

Life and death of *Picea abies* after bark-beetle outbreak: ecological processes driving seedling recruitment

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Abstract. The severity and spatial extent of bark-beetle outbreaks substantially increased in recent decades worldwide. The ongoing controversy about natural forest recovery after these outbreaks highlights the need for individual-based long-term studies, which disentangle processes driving forest regeneration. However, such studies have been lacking. To fill this gap, we followed the fates of 2,552 individual seedlings for 12 years after a large-scale bark-beetle outbreak that caused complete canopy dieback in mountain Norway spruce (*Picea abies*) forests in southeast Germany. We explore the contribution of advance, disturbance-related, and post-disturbance regeneration to forest recovery. Most seedlings originated directly within the three-year dieback of canopy trees induced by bark-beetle outbreak. After complete canopy dieback, the establishment of new seedlings was minimal. Surprisingly, advance regeneration formed only a minor part of all regeneration. However, because it had the highest survival rate, its importance increased over time. The most important factor influencing the survival of seedlings after disturbance was their height. Survival was further modified by microsite: seedlings established on dead wood survived best, whereas almost all seedlings surrounded by graminoids died. For 5 cm tall seedlings, annual mortality ranged from 20 to 50% according to the rooting microsite. However, for seedlings taller than 50 cm, annual mortality was below 5% at all microsites. While microsite modified seedling mortality, it did not affect seedling height growth. A model of regeneration dynamics based on short-term observations accurately predicts regeneration height growth, but substantially underestimates mortality rate, thus predicting more surviving seedlings than were observed. We found that *P. abies* forests were able to regenerate naturally even after severe bark-beetle outbreaks owing to advance and particularly disturbance-related regeneration. This, together with microsite-specific mortality, yields structurally and spatially diverse forests. Our study thus highlights the so far unrecognized importance of disturbance-related regeneration for stand recovery after bark-beetle outbreaks.

Key words: advance regeneration; growth function; *Ips typographus*; mortality; Norway spruce; permanent plots; salvage logging; stand-replacing disturbance; survival.

INTRODUCTION

The key to forest recovery after disturbance is tree regeneration. Its species composition, spatial pattern, and structural heterogeneity are crucial for the biodiversity and future resilience of the developing forest (Swanson et al. 2011, Donato et al. 2012). Following the death of mature trees in consequence of a disturbance event, diaspore supply sharply decreases. Successful stand-replacement often depends on the survival and growth of advance regeneration established before the

disturbance (Kuuluvainen 1994, Franklin et al. 2002, Svoboda et al. 2012). Increased understory light and released nutrients promote the growth of recruits after disturbance (Metslaid et al. 2007, Kaňa et al. 2012), but regeneration rate depends also on competition with the expanding herb-layer and on biological legacies, such as the amount of coarse woody debris and pit-and-mound topography (Kuuluvainen and Juntunen 1998, Jonášová and Prach 2004).

In contrast to episodic disturbances, such as fire or windthrow, bark-beetle outbreak impact is gradual: ongoing canopy tree dieback takes several years (Köster et al. 2009, Edburg et al. 2012). The main differences from episodic high-severity disturbances are (1) gradual

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changes in stand microclimate during the dieback of canopy trees, (2) undisturbed soil surface, and (3) minimal damage to already established advance regeneration and herb layer vegetation (Kuuluvainen 1994, Storaunet and Rolstad 2004, Fischer et al. 2013, 2015). The regeneration processes after bark-beetle outbreaks are therefore different from those following other disturbances. Knowledge about tree regeneration after stand-replacing fire or windthrow is nontransferable to stand recovery after bark-beetle outbreaks.

The severity and spatial extent of bark-beetle outbreaks substantially increased in recent decades worldwide in different types of coniferous forests (Dale et al. 2001, Schelhaas et al. 2003, Meddens et al. 2012). In Europe, Norway spruce (*Picea abies* [L.] Karst.) forests cover large areas within the boreal forest zone and in the mountains within the temperate zone, where spruce naturally forms almost monodominant stands. These stands are prone to European spruce bark-beetle (*Ips typographus* L.) outbreaks, usually induced by preceding windthrow damage (Brüna et al. 2013, Čada et al. 2016). Recently, these outbreaks have been amplified by series of wind-storm events, vast artificial spruce plantations, and also by warmer climate causing tree physiological stress and hastened bark-beetle development (Raffa and Aukema 2008, Temperli et al. 2013, Seidl et al. 2014). As a result, recent outbreaks caused almost complete mortality of canopy trees over large areas within short time intervals (Lausch et al. 2011).

Large-scale, stand-replacing disturbances in spruce forests caused severe economic loss in managed forests and at the same time affected many protected areas (Müller et al. 2008). This presented a challenge for both forest managers and nature conservationists and raised important questions about the best management schemes to balance the requirements of sustainable timber production, biodiversity conservation, and other ecosystem services (Wermelinger 2004, Seidl et al. 2008, Beudert et al. 2015). Detailed knowledge of post-disturbance succession is important for nature conservationists because these early-seral stages are crucial for biodiversity (Kouki et al. 2001, Müller et al. 2008, Donato et al. 2012, Lehnert et al. 2013). Recommendations for management of affected stands are urgently needed also by forest managers, who must decide whether the forest will self-replace itself in an acceptable time frame or instead needs salvage logging and replanting. Salvage logging, often applied after bark-beetle outbreaks, has been hotly debated (Lindenmayer and Noss 2006). Its proponents argued that salvage logging followed by tree replanting is needed to control bark-beetle spread and secure stand recovery (Fettig et al. 2007, Stadelmann et al. 2013), while its opponents questioned the efficiency of salvage logging in controlling bark-beetle epidemics (Grodzki et al. 2006) and argued that this treatment disrupts natural regeneration, adversely affects the self-replacing ability of disturbed stands (Donato et al. 2006, Wild et al. 2014), and negatively influences biodiversity (Kouki et al. 2001, Jonášová and Prach 2008, Thorn et al. 2014).

