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Disturbance history of a European old-growth mixed-species forest – A spatial dendro-ecological analysis

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Abstract

Question: We were interested if and how variation in frequency and/or size of disturbances affect the dynamics of a montane old-growth forest in Central Europe.

Location: The forest, co-dominated by *Fagus sylvatica, Picea abies* and *Abies alba*, is located in Lower Austria and represents one of the few sizable virgin forests in Central Europe.

Methods: We extracted cores from 100 trees using systematic grid sampling (grid cell size 10 m × 10 m) on each of four 1-ha plots distributed across the old-growth remnant of 300 ha. We inferred disturbance events from rapid early growth and release events. For defining release criteria, we applied the boundary line method. We investigated the spatial structure of current age and gap distributions and past disturbance events in grid cells, using a pair density statistic.

Results: The disturbance histories indicate decades with peaks and also extended periods without disturbance. Some peaks occurred synchronously at three of the four plots (1910s, 1930s, 1960s and 1980s). Peaks and gaps in the disturbance chronologies widely agreed with peaks and gaps in the age distributions. Most disturbance events during single decades showed a random spatial distribution.

Conclusions: There is considerable variation in disturbance frequency and/or severity over time. Most disturbance events will rather thin the stand than clear larger areas at once. Following scattered disturbance two pathways occur: (1) gap expansion leading to creation of larger gaps, and (2) gap closure by lateral encroachment or by subcanopy trees growing into the canopy.

Keywords: Boundary-line method; Disturbance regime; Forest dynamics; Release, Spatial pattern analysis.

Abbreviation: PSP = Permanent sample plot.

Introduction

Disturbances are defined as relatively discrete events in time that disrupt the ecosystem, community or population structure and change the resources, substrate availability or physical environment (Pickett & White 1985). Depending on the agent and their spatial and temporal features, disturbances create different environments for the locally available set of plant species to germinate, establish, survive, grow, and interact with each other. Consequently, information on the spatial, temporal and spatio-temporal features of the disturbances affecting an ecosystem (i.e. the disturbance regime) is a prerequisite for understanding vegetation dynamics (Moloney & Levin 1996; Spies & Turner 1999; Nakashizuka 2001; Gratzer et al. 2004).

There is very limited quantitative information on the disturbance regimes of Central European old-growth forests for two main reasons. Firstly, old-growth forests are scarce after a history of intense forest use and exploitation (Glatzel 1999). Secondly, the influence of site on vegetation patterns was emphasized over the influence of disturbances, probably because most forests in Central Europe are compositionally very stable. Even immediately after coarse-scale wind throw, the late-successional species maintain their dominance as they regenerate from seedling banks (Fischer 1992; Splechtna 1994).

In the mountain ranges of Central Europe the disturbance regime may be described as class VI (*sensu* Frelich 2002), when wind becomes the dominant coarse-scale disturbance agent and combines with insects and disease to cause fine-scale gap-phase dynamics of forests. For such forests with complex disturbance regimes, diverse combinations of disturbance histories may interact to create stands with very similar structural and compositional characteristics (Antos & Parish 2002a, b; Winter et al. 2002). Therefore, the reconstruction of past disturbance events is needed for understanding the processes leading to the observed forest structure.

The identification of disturbance events using dendroecological techniques has become a valuable tool in reconstructing disturbance regimes (Lorimer 1985; Lorimer & Frelich 1989; Rubino & McCarthy 2004). These methods provide estimates of the frequency and severity of disturbances. Particularly in forests with wind as the principal disturbance agent at fine and intermediate scales, methods based on the detection of release (abrupt positive growth change), yield much more accurate reconstructions of the disturbance history than size- or age structure analysis (e.g. Lorimer 1985; Frelich 2002; Gratzer et al. 2004). To separate growth changes due to other factors from disturbance events, criteria have been defined taking into account the abruptness and the duration of the growth changes unique to canopy releases (Lorimer & Frelich 1989; Nowacki & Abrams 1997). Black & Abrams (2003) proposed a new method, which indirectly accounts for the differences in release potential associated with age, size, species, and site. They provided empirical evidence that on a statistical level the potential for growth change is only dependent on the growth prior to the event over all but the most extreme sites. This boundary-line approach appears to be best suited to account for (1) the changes in release potential associated with the life history of a tree and (2) species-specific differences in release potential (Black & Abrams 2003). Therefore, we adopted the method for the three co-dominating species in a mixed-species old-growth forest.

The objectives were (1) to adapt the boundary-line method for the very shade-tolerant species *Fagus sylvatica, Picea abies* and *Abies alba*, and (2) to determine whether (a) disturbance is episodic; (b) the temporal variation in the disturbance regime affects forest dynamics, and (c) peaks in the disturbance history coincide with multiple-tree, intermediate-scale gaps, which lead to the formation of spatially distinct cohorts.

Study area

The study area was located at the southern slopes of Dürrenstein, a mountain (summit at 1878 m a.s.l., 47°47' N, 15°04' E) in the northern Limestone Alps of Lower Austria at an elevation of 900 to 1400 m a.s.l. The studied old-growth forest is situated in a bowl, with steep slopes at high elevation converging on a lower-elevation plateau. The climate is submaritime to sub-continental with long winters and short, cool summers. Due to its position within the northern outposts of the Alps the area receives ca. 2200 mm annual precipitation) (Roller cited in Zukrigl et al. 1963). The precipitation pattern is bimodal with maxima during the summer and winter months (Zukrigl et al. 1963). Deep, wet, and long-lasting snow cover shortens the growing season. The bedrock comprises dolomite and banked limestone. Soils are a mosaic of Rendzinas and relict loams – Rendzic Leptosols and chromic Cambisols (Zukrigl et al. 1963). The forests of the study area are classified as *Asperulo-Abieti-Fageta* and *Adenostylo glabrae-Abieti-Fageta*, respectively (Zukrigl 1973). *Fagus sylvatica* dominates on all sites, particularly on the slopes. The co-dominant *Picea abies* and *Abies alba* grow 10 to 15 m taller (up to 58 m) than *F. sylvatica*, forming a two-layered canopy (Zukrigl et al. 1963; Schrempf 1985).

