Natural stand dynamics of beech forests of East-Central Europe

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Introduction

Two essentially different approaches were developed to describe forest dynamics of temperate deciduous forests. The concept of forest cycles (characterized by different development stages and phases) traditionally was used as the major tool in Central Europe. The systems (based on the forest cycles) developed by different authors (e.g. Czájlik, Korpel, Leibundgut, Mayer, Prusa, Zukrigl) are not entirely compatible, the categories used are loosely defined; the mapping units of the phase-mosaic might be of different size, so the perceived mosaic might have different spatial resolution according to the system used. The recognition of stages and phases is observer-dependent, which might cause problems in interpreting results of long-term observations.

The theory of gap dynamics – worked out by English and American authors – examines the natural processes at the level of the tree individuals. According to this theory, gaps – created by natural disturbances – play an important role in the dynamic processes of forest communities. The term „gap” was first used by Watt to refer a site where a canopy individual had died and where a new cohort of trees begun to develop. In further studies on forest dynamics the emphasis was on the relatively small within-community disturbance patches. This so called “gap-dynamics” results in forests comprised of fine scale mosaic pattern of small patches in different phases of development. These phases are similar to the developmental phases/stages described by Central-European authors. These two approaches in studying natural dynamics thus examine the same processes at different spatial resolutions and with different level of subjectivity. The individual based approach used by the theory of gap dynamics warrants higher level of objectivity.

Investigation of natural forests provides substantial information for ecologists, for nature conservation practitioners and also for foresters. In the last decades there has been a growing interest for nature-based silviculture. One of the main aims of this idea is to mimic the natural processes in the management course. Nature-based management would provide favourable conditions for species adapted to natural stand conditions. It would also be more cost-effective in the longer run. However, to gain the necessary information to develop this management regime, long-term investigations of forest dynamics are required.

Remote sensing enables us to gather long-term information on forest dynamics. By analysing a time series of aerial photographs, important events in past stand dynamics can be deduced, though this method cannot substitute field observations completely. Information
gained both from ground observations and remote sensing leads to a deeper understanding of forest dynamical processes and the foundation of nature-based management techniques.

Aims

The thesis investigates the gap dynamics in beech forests characterised by different levels of naturalness with special regard to the causes and the dynamic responses. The first part of the thesis studies approx. 30 years of natural dynamics in three semi-natural beech forest reserves focusing on the characteristics of the individual-based gap dynamics. The second part of the thesis is concerned with the causes of intensive landscape-scale abiotic disturbances in managed forests.

Questions:

1) What new information can be provided by the investigation of the disturbance-patterns of the best reference sites (Žofín, Kékes and the Őserdő in the Bükk Mts.)? Is there any correlation between the duration of the free natural development and the characteristics of gap dynamics?
2) What were the dynamic responses generated by the natural disturbances?
3) What are the most important factors behind the intensive ice breaks in the managed stands of the Börzsöny Mountains?

Methods

The investigations were carried out in four study sites:
1) In Žofín Forest Reserve (Novohradské hory Mountains, Czech Republic) spatial and temporal pattern of gaps and the mortality processes were investigated.
2) In Kékes Észak Forest Reserve (Mátra Mountains, Hungary) spatial and temporal pattern of gaps and relationship between gaps and developmental phases were investigated.
3) In Őserdő Forest Reserve (Bükk Mountains, Hungary) spatial and temporal pattern of gaps and regeneration in gaps were studied.
4) In the southwestern part of the Börzsöny Mountains (Hungary) managed by the Királyrét Forest Directorate, characteristics of disturbance patches caused by the ice breaks in 1996 and 2001 and causes of the disturbances were studied.

A ground survey of tree regeneration was conducted in 27 gaps in Öserdő Forest Reserve. The gaps were selected by age and size. They were divided into two groups according to their age: ‘old gaps’ were created before 1980 and ‘young gaps’ appeared later. In each gap, seedlings and saplings were counted in a 25-m² quadrat, and the species, height class and browsing damage were recorded for each individual. Field sampling was carried out at the end of July in 2005.

Spatial distribution of the ice-break patches in the Börzsöny Mts. was mapped in the 4200 hectare study area in 2001-2002. Based on the ground survey, the homogeneous disturbance patches were marked in the photos and the intensity of the damage (tree fall, crown breakage, total canopy loss) was estimated in each patch.

Data processing: for analysing the gap characteristics an ArcView extension (Patch Structure) was used, developed for the purposes of this study by Zs. Pataki. For each study year, gap characteristics of the study area were described in terms of: number of gaps; size distribution (mean, standard deviation, minimum, maximum) of gaps; proportion of the whole area in gaps; mean elevation, slope and aspect. Kruskal-Wallis and post hoc tests were used to test the significance of differences between average gap sizes in each of the study years. The fate of the individual gaps was determined, and the number, proportion and area of opened, closed and surviving gaps were compared between the study periods.