This controversy has triggered intensive research on natural regeneration and factors affecting stand self-replacement (Kupferschmid et al. 2006, Harvey et al. 2014). However, the regeneration process after bark-beetle outbreaks has been investigated only through studies that did not follow individual seedlings over time (Jonášová and Prach 2004, DeRose and Long 2010, Diskin et al. 2011, Zeppenfeld et al. 2015). Moreover, these studies usually focus only on regeneration over a certain height threshold. The resulting snapshot data covering only a subset of regeneration can easily provide biased results, as it is extremely difficult to infer actual processes behind the observed static patterns (Wiegand et al. 2003). For instance, clumped spatial pattern of spruce seedlings was repeatedly observed, but the processes responsible for the formation of such a pattern remain unclear (Grenfell et al. 2011, Wild et al. 2014). High densities of seedlings on coarse woody debris suggest low mortality on these microsites (Jonášová and Prach 2004, Kupferschmid and Bugmann 2005), but Kathke and Bruelheide (2010) inferred opposite conclusions from regeneration age structure. Advance regeneration, i.e., recruits well-established before the disturbance, is generally thought to be the most important tree cohort for shade-tolerant tree recovery (DeRose and Long 2010, Bače et al. 2015, Burton et al. 2015), but reliable evidence based on temporally replicated surveys is missing. To disentangle conflicting evidence and to provide robust recommendations for the management of *P. abies* forests, long-term studies following the fates of individual seedlings are needed (Fischer and Fischer 2011).

We therefore tested the following hypotheses about tree regeneration after stand-replacing bark-beetle outbreaks: (H1) Tree regeneration after the disturbance will be dominated by advance regeneration already established before the disturbance, and (H2) tree regeneration will be structured by microsite-specific seedling performance (i.e., growth and survival rates).

To test these hypotheses, we collected and analyzed individual performance data on *P. abies* seedlings and saplings during the first 12 years after a stand-replacing bark-beetle outbreak in a naturally regenerated forest in the Bavarian Forest National Park, Germany. To provide recommendations for applied ecology, we also evaluated the potential of short-term post-disturbance monitoring of individual seedlings to yield meaningful predictions of further stand development.

METHODS

Study site

We worked in the Bavarian Forest National Park in southeast Germany (Fig. 1). The park was established in 1970 and enlarged to its current 240 km² in 1997. Bedrock mostly comprises gneiss and granitic rocks, leading to acidic, podzolized soils. Climate in the park is cold, with long winters and short, but relatively warm summers. Mountain spruce forests form the natural vegetation from

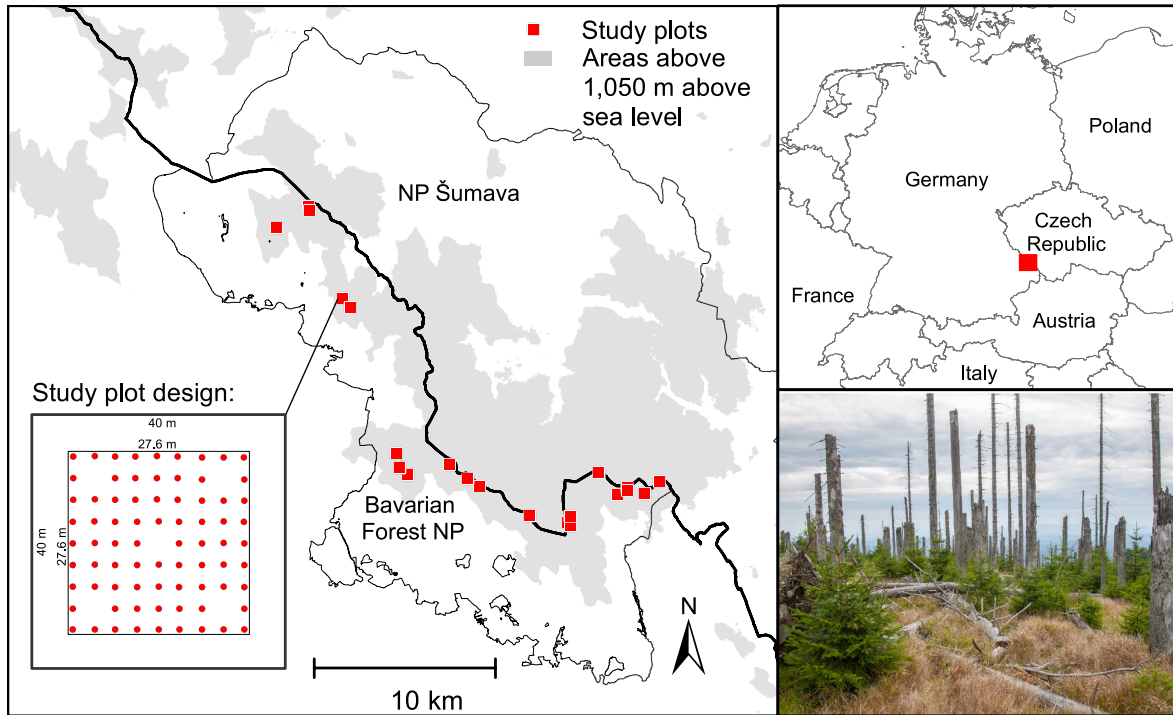


FIG. 1. Study site location and plot arrangement: plots are subdivided into a grid of 76 circular sub-plots, 0.5 m^2 each, spaced 3.35 m apart. All seedlings and saplings present on these sub-plots were permanently labelled and repeatedly measured during the first 12 years after stand-replacing disturbance by a massive bark-beetle outbreak. Inset photograph shows the stand 12 years after the outbreak (during fieldwork in 2010).

