration spruce was similar, regardless of the distance from undamaged stand.

Discussion and Conclusions

The intensity of windthrow influences the initial conditions of succession (Kuuluvainen 2002). In the disturbed area, the abundance and arrangement of the standing trees both in windthrown and undisturbed area determines the following stand development (Coates 2000). The pioneer species are the most abundant in the overstorey (Figure 1), in accordance to theoretical succession after stand replacing disturbance (Angelstam and Kuuluvainen 2004). However, in the overstorey, spruce was found within more than a half of the plots, dominating at 23% (Figure 2). Overall, in the overstorey, 9 species were found in the study area. The species diversity is promoted by the diversity of the microsites due to the different ecological demands.

The most favourable microsites for the tree regeneration are the tree-fall pits and mounds and logs (Clinton and Baker 2000, Harrington and Bluhm 2001, Zielonka 2006). The pit and mound area is affected by the tree dimensions and species (Ilisson et al. 2007), among which spruce forms larger area of open soil than other native tree species of the region (Lõhmus et al. 2010). Before the storm, the study site was dominated by more than 40 years old spruce. If such area is intensively damaged, pit and mound topography might cover up to 15–25% of the surface (Ulanova 2000), creating suit-

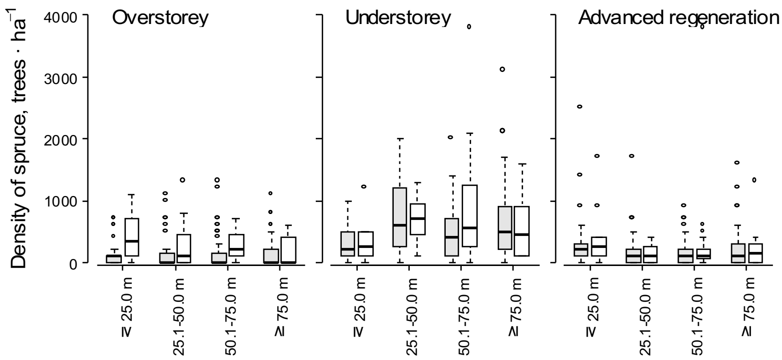

Figure 4. The density of spruce according to the stand layer and the distance from the undisturbed stand at the mesic (grey) and wet (white) sites

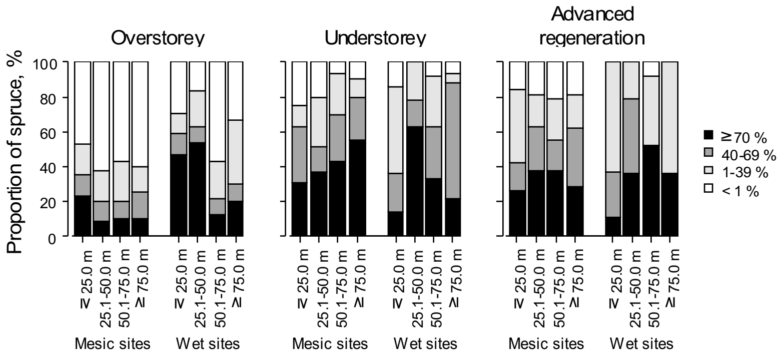

Figure 5. The proportion of plots according to the proportion of spruce, site type, stand layer and the distance from the undisturbed stand

able seed beds. Open soil is favourable to emergence of small-seeded species, i.e. birch and aspen (Ulanova 2000, Vodde et al. 2010). In the natural forests, spruce shows strong preference of emergence on the decaying wood in comparison to undisturbed soil (Hytteborn and Packham 1987, Zielonka 2006) and similar preference of the pits and mounds (Ilisson et al. 2007).