Material and Methods

The sampling was carried out on four 100 m × 100 m permanent sample plots (PSPs). Two permanent sample plots (PSP1 and PSP2) in the lower and flatter, conifer-richer portion of the forest had been established in 1980 and 1943, respectively. Two other plots PSP3 and PSP4 were selected to capture the dynamics of the beech-dominated stands on slopes (Table 1). Plots were selected to represent a relatively uniform site without strong topographic variation, or intermeditate-scale edaphic variation. An earlier census of all trees > 1 cm in DBH (Gratzer & Splechtna unpubl. data) revealed that in all plots *F. sylvatica* dominates by abundance, but to a lesser extent by basal area. At PSP1 the relative importance of *F. sylvatica* is lowest, whereas at PSP3 *F. sylvatica* is clearly dominating. PSP2 and PSP4 have similar species composition, though they represent contrasting land forms (flat plateau versus steep slope) (Table 1).

We divided all PSPs into 100 10 m × 10 m squares for systematic sampling. Two cores (from bark to pith) were extracted from the tree (regardless of species) that was closest to the centre of each quadrat and greater than

Table 1. Characteristics of the four 1-ha plots (PSPs).

	PSP1	PSP2	PSP3	PSP4
Altitude (m)	1050	1020	1090	1200
Aspect (°)	120	110	160	175
Slope (°)	0-10	0-5	15-25	25-30
No. of *F. sylvatica*				
1- 10 cm DBH	1062	2214	757	1033
≥ 10 cm DBH	197	240	145	206
Total basal area *F. sylvatica*	22.8	28.9	30.1	27.9
Relative importance *F. sylvatica*	60.0	78.3	93.2	81.4
No. of *P. abies*				
1 - 10 cm DBH	183	196	21	44
≥ 10 cm DBH	63	31	2	29
Total basal area *P. abies*	20.2	7.8	0.2	7.4
Relative importance *P. abies*	25.3	13.2	1.6	12.1
No. of *A. alba*				
1 - 10 cm DBH	3	4	0	1
≥ 10 cm DBH	55	30	7	23
Total basal area *A. alba*	15.0	6.9	3.3	4.5
Relative importance *A. alba*	14.8	8.6	5.3	6.6

4 cm in diameter. These 100 trees per PSP were later used for age structure analysis. If a sample tree was suppressed (directly overtopped by other trees), the next non-suppressed tree was also cored. In total we made 118, 115, 106 and 108 cores at the plots PSP1, PSP2, PSP3 and PSP 4, respectively. The 100 non-suppressed trees per plot were used for disturbance event analysis. The cores were taken in opposite direction, perpendicular to the slope so as to avoid reaction wood. Coring height was at 1.1 m, however, the second core was taken as close as possible to the base of the tree for age estimation and for estimation of the time needed to grow to reach the coring height of 1.1 m. For every tree, we recorded diameter at breast height (DBH), tree height, and coring height. Further we recorded whether the cored trees were suppressed (overtopped by other trees), co-dominant, or dominant. For every sampled subcanopy tree (below 15 m in height) we noted whether it was growing in a gap or not.

Sample preparation and measurements were carried out differently for *F. sylvatica* and for conifers, because the latter were subjected to x-ray densitometry (Schweingruber et al. 1978) so the density data could be used for a study of the relationship between climate and growth. *F. sylvatica* cores were placed on holders, air-dried and then glued onto the holders and sanded with successively finer sanding paper (400 grit paper), so that single cells became clearly visible under the microscope. Ring width was measured with a measurement station to the nearest 0.01 mm. Conifers were prepared for x-ray densitometry by sawing thin probes (2 mm) with a special saw out of core sections. After x-raying the conifer probes the developed films were scanned and the digitized images were analysed. Cross-dating was carried out by visual inspection of ring width series using the list method (Yamaguchi 1991) and statistical evaluation was done with Cofecha (Holmes 1983). While most of the conifer cores could be cross-dated, only half of the *F. sylvatica* cores could be successfully cross-dated because of difficulties with reaction wood, short cores, or extended periods of suppression with very narrow rings. The high snow pack in the area does also induce reaction wood in trees growing on flat sites. Indeed, many of the cores taken at the base were difficult to date and also showed abrupt growth changes that were rather due to reaction wood formation than true releases.

The pith was not reached in many cores due to insufficient borer length, rot, or missing the centre of the tree. In these cores, the 'distance to pith' was estimated by the degree of arcing in the oldest captured growth increments, assuming a circular growth pattern. The 'number of rings to pith' was determined by estimating the number of rings that could occur in the remaining distance to the pith, assuming average growth rate was equal to that of the last three visible rings. For the vast majority of cores the missed distance to pith was small (for the 242 cores with no pith but arcing rings, the estimates for the distance to pith had the following statistics: median = 0.4 cm, 83 % < 1 cm, 97.5 % < 2.6 cm), so that for most cores the estimates appeared reliable at the decadal resolution of analysis. The few cores, where no arcing was visible (mainly trees with rotten centres), were deleted from the age structure analysis, because age could not be estimated accurately. Age structure analysis was therefore based on 94 trees at PSP1, 97 trees at PSP2, 80 trees at PSP3 and 94 trees at PSP4. Age was measured at coring height 1.1 m, because of the – already mentioned – problems we encountered with cross-dating of the cores taken at the base. Because establishment of seedlings occurs regularly even at very low disturbance severities for all three species in the study stands (Zukrigl et al. 1963; unpubl. data), the time when seedlings are able to grow to a height of more than 1 m may be even a better indication of disturbance than absolute age.