about 1,150 m above sea level up to the highest elevation in the park (1,453 m above sea level) where mean annual temperature ranges from 5.1°C to 3.6°C (Elling et al. 1987). The tree layer is dominated by Norway spruce, accompanied by a small fraction of mountain ash (*Sorbus aucuparia* L.). The European spruce bark-beetle responsible for periodic outbreaks is indigenous to these forests, but its populations show extensive fluctuations depending on forest stand and weather conditions (Wermelinger 2004, Berec et al. 2013). Outbreaks usually cause complete dieback of Norway spruce canopy trees over large areas (Müller et al. 2008).

We studied stands affected by a major outbreak that started in 1993 and culminated between 1996 and 2000. The severity and extent of the canopy dieback were exceptionally high, with complete canopy dieback on about 54 km^2 (Lausch et al. 2011). The affected stands in the core zone were left to spontaneous development, and this gave us a unique opportunity to study natural tree regeneration after a bark-beetle outbreak.

Data collection

In 1998, Bauer established 24 permanent plots in mountain spruce forests across the park (Bauer 2002, Bauer et al. 2008). The plots covered the whole elevation gradient within the natural spruce forest belt in the region (1,155–1,345 m above sea level). Plots were established in stands infested by bark-beetles; complete canopy dieback

was reported on all plots by the year 2000. Pre-disturbance stem densities ranged from 269 to 669 stems/ha, with median 459.5 stems/ha.

A regular grid of 76 circular sub-plots (0.5 m^2 each) was established within each 762 m^2 plot (Fig. 1). All seedlings and saplings rooting in the sub-plots were permanently labelled and numbered. Four parameters were determined for each labelled individual: (1) age in years, (2) absolute height in millimeters, (3) annual height increment in millimetres, and (4) rooting microsite. Age was determined according to terminal bud scar and verticil positions, which is reliable for young spruce saplings (Zielonka 2006, Bače et al. 2011). This allowed us to date very precisely the individual seedlings and divide them into three age cohorts: (1) advance regeneration, trees established prior to the outbreak (i.e., germinating before 1996); (2) disturbance-related regeneration, trees established during the bark-beetle outbreak (i.e., germinating between 1996 and 1999); and (3) post-disturbance regeneration, trees established after complete canopy dieback (i.e., 2000 and later). Rooting microsite type was categorized according to substrate and surrounding vegetation (see Table 1). Annual increments and mortality of individual seedlings were measured in the following two years (1999 and 2000).

In 2010, we repeated the same measurements on 21 plots, excluding three plots in the area damaged by wind-storm Kyrill. To retain continuity in data, we measured all annual increments of the labelled trees from the last year

TABLE 1. Microsite type definitions and overview of tree proportions on microsites from 1998 (during dieback), 2000 (shortly after dieback), and 2010.

Microsite	Description	Proportion of juveniles observed on microsite (weighted plot mean \pm SE)			Cumulative mortality 1998–2010	Fitted mortality effects	
		1998	2000	2010		Odds ratio	Tukey HSD
Dead wood	laying tree logs or coarse woody debris	4.8 \pm 1.3	7.3 \pm 2.0	12.0 \pm 4.4	68.6	0.547	a
Tree base	area surrounding standing trunks up to the distance equal to trunk diameter	15.4 \pm 5.1	20.8 \pm 5.9	18.0 \pm 8.7	85.5	0.632	a
Stump	directly on stumps/snags	14.0 \pm 2.9	19.4 \pm 3.8	25.0 \pm 5.6	77.9	0.665	a
Pits and mounds	windfall pits and mounds	1.7 \pm 0.6	1.9 \pm 0.4	4.1 \pm 0.7	69.8	0.910	abc
Moss	cover predominantly of mosses	15.5 \pm 3.2	13.2 \pm 3.2	8.5 \pm 2.3	93.2	1.215	b
Litter	ground covered by needles, bark or twigs	37.9 \pm 4.9	31.2 \pm 5.5	29.1 \pm 9.0	90.5	1.228	b
Lycopodium	cover predominantly of <i>Lycopodium annotinum</i>	5.0 \pm 0.9	3.2 \pm 0.6	2.5 \pm 0.5	93.8	1.428	bc
Graminoid	cover predominantly of <i>Calamagrostis villosa</i> , <i>Luzula sylvatica</i> , or <i>Avenella flexuosa</i>	3.8 \pm 0.8	1.9 \pm 0.6	0.3 \pm 0.3	99.0	2.243	c
Other*	cover predominantly of other species, i.e., <i>Vaccinium</i> , <i>Athyrium</i> , <i>Dryopteris</i> , <i>Oxalis</i>	1.8 \pm 1.3	1.1 \pm 0.9	0.3 \pm 0.3	97.8	–	–
Total no. individuals		2,550	1,045	316	87.6%		

Notes: Numbers are based only on a subset of trees already present in 1998. Tukey HSD letter codes indicate microsite groups with significantly different mortality odds at the 0.05 level. Note that cumulative mortality is a raw value, but fitted odds ratios also reflect tree height as a component of mortality.

*Juveniles from “other” microsites were excluded from analyses owing to low number of observations and high within-group variability.

of measurement in 2000. To get a more representative estimate of regeneration density in each sampled stand, we also counted all juvenile trees growing on each plot.