In the overstorey, the emergence of the species occurred at the same time, as indicated by similar dimensions among the species (Figure 3). The percentage of emerging seedlings is declining with the time since the disturbance (Nilsson et al. 2002), as could be seen for most of the species (Figure 1). In contrast, the abundance of the understorey spruce is noticeably increased. Apparently, it was emerging after the logs became suitable substrate. In natural forests, almost half of the seedlings has been found on the lying logs, although they formed an only 4% of the surface (Zielonka 2006). Initially, the high number of logs hampers regeneration (Schönenberger 2002). Presumably, this happened also in our study area due to high standing volume before the storm. Afterwards, logs turn into a favourable substrate for germination (Harrington and Bluhm 2001, Zielonka 2006). The first seedlings seldom can be found on the logs on the first stages of decay and the most suitable conditions are reported on *ca* 30 – 60-year-old logs (Zielonka 2006), resulting in the abundant recruitment. Yet, the time needed to reach the suitable decay state is highly variating. Nevertheless, a high number of logs remains laying into piles with no contact with forest floor, and the wood decomposition of such logs is inhibited (Storaunet and Rolstad 2002). The time window until the dead tree forms suitable substrate might be the reason for the great abundance of spruce in the understorey and as the advanced growth (Figure 1). Yet, the survival of seedlings might have greater impact on the species composition (Coates 2000, 2002, Fischer and Fischer 2012). The differences in the species composition between the site types were denoted (Figure 1, Figure 4), as the seedling establishment on the specific microsites is more restricted on wet soils (Kuuluvainen 1994). The seedlings on mounds might die due to erosion (Harrington and Bluhm, 2001) and pits undergo rapid changes in soil moisture (Lüscher 2002). Moreover, the tree growth in wet sites is reduced (Dang and Lieffers 1989, Astrade and Bégin 1997), indicated by the smaller dimensions and higher number of the trees on the wet soils (Figure 1).

In addition to the suitable substrate, climate and microhabitat (Clinton and Baker 2000), the remaining trees (Axelsson et al. 2002), the availability and distance from the seed source (Coates 2002) have effect on the spatial and temporal differences in the seedling emergence and survival. The incidence of the identified pre-storm advanced regeneration was scarce. Detailed analysis of this aspect can be carried out in further studies involving reconstruction of age structure of the stands. Spruce is sensitive to the sudden changes in the stand density. After the release, saplings have low survival, reported less than 10% for the saplings smaller than 20 cm (Örlander and Karlsson 2000). Needles of the advanced regeneration trees are adapted to shady conditions morphologically and physiologically (Bertamini et al. 2006, Gebauer et al. 2012) and a sudden change in the light conditions could have adverse effect on needle function, especially on wet sites (Gnojek 1992). The survival of higher saplings might exceed 70–80% (Örlander and Karlsson 2000). Still, the release of advanced regeneration is often followed by stagnation of height growth (Örlander and Karlsson 2000) due to enlargement of the root system (Kneeshaw et al. 2002). The recovery period can exceed up to 10 years (Örlander and Karlsson 2000, Panayotov et al. 2011), followed by rapid height and radial growth (Panayotov et al. 2011). In line, the dimensions of spruce were positively related to the pre-storm abundance of advanced regeneration. The undamaged trees influence the available resources; hence, the development of the disturbed area might be irregular (De Chantal et al., 2003). The pre-storm advanced regeneration had negative effect on the density of current overstorey, most probably due to provided shade (George and Bazzaz 1999). Beneath advanced regeneration, light conditions might be insufficient to promote emergence of seedlings (Clinton and Baker 2000). Moreover, the effect of abundance of these trees remains in the farther stand development. The abundance of the current advanced regeneration had strong relation to the incidence of the pre-storm trees, presumably due to the seed production.

Similarly, the emergence of the overstorey of current stand was affected by the availability of seeds. In the year of the windthrow, the assessment of spruce flowering in the western Latvia was similar to the flowering in the mast years (Zviedre 1971). The seed production was low but the quality of seeds is regarded as high (Zviedre 1978). However, noticeable differences of the seed production between the stands are common (Rone 1965) and there are no data on seed production from the spruce stands in the study site. The windthrow occurred in the beginning of November, at the time when seeds are suitable for germination (Oršanić et al. 2008). As the result, the overstorey spruce was similarly abundant, regardless of the distance to the undamaged stand (Figure 4). Yet, even small detected differences in the overstorey density might affect the available light beneath it. Thus, the density and proportion of the understorey spruce increased with the distance from the undamaged stand (Figure 4, 5). Presumably, due to the pooled effect of the provided shadow from the undamaged stand and the overstorey trees. In contrast, the abundance of the advanced regeneration was not affected ($p > 0.05$) by the distance from the undamaged stand (Figure 4). The seed source, i.e. the overstorey trees, and the provided shade from the higher stand layers provide similar conditions for recruitment.

Our hypothesis was partly confirmed. Indeed, spruce was the most abundant species in the understorey and as the advanced regeneration. However, it was frequently found in the overstorey, also as the dominant species. The abundance of the overstorey spruce was not significantly affected by the distance from the undamaged stand. Yet, the density of the understorey spruce had significant positive relation to the distance to the undamaged stand.

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