For defining release events, we used boundary-line release criteria (Black & Abrams 2003, 2004). The boundary-line method is a running mean method for release detection (Rubino & McCarthy 2004); it differs from all other available methods by scaling the release relative to the boundary line, i.e. the expected maximum growth change given the specimens growth immediately preceding the growth change. Thus the method takes into account that the release potential for a specimen is not constant over time, but is much greater when its growth is strongly suppressed (Black & Abrams 2003). The method proceeds through two steps: (1) empirical estimation of the maximum growth change given a prior growth for the study species (boundary line), and (2) scaling of the releases found by the running mean method (Nowacki & Abrams 1997, see formula below) relative to the boundary line.

For calculating the species-specific boundary line, a large data set of tree ring measurements collected from a variety of sites was needed. Therefore, we supplemented our data with data from other sites in the limestone Alps in Austria (Grabner et al. 2004) and with all available tree ring series for *F. sylvatica, P. abies* and *A. alba* (Anon. 2005). Prior growth was defined as average ring width over the past ten years, and percent growth change was calculated according to the running mean formula of Nowacki & Abrams (1997) in which percent growth change for a year is equal to $[(M_2 - M_1)/M_1] * 100$, where M_1 is the mean growth over the prior ten years and M_2 is the mean growth over the subsequent ten years. Prior growth and percent-growth change were calculated for every growth increment, except for the first and last

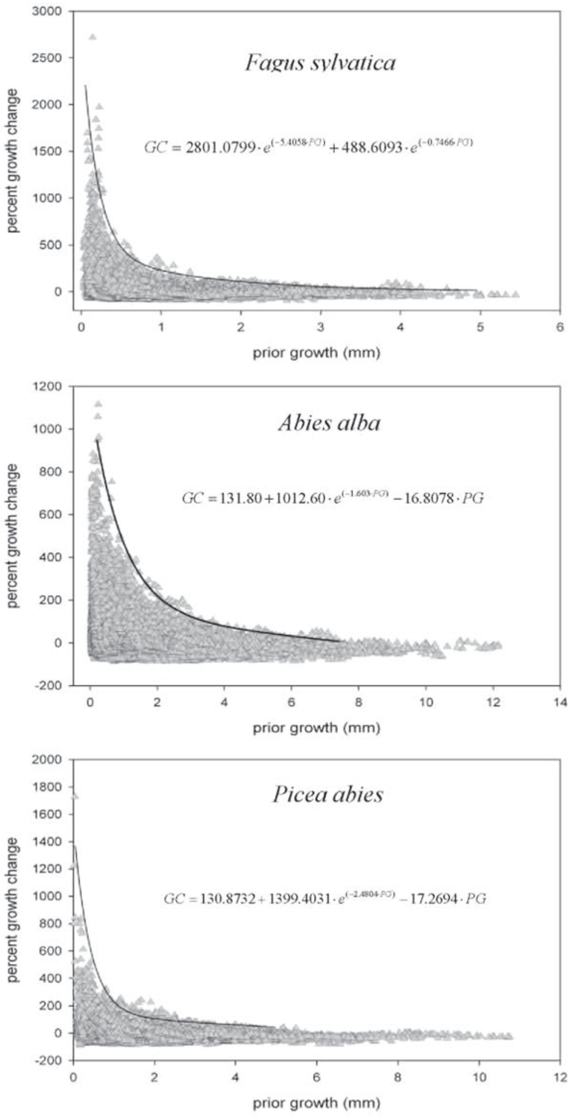

Fig. 1. Fitted boundary lines and plots of all percent growth change (GC) values with respect to prior growth (PG) for all tree rings of the three species. Please note the differences in scale between plots for different species.

ten years in each tree ring series due to the constraints of the percent-growth change and prior growth formulas. We divided the data set into nine prior growth classes (class width 0.5 mm). We averaged the ten highest growth change values for every growth class, and tested several non-linear functions for their fit to these nine top values.

The fitting of the boundary-line functions proved to be difficult, because maximum percent-growth change of all three species declined very rapidly with increasing rates of prior growth. To get a satisfactory fit we modified the techniques originally used by Black & Abrams (2003). For *F. sylvatica* we reduced the prior growth class width for the prior growth classes up to 1.0 cm from 0.5 mm to 0.25 mm, where decline in maximum percent-growth change was steepest. For these classes we averaged only the five highest data points for fitting the boundary line to keep the sample size equal. We were able to fit a double negative exponential function that followed very closely the upper boundary of the *F. sylvatica* data (Fig. 1).

For the conifers, a modified negative exponential function with an additional linear term fitted the data well (Fig. 1). However, for *P. abies* the visual check showed that none of the data from Central Europe approached the boundary line, indicating that the release potential was overestimated for the entire region. Considering the large range of *P. abies* and the genetic diversity of the species, it seemed warranted to reduce the data set. Consequently, we used only data from the Alps and developed a regional boundary line for *P. abies*.

In the second step, all the releases according to the Nowacki & Abrams criteria were scaled relative to the expected maximum growth change quantified by the boundary line. Visual inspection of the data showed that the variation of ring width increased with increasing prior growth, because late-frost events or other short-term climate extremes or mast years lead to very narrow rings even during periods of high growth (Splechtna & Gratzer unpubl. data). Even after smoothing the growth using 10-year running means – using the Nowacki & Abrams (1997) formula – this higher year-to-year variation appeared to influence the release detection. Therefore, we used only growth pulses of at least 50 % growth change according to Nowacki & Abrams (1997) and accepted only these events as potential releases. Only these potential releases were then scaled relative to the boundary line. After making these adjustments to the boundary line method, the risk was very low for accepting climatically induced spurious releases. Therefore, we could select the relatively liberal release criteria for scaling candidate releases to the boundary line analogous to Black & Abrams (2003). We defined, a moderate release as any percent-growth change pulse > 20 % of the boundary line at the given prior growth rate, and we defined a major release as any pulse exceeding 50 % of the value of the boundary line. The proportion of cores at coring height 1.1 m, which released every decade was then calculated and displayed as a disturbance chronology (Lorimer & Frelich 1989).