Data analysis

We analyzed the survival and growth only of *P. abies*, which formed 99% of all recorded individuals. Other species were too rare for such analyses, and we included them only in a plot-level overview of regeneration density.

Regeneration structure.—To assess changes in regeneration structure over time, we calculated proportions of cohorts in the survey years. To test the hypothesis H1, we tested the year 2010 paired differences in plot-level sums of advance regeneration vs. disturbance related plus post-disturbance regeneration by a one-sided Wilcoxon test for paired data.

Growth.—To analyze tree growth, we fitted the tree-height series with parametric growth functions through nonlinear mixed-effect models, accounting for the spatially and temporally dependent error structure. Only juveniles surviving the whole period (1998–2010) were selected for fitting tree growth. We compared six

different growth functions previously used for temperate forest trees (Table 2; Pretzsch 2010).

To fit the models, we used the R software version 3.2 (R Core Team 2015) and the nlme function from the nlme package (Pinheiro et al. 2013). In the models, we used tree age as a fixed effect and individual trees nested within individual plots as random effects to account for autocorrelation. As an asymptotic tree height parameter, we used the 90th percentile (i.e., 26.85 m) of canopy tree heights measured on our plots before stand dieback (Bauer 2002). To account for heteroscedasticity in tree heights, we used a power variance function. For further analyses, we selected the growth function which fitted best according to the root mean square error (RMSE) and visual inspection of the residuals.

To test the effect of rooting microsite on sapling growth, we added microsite as an additional fixed effect to the best-fitting growth-function model. We used the AIC (Akaike’s information criterion) and a log-likelihood ratio test to explore if the inclusion of rooting microsite improved model fit.

Mortality.—To investigate the drivers of juvenile tree mortality, we fitted binomial generalized linear mixed-effect models using the glmer function of the lme4

TABLE 2. Growth function equations.

Growth curve	Equation	RMSE	Parameter estimates \pm SE
Logistic	height $\sim a/(1 + c \times \exp(-b \times \text{age}))$	0.050	b = 0.2191 \pm 0.0038 c = 1083.8 \pm 26.727
Gompertz	height $\sim a \times \exp(-b \times \exp(-c \times t))$	0.051	b = 7.606 \pm 0.0406 c = 0.0482 \pm 0.0014
Chapman-Richards	height $\sim a \times (1 - \exp(-b \times \text{age})^c)$	0.067	b = 0.0131 \pm 0.0016 c = 2.103 \pm 0.1155
Bertalanffy	height $\sim a \times (1 - \exp(-b \times \text{age})^3)$	0.071	b = 0.0236 \pm 0.0006
Korf	height $\sim a \times \exp(-b \times \text{age}^{-c})$	0.092	b = 11.9955 \pm 0.6293 c = 0.4099 \pm 0.0243
Hossfeld IV	height $\sim t^c/(b+t^{c/a})$	0.100	b = 373.9 \pm 8.832 c = 2.02 \pm 0.0138

Note: Asymptotic height (parameter a) was set as 26.85 m for all functions; standard errors (SE) of fixed effect terms are given.

R package (Bates et al. 2015). We tested log-transformed tree height, rooting microsite, and site elevation as fixed effects. Plot ID and survey year were included as crossed random effects. We constructed the minimal adequate model through forward selection of predictors based on the AIC (Crawley 2007). Then, we used a type II Wald χ^2 test to check the statistical significance of the fixed model terms. In the models, we used Laplace approximations for maximum likelihood estimation. For post-hoc comparison of mortality levels we used Tukey's HSD test.

Regeneration dynamics model

To investigate whether short-term observation can be used for the prediction of future stand structure, we built a predictive model and compared its output with the observations made after 10 years. We used data from only the first three years of sampling (1998–2000) to fit the previously selected growth function to all juvenile trees present in 2000. We then made predictions of their heights in the 2001–2020 period. For each sapling, we also estimated survival probability according to the marginal prediction of an annual mortality risk model based on rooting microsite and estimated sapling height for each given year. Individuals surviving to the next year were selected randomly, with weighting based on survival probability.

To evaluate the model, we compared our observations with the predicted numbers of surviving saplings, their densities on different microsites, and their height and age structures in the year 2010. We ran this model 1,000 times. In each run, we tested conformity of mean and

distribution function for height by a two-sample *t* test and Kolmogorov–Smirnov test and by a discretized Kolmogorov–Smirnov test from the dgof R package (Arnold and Emerson 2011) for age structure. Finally, we calculated the number of simulations having predictions significantly deviant ($P < 0.05$) from the observed data.

RESULTS

Regeneration structure

Initially, in 1998, a total of 2,552 spruce seedlings and saplings were found on the plots, with 86% of them belonging to the disturbance-related cohort. Advance regeneration represented only 14% of all juvenile trees (Table 3).

Of the 2,552 juveniles found in 1998, only 316 individuals (12.4%) survived to 2010. Only 38 juveniles got established after complete canopy dieback and survived to 2010. Advance regeneration benefited from lower mortality, and therefore its relative proportion increased over time to 31% in 2010. Despite local variability in proportion of regeneration cohorts (Fig. 2), the advance regeneration does not dominate globally (Wilcoxon test, $V = 13.5$, $P < 0.01$). Contrary, disturbance-related cohort represented the majority of regeneration (58%) even 12 years after the disturbance (Fig. 3). We thus have to reject the H1 hypothesis, that the regeneration will be dominated by the individuals established before the disturbance.

In 2010, spruce dominated regeneration with densities varying among plots from 39 to 17,275 individuals/ha, with a median of 1,601 individuals/ha. Other tree species

TABLE 3. Cohort contribution (total number of individuals and actual percentages \pm SEM in parentheses) to spruce population and cumulative mortality starting from 1998 (outbreak culmination) to 2010 (decade after outbreak).

Cohort	Number of individuals				Cumulative mortality (%)		
	1998	1999	2000	2010	1999	2000	2010
Pre-disturbance	363 (14.2 \pm 7.2)	308 (16.7 \pm 6.9)	238 (22.8 \pm 7.2)	110 (31.1 \pm 8.6)	15.2	34.4	69.7
Disturbance-related	2,189 (85.8 \pm 7.2)	1,534 (83.2 \pm 6.9)	807 (77.2 \pm 7.2)	206 (58.2 \pm 8.1)	29.9	63.1	90.6
Post-disturbance	0 (0.0 \pm 0.0)	1 (0.05 \pm 0.1)	1 (0.1 \pm 0.2)	38 (10.7 \pm 6.6)
Total	2,552 (100)	1,843 (100)	1,046 (100)	354 (100)	27.8	59.1	87.6

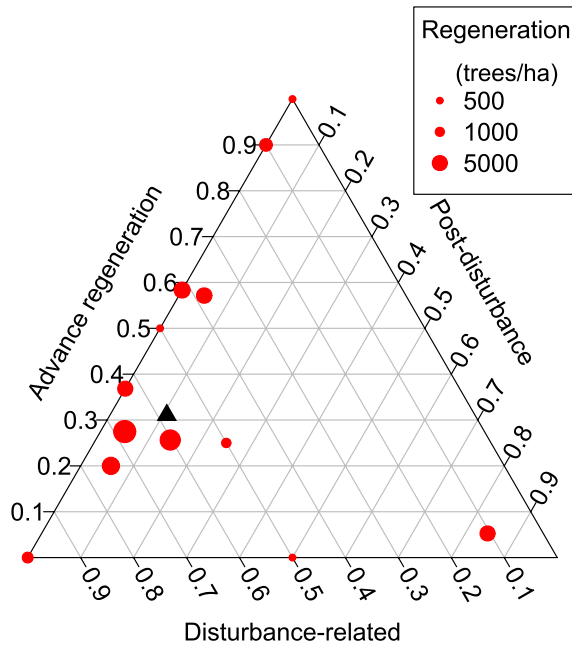


FIG. 2. Cohort contribution to regeneration in 2010 (12 years after bark-beetle outbreak): total mean (black triangle) and site values (red dots). Size of the dots is proportional to total number of recruits; sites without surviving tracked individuals are not plotted.

were far less abundant: only *S. aucuparia* was present regularly, with median density of 66 individuals/ha (3.6% of total counts). Light-demanding pioneer species (*Betula* spp., *Salix* spp.) appeared sparsely, together comprising only 0.6% of regeneration. For individual plot values, see Appendix S1: Table S1.

Density of regeneration on plots 12 years after the outbreak was 3.9 times the pre-disturbance density of canopy trees (calculated as median of pair-wise ratios). However, regeneration density decreased with increasing elevation by an order of magnitude every 122 m (linear regression, densities log-transformed, $R^2_{adj} = 0.43$, $F_{1,19} = 16.31$, $P < 0.001$). All plots below 1,300 m above sea level had regeneration densities higher than their pre-disturbance stem densities, but above this elevation, five out of eight plots had less regeneration than their pre-disturbance numbers of canopy trees.

Growth

Median height rose from 7.3 cm (1998) to 110 cm (2010) for pre-disturbance regeneration and from 3.3 cm to 71.5 cm for disturbance-related regeneration. The median height of post-disturbance regeneration was 26 cm in 2010. During the 12 years after the outbreak, height variability of all regeneration present increased substantially (Fig. 3).

Fitted growth functions differed substantially in residual error structure (Appendix S1: Fig. S1). Logistic and Gompertz growth functions had the lowest RMSE

(5 and 5.1 cm, respectively; Table 2). No trends in residual error structure were apparent for the Gompertz growth function. Chapman-Richards, Bertalanffy, Korf, and Hossfeld IV growth functions substantially underestimated the height of the youngest recruits, while logistic growth function overestimated it (Appendix S1: Fig. S1). Therefore, we chose the Gompertz growth function for further analyses. Rooting microsite was not related to individual growth rate (approximate log-likelihood ratio 20.75, $P = 0.108$; $\delta AIC = +7.24$).

In general, young seedlings grew slowly, but their growth gradually accelerated (Fig. 4). The median annual height increment was 1.1 cm for year 2 seedlings (i.e., in their second growing season), but 4 cm and 11 cm for year 10 and year 15 saplings, respectively. Accordingly, the median age needed to reach the height of 10 cm was almost six years (six growing seasons) and to reach breast height (1.3 m) it was almost 16 years.

Mortality

Smallest seedlings faced the highest mortality (Fig. 5), which sharply decreased with increasing seedling height: 10-fold increase in height reduced mortality odds 47.47 times ($\chi^2 = 356.75$; $df = 1$; $P < 0.001$). Additionally, mortality was affected by rooting microsite ($\chi^2 = 93.98$; $df = 7$; $P < 0.001$). Mortality risk was lowest at wood-related microsites, logs, stumps, and tree bases, with odds ratio ranging from 0.55 to 0.66 (Table 1). In contrast, graminoid-dominated microsites showed the highest mortality risk (odds ratio 2.24). Seedlings rooting in litter, moss, *Lycopodium*, and pits and mounds microsites had a moderate mortality risk (Fig. 5). Mortality risk was independent of plot elevation ($\chi^2 = 0.26$; $P = 0.62$; $\Delta AIC = +1.8$).