Gap origin events (Lorimer & Frelich 1989) were defined based on early growth rates of the trees. When plotted against DBH, there was only a small overlap in recent growth (mean growth of the last ten years) between the a-priori field-determined groups of suppressed and dominant trees up to a DBH of 50 cm, indicating that based on a growth threshold most individuals would be classified correctly. We defined the threshold for gap origin as the upper 95th percentile of growth rate of suppressed trees over the last ten years (1991-2000), which corresponded closely with the 5th percentile of dominant trees. For *F. sylvatica* the threshold was 0.75 mm, and for *P. abies* and *A. alba* the threshold was 1.1 mm. Every tree that grew at a higher rate than the threshold between the years 6 and 15 counted from the pith was considered gap origin.

To investigate the fine- to intermediate-scale spatial structure of release events, spatial analysis was carried out using the software Programita (Wiegand & Moloney 2004). For this analysis, every tree represented a grid cell of 10 m × 10 m. This analysis was restricted to the last century, because only for this time period the majority of our sample trees have been already alive, ready to record disturbances within grid cells. To test whether the release events occurred in clumps or were randomly distributed, we calculated the O-ring statistic for five different radii, from 10 m to 50 m in 10-m steps. The O-ring statistic with edge correction (Wiegand & Moloney 2004) is closely related to the widely used Ripley's *K*-statistic (Ripley 1981; Dale 1999). The latter is based on the mean number of points in a disc of radius r centred on each point and divided by the intensity α of the pattern and is thus cumulative. The pair correlation function (Stoyan et al. 1995) is not cumulative as it replaces the circles of radius r with rings of radius r. Hence, interpretation becomes more intuitive (Stoyan & Penttinen 2000). The O-ring statistic is the pair correlation function multiplied with the intensity α of the pattern (Wiegand & Moloney 2004). Lower and upper confidence intervals ($\alpha = 0.05$) for the O-ring statistic were identified as the 25th-highest and the 25th-lowest value of 999 Monte Carlo simulations, respectively.

Results

Boundary lines for the three shade-tolerant species

The final curve for *Fagus sylvatica* was based on 94 649 growth increments from the data of our study supplemented by data from three sites from the International Tree Ring Data Bank (Anon. 2005). For *F. sylvatica*, percentage growth change values of all sites, size classes, and age classes approached the boundary line, indicating that prior growth was a good estimator of release potential. The final (Alpine) curve for *P. abies* was based on 147 949 growth increments from the data of our study supplemented by data from 51 sites from the International Tree Ring Data Bank and by data from Grabner et al. (2004) (Fig. 1). The final *A. alba* boundary line was based on 132 544 growth increments from our study supplemented by data from 96 sites from the International Tree Ring Data Bank and by data from Grabner et al. (2004) (Fig. 1). For both coniferous species percentage growth change values of all but the oldest age classes (> 300 years) approached the boundary line. For *A. alba* all DBH classes reached the boundary line, but for *P. abies* percentage growth change values of the larger diameter trees (> 80 cm DBH) did not reach the boundary line. This indicates that the maximum release potential of the very old or largest trees may be lower than given by the boundary line. Therefore, during the latest part of the tree ring record of these old or large trees, disturbance events may not be detected. Nevertheless, we decided to keep all tree ring records with their full length in the data set, because eliminating the latest portion of the tree-ring records would have reduced the overall number of trees during the later periods and therefore would have only slightly increased the percentage of trees with releases during the latest decades. Given our research hypotheses, we decided to rather err on the conservative side of slightly underestimating disturbance.

Disturbance history

The temporal pattern of seedling recruitment to the coring height of 1.1 m was discontinuous at all four plots with periods of no or very little recruitment lasting for as long as several decades (Fig. 2). Length and timing of these periods varied between plots and occurred at PSP1 from 1860 to 1910, at PSP2 from 1740 to 1840, at PSP3 from 1870 to 1950, and at PSP4 from 1810 to 1940. The disturbance chronologies including release and gap origin events for the four PSPs revealed a relatively low proportion of trees showing release in most decades; in few decades more than 20% of trees show release, and in many decades, fewer than 10% of trees show release (Fig. 3). Especially low levels of disturbance occurred in all four plots between the late 18th century and the early 20th century. However, the exact timing varied with location. Periods lacking disturbance were longer and more pronounced at stands on flat areas (PSP1: 1780-1910 and PSP2: 1750-1890) compared to the stands located on slopes (PSP3: 1840-1910 and PSP4: 1830-1940) (Fig. 3). At times releases occurred synchronously among all plots in the stand. In particular, there was an increase in disturbance events during the 20th century, with peaks in three of four PSPs during the 1930s, 1960s and 1980s. Also, all plots showed disturbance peaks during the early portion of the chronology lasting roughly from 1700 to 1760 (Fig. 3). Most peaks in releases agreed with the relatively broad peaks in age distribution (indicated by arrows in Fig. 2), but frequent releases during the 1910s and 1930s at PSP3 were not reflected in the age distribution (Figs. 2 and 3).

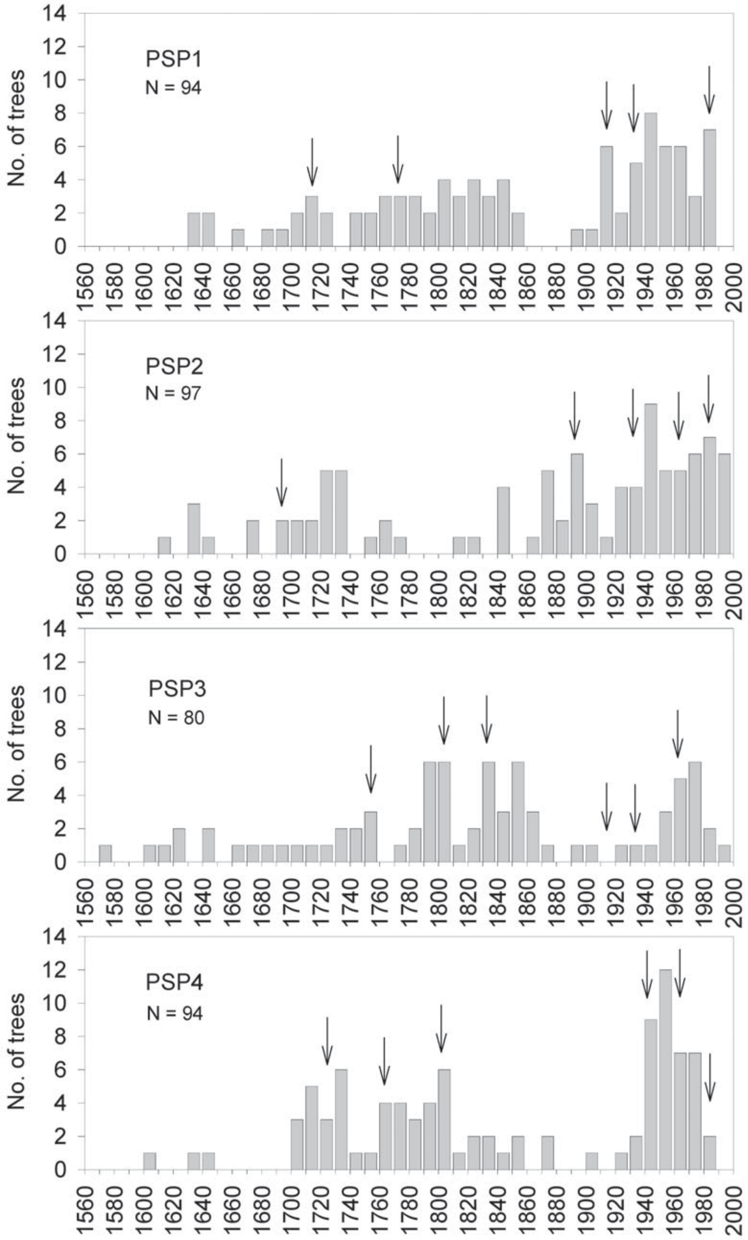

Fig. 2. Number of trees 'established' every decade at 1.1 m coring height on a regular grid in four 1-ha plots. *N* represents the number of sample trees (out of 100) with reliable age estimates kept in the analysis. Arrows indicate peaks in the corresponding disturbance chronologies (Fig. 3).

Spatial analysis of age distribution, gap distribution, and disturbance events

When the age of the tree cored at the centre of the grid cells were plotted in 100 year age classes, spatial clusters of trees of similar age occurred on PSP1, PSP2, and PSP4 (Fig. 4). While at PSP1 and PSP2 the spatial clusters were of the youngest age class (0 to 100 years), the cluster at PSP4 was of the age class 200 to 300 years. The clusters of PSP1 and PSP2 closely corresponded with the grid cells identified as being in gap status in year 2000 (Fig. 5). Of the 100 grid cells 41, 49, 19, and 38 were considered in gap at PSP1, PSP2, PSP3 and PSP4, respectively. Only for PSP1 and PSP2 was there significant clumping of gap cells when tested using the O-ring statistic (Table 2).

The spatial analysis of release events was restricted to peak periods of disturbance during the 20th century (1910s, 1930s, 1960s, 1980s, and the period 1963 to 1990), because for other periods there were too few events for a meaningful pattern analysis. The releases during most peak periods of disturbance did not show