Regeneration dynamics model

The predictive model built on data from the first three survey years started with 1,028 juvenile trees in 2000. After 10 years, all model runs predicted higher numbers of surviving saplings than were actually observed in 2010 (Appendix S1: Table S2). According to the model, the annual mortality dropped below 1% in 2010. While the model overestimates the number of surviving saplings, it predicts regeneration height structure reasonably well. The mean predicted tree height (88 cm) was only slightly lower than the observed mean height (92 cm). Moreover, the difference in the means was significant only for 1% of simulations and K-S test revealed 57.8% simulated empiric distribution functions to be equal with the observed ones (Fig. 6).

The model predicted an increase in the amount of pre-disturbance regeneration relative to disturbance-related regeneration, which was similar to that actually observed (K-S test of age distributions insignificant in all simulations). The observed and predicted trends in proportions of trees rooting in specific microsites were

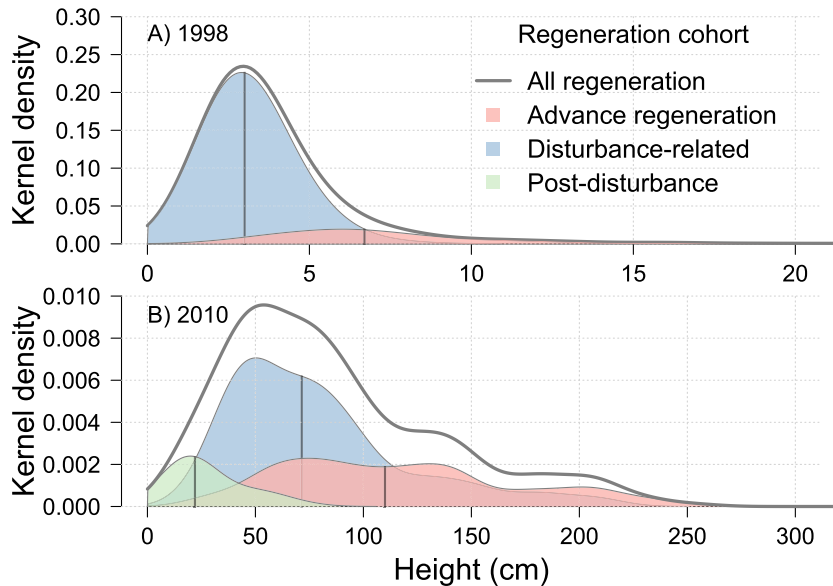


FIG. 3. Height distribution of seedlings and saplings (A) in 1998 and (B) in 2010. Solid gray line shows height distribution of all regeneration, and colored areas show height distributions of separate regeneration cohorts. Vertical lines denote median heights for each cohort separately. Note different scales used. (A) Regeneration during bark-beetle outbreak comprised mostly 1–2-yr-old seedlings of height <5 cm established during the outbreak itself. (B) Twelve years later, the dominance of this disturbance-related cohort was still apparent, but the relative proportion of advance regeneration increased. Only a small fraction of seedlings got established after the canopy dieback.

similar. The only exception was tree-base microsite, for which the model predicted a higher proportion of juvenile trees than observed (for details, see Appendix S1: Table S2).

DISCUSSION

Regeneration structure

Our hypothesis H1 that advance regeneration would dominate after the bark-beetle outbreak was rejected. Despite high mortality, disturbance-related regeneration outnumbered all other cohorts during the 12-year observation period. After the canopy dieback, seed rain apparently decreased and the proportion of unsuitable patches occupied by graminoids or dense clumps of tree regeneration increased. This explains the minimal establishment of new seedlings after the canopy dieback. The relative importance of advance regeneration increased over the evaluated period because it had the lowest mortality. To the future, we expect the relative proportions of regeneration groups to remain stable because all groups reached low mortality (about 1% annually).

The dominance of disturbance-related regeneration can be ascribed to the timing of several events. The bark-beetle outbreak created a temporal window allowing establishment of numerous seedlings originating mostly from the last mast year in 1995, immediately before the outbreak. These seedlings germinated in 1996, after the outbreak began. The timing of mast seeding preceding an outbreak could be of major significance for

regeneration assembly, but mast years are relatively frequent in our study area, occurring on average every three years over the last 20 years (Zeppenfeld et al. 2015). Therefore, a relatively abundant seedling bank could be maintained continuously despite limited long-term survival.

The abundant seedling establishment during canopy dieback suggests that most regeneration usually considered

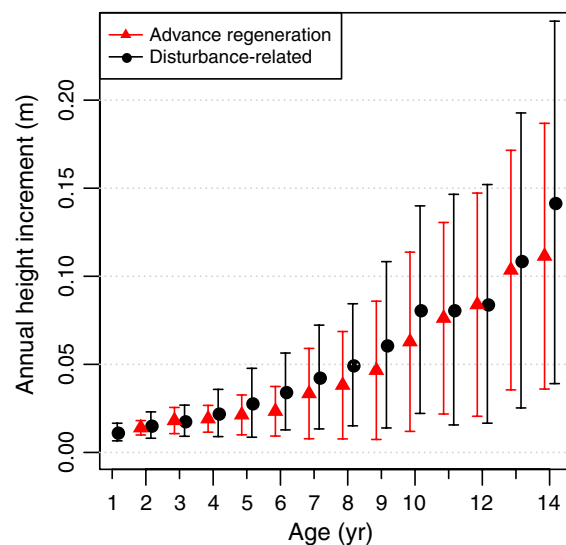


FIG. 4. Annual height increments (mean \pm 1 SD) observed for juveniles regarding their age and cohort rank.