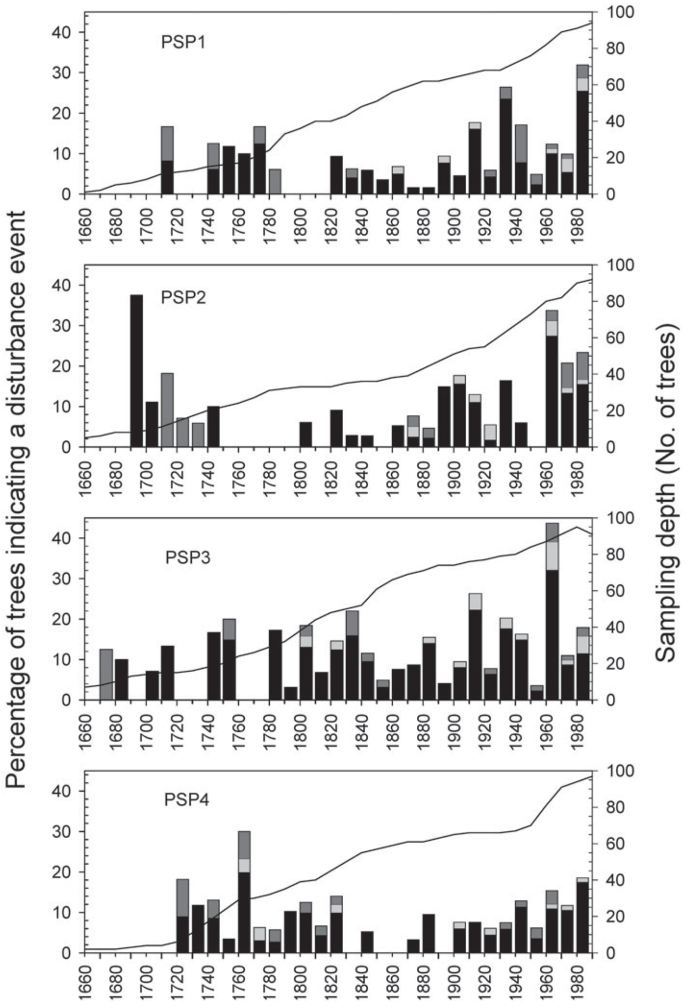

Fig. 3. Proportion of trees with moderate (black) and major (light shaded) release or gap origin events (dark shaded) relative to the number of trees alive during a given decade for the four 1-ha plots. Sampling depth is given for every decade by lines.

significant departures from the complete spatial randomness null model. The grid cells showing release for the 1910s, 1930s and 1960s were not clumped at anyone of the PSPs and results are therefore not displayed in Table 2 (at PSP4 there were too few events for the 1910s and the 1930s for carrying out the analysis). At PSP3 release events were significantly regularly dispersed at a radius of three grid cells (30 m) for the 1960s. However, the release events for the 1980s and for the extended period 1963 to 1990 were clumped at the flat stands PSP1 and PSP2 but not clumped at the stands located at the slopes (PSP3 and PSP4); at PSP4 the release events at the 1980s and from 1963 to 1990 were regularly dispersed at a radius of 40 m (Table 2).

Table 2. O-ring statistics for testing spatial patterns of grid cells in gaps or showing evidence of disturbance during a given period and for a given radius: Significance ($\alpha = 0.05$) was determined based on confidence intervals calculated using Monte Carlo Simulation (1000 simulation runs).

	R1 (10 m)	R2 (20 m)	R3 (30 m)	R4 (40 m)	R5 (50 m)
Gaps					
PSP1 Gaps	0.498*	0.448	0.410	0.375	0.376
PSP2 Gaps	0.576*	0.593*	0.540*	0.519	0.474
PSP3 Gaps	0.183	0.160	0.145	0.157	0.194
PSP4 Gaps	0.432	0.403	0.350	0.357	0.361
Disturbance events					
PSP1 1980s	0.446*	0.364	0.316	0.260	0.345
PSP2 1980s	0.375*	0.281*	0.237	0.211	0.215
PSP3 1980s	0.291	0.194	0.288	0.261	0.192
PSP4 1980s	0.256	0.223	0.122	0.105#	0.157
PSP1 1963 - 1990	0.563*	0.514	0.498	0.470	0.541
PSP2 1963 - 1990	0.668*	0.652*	0.622*	0.594	0.594
PSP3 1963 - 1990	0.547	0.521	0.551	0.539	0.540
PSP4 1963 - 1990	0.427	0.378	0.375	0.307#	0.419

* Significant clumping; # Significant regularity.

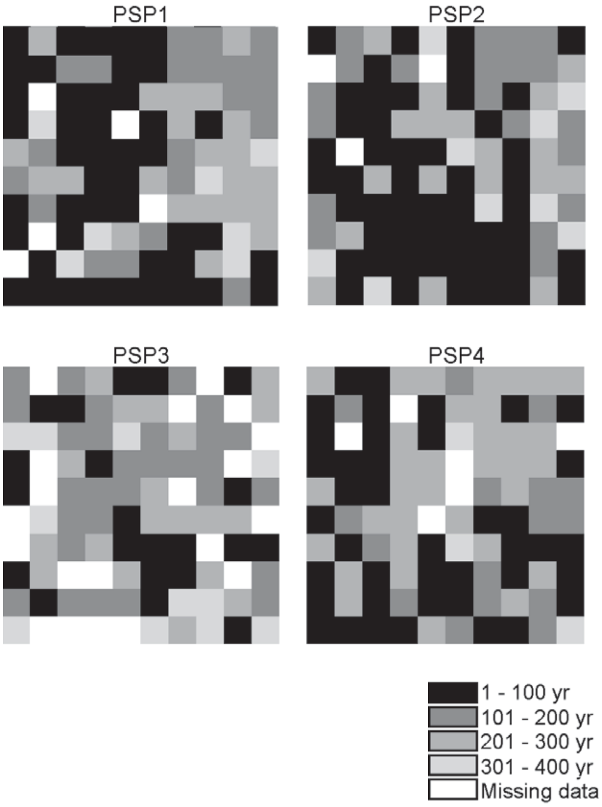

Fig. 4. Spatial distribution of age classes (class width 100 years) on a 10 m × 10 m grid for the four 1-ha plots. Missing data indicate mostly relatively old trees with rotten centers, which made reliable age estimation impossible.

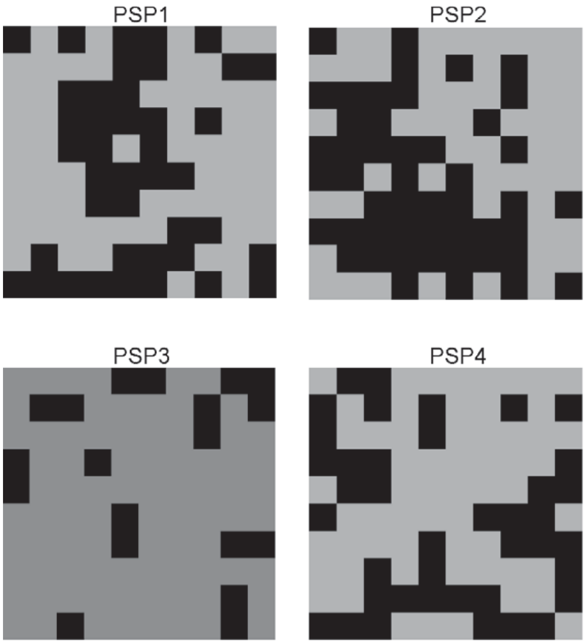

Fig. 5. Spatial distribution of grid cells (10 m × 10 m) in gap state (black) and closed canopy (shaded) at year 2000 for the four 1-ha plots.