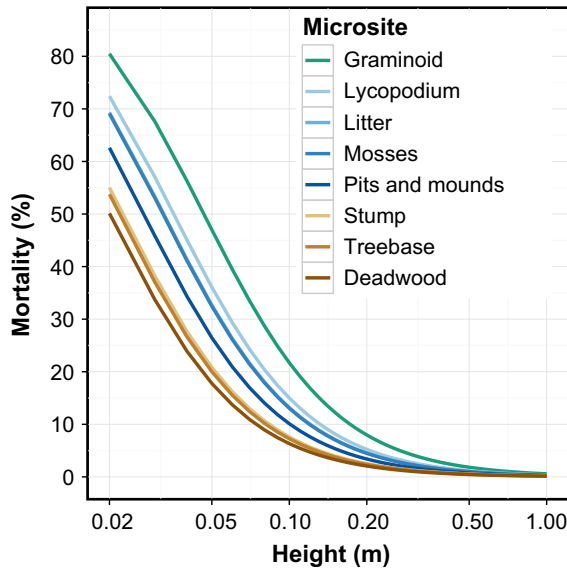


FIG. 5. Annual mortality steeply decreases with height and differs for particular microsites. Overall, the highest mortality was for seedlings growing in graminoid vegetation, whereas seedlings rooting in deadwood had the lowest mortality. Lines show marginal predictions of mortality model.

as advance, i.e., established before a bark-beetle outbreak, could in fact originate during the disturbance itself. This has far-reaching consequences, because the processes driving regeneration establishment are markedly different before and during a bark-beetle outbreak. Even the shade-tolerant true advance regeneration is light-limited and

survives mostly in patches under small canopy openings (Metslaid et al. 2007, Nigh et al. 2008, Kathke and Bruelheide 2010). As the stand infested by bark-beetles gradually opens, the seedlings can readily establish on a wider range of microsites until they are outcompeted by expanding vegetation. Canopy trees thus self-replace mostly during disturbance itself. This self-replacing mechanism leads to the long-term stability of tree species composition and genetic structure of populations. Such positive relationship between conspecific overstory and understorey (called “neighborhood effect”) was proposed by Frelich and Reich (1999) as major factor forming forest dynamics. Zeppenfeld et al. (2015) recently showed positive neighborhood effect also in European mountain spruce forest. Our results corroborated this finding but showed that not only advance regeneration but also disturbance-related regeneration contributed to continuous dominance of spruce.

More precise specification of cohorts in terms of their temporal relationships to disturbance is needed. We propose that the term “advance regeneration” should be used only for those juveniles that have already passed the earlier high-mortality stage and have a higher chance to survive in the understorey for a longer time, typically decades. The seedlings established during or just before a disturbance, which experienced different ecological conditions but share similar seed-source would be called “disturbance-related regeneration.” We are convinced that using this more precise differentiation could change the interpretation of many observed tree recovery patterns as well as forest practitioners’ perception of disturbance.

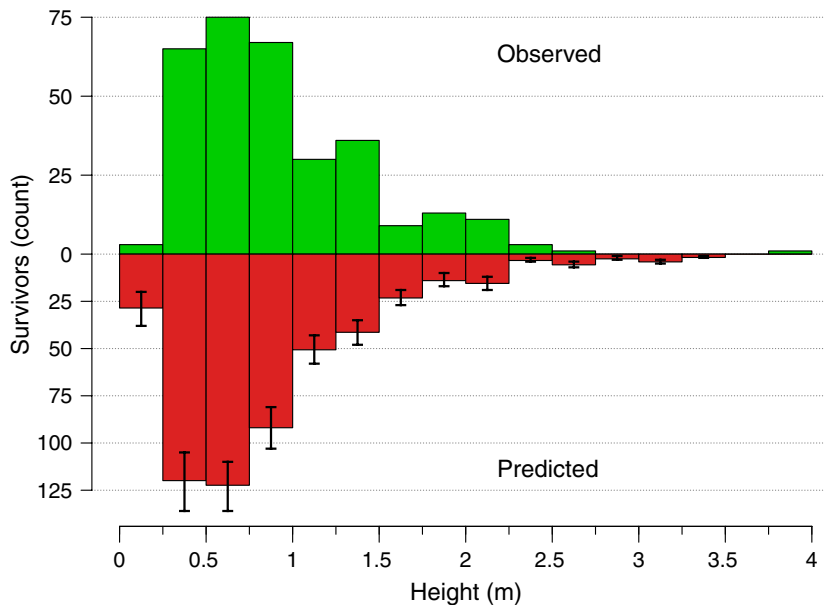


FIG. 6. Observed height distribution (upper green bars) corresponds to the year 2010 predictions (lower red bars), while total number of survivors is systematically overestimated. Error bars delimit 95% simulation interval.

Regeneration height growth

We found the absolute increments in early life stages of spruce to be quite small but gradually increasing (Fig. 4). Since it usually takes six years for a juvenile to reach 10 cm height (but varying greatly among individuals), this height class includes an important fraction of regeneration even several years after disturbance. Unfortunately, a common practice in forest inventory is to record only seedlings taller than 10 cm or more (Schweiger and Sterba 1997, Heurich 2009, Tomppo et al. 2010, Zeppenfeld et al. 2015). Our data showed that the information about tree regeneration captured by these inventories is incomplete, if not biased. For example, a stand with massive regeneration during a bark-beetle outbreak can be classified by standard forest inventories as having insufficient regeneration even several years after the outbreak.

The quality of fit differed considerably between growth functions used. We chose the Gompertz function as most suitable for fitting height growth of juvenile spruce trees because it showed the best fit and stability of residuals. Rammig et al. (2007) recommended the Bertalanffy growth function for fitting growth of young saplings, but they did not provide comparison with other growth functions. However, their data also showed that Bertalanffy function systematically underpredicts heights in the smallest height category. Since juvenile mortality is tightly coupled with tree height, the selection of an accurate growth function is crucial for the proper prediction of the regeneration process.

Processes structuring regeneration

Seedling microsite preferences are thought to be the main driver of regeneration spatial pattern and density (Kuuluvainen and Kalmari 2003, Wild et al. 2014). Because height-dependent mortality excludes slowly growing individuals from regeneration, we expected that microsites will affect mortality indirectly through differentiated height growth. However, we found no significant effects of microsites on height growth. Published evidence is ambivalent: height growth at wood-related microsites was reported to be lower (Kathke and Bruelheide 2010), unaffected (Kupferschmid and Bugmann 2005) or even higher (Baier et al. 2006). Height growth variation thus seems to be influenced by other factors, such as intraspecific competition (Metslaid et al. 2007).

In contrast, we found considerable differences in tree mortality among microsites. Low mortality found on decaying wood and at the bases of standing stems is in accord with the often-reported increase in regeneration densities on these microsites (Kuuluvainen 1994, Kuuluvainen and Kalmari 2003, Bače et al. 2012). However, low mortality values contradict Kathke and Bruelheide (2010), who deduced from regeneration age structure that mortality is highest on log and stump microsites. Low mortality without improved growth at these wood-related microsites suggests that spruce

regeneration occurs preferentially there due to lower stress-induced mortality, rather than better growth conditions enabling the juveniles to grow out of high mortality stages. Indeed, differences in microsite-specific mortality levels can be attributed to various mechanisms that could include the much greater stress caused by competition in patches occupied by graminoids, lower snow-mold infection rates on microsites with shortened snow cover duration (Cunningham et al. 2006), or better moisture conditions on decayed logs and stumps preventing seedling desiccation (Takahashi and Sakai 2000, Bače et al. 2012). Our hypothesis H2, that regeneration is structured through microsite-specific individual performance, was thus supported, but the main underlying driver was tree mortality rather than height growth.

Our findings of microsite effects on tree mortality allow us to clarify how the clustered spatial pattern of Norway spruce regeneration arises. The previous hypothesis of secondary seed dispersal into snow tree wells around trunks and snags was based only on snapshot data (Wild et al. 2014). We provide an alternative explanation that improved juvenile survival around tree trunks and snags governs the formation of such a pattern, but these processes could act simultaneously. Further research is needed to disentangle them precisely.

Interestingly, we found no relationship between mortality and elevation. However, sapling densities decreased considerably with elevation: in five stands above 1,300 m, we even found regeneration densities lower than the pre-disturbance stem density. The gradient in density is probably driven by decreasing seed production or germination, as was shown in the Alps (Mencuccini et al. 1995). Recruitment on these sites thus strongly depends on microsite availability and sparse canopies can persist there for decades. Further research is needed to ascertain whether the canopy gaps will be infilled, or if the sparse canopies will persist. With this exception, regeneration densities were several times higher than pre-disturbance canopy density. Self-thinning is thus likely to be the most important driver of future sapling mortality, but this can take decades to manifest in shade-tolerant spruce (Pretzsch 2006).

Evaluation of predictions based on short-term data

We expected that short-term monitoring of individual seedlings after the disturbance would not be sufficient to predict further stand development. Surprisingly, our model based on only three years of monitoring provided satisfactory predictions for some aspects of regeneration structure development. Individually modelled tree growth following the Gompertz function and non-random mortality provided realistic height and age distribution estimates even 10 years later, despite height growth being strictly nonlinear and mean height increasing ninefold in the evaluated period.

However, the same model systematically overestimated the total number of surviving individuals. This is

probably a result of underestimated mortality due to increasing competition with other juveniles and expanding graminoids. Kupferschmid et al. (2006) achieved better prediction accuracy with a model that included changes in competition. However, we were not able to include competition in our model because competition is not practically possible to parametrize from only three years of data.

Management recommendations

We provide strong evidence that self-replacement of mountain spruce forests after bark-beetle outbreak is possible without any management intervention. Moreover, because most of the regeneration comprises trees that germinated during the gradual stand-dieback, even stands lacking advance regeneration could recover naturally. Although young seedlings with height <10 cm at the time of outbreak suffer high mortality, their role in stand recovery is crucial. Individuals that emerged from such seedlings form the dominant cohort even a decade after the disturbance. Therefore, the practice of counting only seedlings above a pre-defined threshold height, which is frequently employed in current forest inventories, must change, as it excludes potentially important seedlings and can lead to seriously biased management recommendations. We propose that forest inventories should include all regeneration, with height classes weighted by expected future mortality. Similarly, the prediction of regeneration growth should be based on longer (>3 years) observation; otherwise the tree counts could be strongly overestimated. Although our study was based on observations only in one region, given the ecological similarity of conifer dominated forests in the northern hemisphere, our results have far reaching consequences, which could be applicable elsewhere.

Spatially structured stands with complex age and height distributions of young trees formed rapidly despite relatively uniform initial conditions. Resulting stand heterogeneity, together with the biological legacies of the former stands, contributes to the high biodiversity of unsalvaged stands (Kouki et al. 2001, Müller et al. 2008, Thorn et al. 2014). Salvage logging can thus damage natural regeneration in the time most critical for seedling establishment and disrupt or postpone the regeneration process. Moreover, excluding soil disturbance caused by salvage logging protects the site from invasion by pioneer and weedy species (Fischer et al. 2015, Nováková and Edwards-Jonášová 2015). Therefore, we consider natural regeneration as an appropriate management practice after bark-beetle outbreaks in natural Norway spruce forests.

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