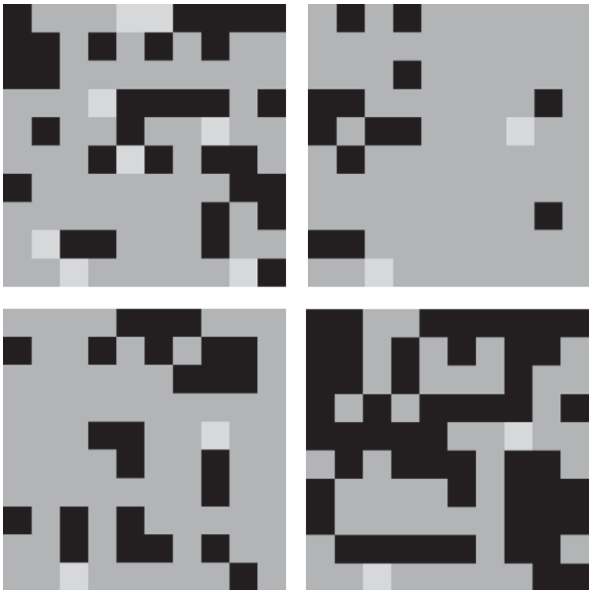

Fig. 6. Spatial distribution of release and gap origin events (black cells) at PSP3 for the 1960s (upper left), the 1970s (upper right), the 1980s (lower left) and the period from 1963 to 1990 (lower right). Dark shaded cells indicate no release, and light shaded cells indicate missing values for the period.

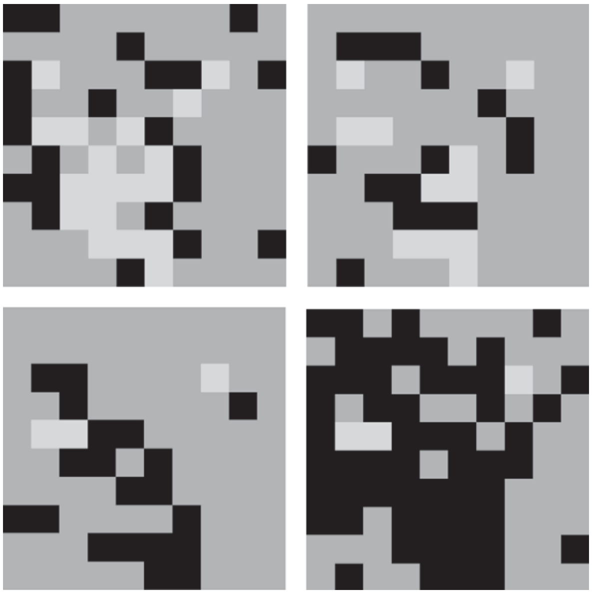

Fig. 7. Spatial distribution of release and gap origin events (black cells) at PSP2 for the 1960s (upper left), the 1970s (upper right), the 1980s (lower left) and the period from 1963 to 1990 (lower right). Dark shaded cells indicate no release, and light shaded cells indicate missing values for the period.

Discussion

The boundary-line approach applied to a mixed-species stand

Release criteria are at the core of the dendro-ecological approach to reconstruction of disturbance histories. Depending on the system studied and the research objectives many different criteria have been applied for release detection (Canham 1985, 1990; Lorimer & Frelich 1989; Nowacki & Abrams 1997; Abrams et al. 1999; Winter et al. 2002; Parshall 1995). This was warranted by the observation that release potential varies with site, species, and canopy position (Abrams et al. 1999). Consequently, the choice of the method and the threshold may influence the result substantially (see Rubino & McCarthy 2004 for a detailed review on this matter) thus hindering comparisons between studies. Furthermore, mixed species stands are often analysed using the same criteria for all species despite potential differences in the response of different species to a given canopy opening (e.g. Abrams et al. 1999, 2001; Antos & Parish 2002 a, b).

This is the first study adopting the boundary-line approach for identifying release events for different species growing in the same stand. The boundary line approach provides a much more accurate estimation of disturbance history of mixed-species stands than other methods, because it accounts for changes in release potential with life history (mainly canopy position) and between species (Black & Abrams 2003). The differences between the shapes of the boundary lines among the late-successional species *F. sylvatica* and *A. alba* detected in this study amplify that even species of similar shade tolerance may show big differences in release potential. Because we scaled the releases according to their species-specific release potential for a given prior growth, we could readily compare releases of the same strength between species and display the overall disturbance history for the entire stand.

The main advantage over other methods is therefore that the release potential is not held constant but is estimated from empirical data. Because the empiric assessment of the species-specific release potential (boundary line) is done independently from the studied forest, using data from various locations and sites across the range of the species, the developed functions (Fig. 1) can be used for studies in other forests consisting of the same species. Such broad criteria should facilitate more accurate comparisons of disturbance histories among forests.

Are episodic disturbances driving the dynamics of the gap-phase forest?

A history of rather low-severity disturbances has led to the formation of the studied forest. This is in concordance with the gap-phase paradigm, stating that low-severity disturbances forming small gaps are the main pathway of recruitment. However, similar to the situation in other old-growth forests, the disturbance regime is not static but varies on broad temporal scales (Abrams et al. 1999; Antos & Parish 2002 a,b; Winter et al. 2002). The disturbance history of the studied forest is characterized by a relatively low-severity disturbance regime during the 19th century, but higher severity in the 18th century and a strong increase in the 20th century. The widespread releases in the later 20th century (1960s and 1980s) coincide with heavy windstorms that hit the area in 1966, 1976, and 1990 (Splechtna 1994), indicating that the disturbance histories inferred from release and gap-origin events are accurate. Disturbance pulses occurred synchronously on up to three out of four plots distributed across the old growth remnant, indicating that single events or periods of increased disturbance affect larger areas of the forest. This is also in agreement with earlier reports that between 1960 and 1980 the standing volume of a portion of 60 ha of the forest was decreased by 20% likely due to wind throw (Schrempf 1985). The synchronous occurrence of release and gap-origin events also before 1966 indicates additional intense disturbance events affecting larger portions of the forest. Therefore, we can conclude that disturbances are indeed episodic.

The importance of these episodic disturbances for the dynamics of the forest is illustrated by the coincidence of recruitment pulses (of seedlings above 1.1 m) with periods of increased disturbance. Szwagrzyk et al. (2001) found that *Fagus* seedlings were permanently replaced on a relatively short cycle. This indicates that in old-growth (*Picea-Abies*) *Fagus* forests the seedling establishment and the maintenance of a seedling bank may depend less on episodic disturbance but may occur with fine-scale or even without disturbances. However, our results suggest that the successful survival and growth to a larger size corresponds well with episodes of increased disturbance.

Are periods of high disturbance associated with the formation of larger gaps?

The observed peaks in the disturbance history may be the result of a higher frequency of low-severity disturbance (creation of many small gaps) or could be related to a higher severity of the disturbances and thus creation of larger gaps. Differences in gap size may be an important mechanism for enabling the coexistence of tree species in mixed-species forests (Denslow et al. 1998; Pearson et al. 2003; but see Brokaw & Busing 2003). However, current gap status of a stand may not be a good indicator of the disturbance regime over longer periods of time. Therefore spatial pattern analysis of reconstructed disturbance events is an excellent complement for age structure analysis and analysis of spatial patterns of gaps.

Even the most severe events thinned the stand rather than cleared large areas at once. The creation of intermediate to large gaps through single events appears to be the rare exception. Small gaps predominate in most old-growth forests, may it be in the boreal, temperate, or tropical climate zones (Kneeshaw & Bergeron 1998; Runkle 1985; Brokaw 1985). The results of our study suggest that these small gaps may (1) be relatively quickly closed via lateral expansion of branches of adjacent trees or from below through the advancing of large subcanopy trees to the canopy, or (2) expand over time to form larger gaps. The first of these mechanisms appears to have occurred in PSP3: Spatial analysis of the recent disturbance history in PSP3 indicates widespread but scattered releases in the later 20th century. Over half (53%) of the grid cells representing the stand showed a release or gap-origin event from 1963 to 1990 (Figs. 5 and 6). However, few gaps presently exist in this stand, which suggests that gaps opened by disturbances were rapidly closed. *Fagus sylvatica* is known to be a very plastic species and has a well-documented ability to close small gaps via lateral encroachment (Lemoine et al 2002; Meszaros et al. 2002). This pathway of vegetation development may explain the tendency of uneven-aged beech forests to form single-layered canopies.

The second of these mechanisms may explain why intermediate-sized gaps occur regularly (roughly 10% of the gaps are larger than 400 m^2, Splechtna & Gratzer in press). Similar to PSP3, 55% of the grid cells representing PSP2 showed a release or gap-origin event between 1963 and 1990. Yet in PSP2, widespread gaps currently exist, and the locations of these gaps correspond with the locations of the releases and gap-origin events over the past 40 years (Figs. 5 and 7). In PSP2, and also likely in PSP1 and PSP4, initially small gaps were enlarged over time, probably as a consequence of the increased mortality risk of trees growing along the gap edges (Runkle 1984; Lawton & Putz 1988; Lertzman & Krebs 1991; Young & Hubble 1991).

Which one of the two pathways of vegetation development will be followed after scattered disturbance likely depends on the stand structure (developmental phase) at the time of a disturbance and therefore on the history of the stand and the legacies left after the disturbance. Spatial interactions at a fine-scale (neighbourhood processes, Pacala et al. 1996; Gratzer et al. 2004) appear to determine vegetation development after scattered fine-scale disturbance in this forest. The described differences in the response to disturbances through these neighbourhood processes may help to explain the discrepancy between gap studies and studies following more closely the mosaic-cycle concept. The former studies emphasise the predominance of small gaps (Kneeshaw & Bergeron 1998; Runkle 1985; Brokaw 1985) and their role for forest dynamics. The latter approach, which is commonly followed in Central Europe, aims at identifying and mapping developmental phases of a stand (Watt 1947; Leibundgut 1959; Zukrigl et al. 1963). Studies following this approach usually find patchiness at a much coarser scale then would be implied by the gap size distribution alone (e.g. Schrempf 1985; Korpel 1995). The sheer dominance of small gaps does not imply that vegetation change is predominantly or exclusively occurring through small gaps. Patchiness at a larger scale may result from both of the described mechanisms. The ability to quickly close canopy gaps through lateral encroachment or large subcanopy trees will maintain closed canopy conditions for extended periods of time and thus prevent successful development of seedlings to the sapling and subcanopy stages. On the other hand, gap expansion processes will lead to the formation of true albeit broad cohorts at intermediate to coarse scales. The dependence of the vegetation development on these neighbourhood processes after scattered fine-scale disturbance suggests that inferring stand dynamics from gap size distributions or disturbance histories may be too simplistic. It reiterates that the vegetation response to similar disturbances differs depending on the succession state (White & Jentsch 2001) and local interactions and that these response processes need to be identified in order to enhance the understanding of forest dynamics even in gap-phase forests.

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