To study the relationship of dead trees and gaps in the 10 hectares sample plot – where the related maps were fitted – the number, species and size of gap makers and non gap maker trees were examined. For this analysis trees that had been died between 1975 and 1997 were considered. Kruskal-Wallis test and post-hoc comparisons of mean ranks were used to test if there was a significant difference in mean DBH of gap maker trees and gap sizes depending on the number of neighbouring trees (1, 2, 3) in a gap. To get a better understanding of the role of different trees in gap creation, we tested several hypotheses by applying Chi-square ($\chi^2$) tests of independence between rows and columns of contingency tables to test hypotheses about the
relationships between gap making and size, species and neighbourhood. In Kékes the size, number and proportion of gaps was determined in each developmental phase. In Öserdő the significance of the effects of gap age (old vs young) on regeneration density was tested by t-test or by Welch-test. Independence of browsing damage, height class and species was tested by Pearson’s $\chi^2$.

To study the relationships between the occurrence of disturbance and potential explanatory variables (elevation, slope, aspect, mixture ratio and age-specific slenderness of beech, age and height of the stand) in the Börzsöny, a random sample was used. The impact of variables of topography and stand characteristics on the intensity of the ice breaks was tested by pairwise Spearman rank correlations, independence of the disturbances and the nominal variable of aspect was tested by $\chi^2$-tests. Differentiation of samples of sporadic and intensive disturbances and disturbance free patches by variables and the importance of variables were investigated by CVA analyses. The importance and critical values of explanatory variables in the development of intensive disturbances was examined by CART analyses. Prediction of the model made by R. Aszalós for the 1996 ice-break was compared with the disturbances in 2001.

**Results**

1) The average gap size was between 75 and 99 m² and didn’t vary significantly in Žofín and Kékes, while it increased in Öserdő (40-93 m²).

2) Most of the gaps of the reserves belonged to the size category 20-50 m². Gaps of 200-500 m² in Žofín and 100-200 m² resp. 200-500 m² in Kékes gave the largest proportion of the overall gap area throughout the whole study period. However, in Öserdő this characteristic changed in time.

3) Percent of total area covered by gaps increased only slightly in Žofín and Kékes (from 8.9% to 10.8%, and from 4.9% to 7%, respectively), whereas it grew from 2.5% to 7.7% in Öserdő during the investigated periods.

4) Proportion of closed gaps was constant (0.02-0.04%) through time in the reserves. In the studied periods (cc. 30 years) the area of new and surviving gaps increased slightly in Žofín (0.01 and 0.06%). Considerably larger increase in area was found in Kékes and Öserdő (0.02-0.08 and 0.02-0.09% respectively). The wind throw in 2004 in the Öserdő raised the proportion of the area of new and surviving gaps to 0.07 and 0.13%. Annual proportion of area where canopy dynamics occurred was between 0.09% and 0.15% in the three reserves but the wind throw in Öserdő raised it to 0.23%.
5) In Žofín the simultaneous death of one to three larger trees was the typical driving force behind both the formation of new gaps and the enlargement of existing ones. Size, species and the neighbouring stand structure strongly determined whether the tree acted as a gap maker or not.

6) Average seedling density in the studied natural gaps was in the range (between 40 and 50 thousands per hectare) that is regarded as sufficient for restocking managed beech stands by natural regeneration. More small seedlings were established in old vs young gaps, but the density of saplings up to 0.5 m in height was similar, which suggested that seedling survival was less in old gaps than in young ones. Browsing pressure on the regeneration was considerable and preference for associated species could be detected.

7) Investigation of gap characteristics in Kékes showed different mean gap size, number and proportion of gaps in the developmental phases.

8) In the development of ice breaks both the studied topographic (elevation, slope, aspect) and stand variables (mixture ratio and slenderness of beech, stand age and height) played an important role.

9) Ice break appeared at higher elevations (> 500 m) and on steeper slopes (> 15°) than patches that were not hit by the corresponding disturbance. Ice damage was observed on NE-E-SE facing slopes significantly more often than expected.

10) The stands, where intensive canopy loss occurred, were typically beech-dominated (mixture ratio > 60%), relatively old (70-100 years old) and taller than 20 meters stands. Beeches in these stands were more slender than their age-class average. Tree height showed difference between the two ice breaks, in 2001 the shorter (18-20 m) stands also suffered from crown breaks.

11) Prediction model developed after the ice break in 1996 indicated the disturbance in 2001 with 62% efficiency.

Conclusions

Percentage coverage of gaps (5-11%), and average gap size (under 100m²) are in the range found in different natural temperate and tropical forests. Proportion of small (< 50 m²) gaps was high. Mean diameter of the gaps was less than one tree height in all the three reserves. The characteristics of gap dynamics seemed to be more static in the unmanaged reserves. Intensive gap creation and closure took place simultaneously in these forests. In spite of this, the gap characteristics (number, size distribution) at different periods were very similar. However, even in real natural forests the dynamic equilibrium maintained by fine-scale
disturbance events can be disrupted by rare and intensive large-scale disturbances. The role of large-scale disturbances can also be recognized from the intensity of gap dynamics. The annual proportion of area where canopy dynamics occurred (0.1%) would suggest more than 1000 years turn over rate, which seems to be too long compared to the average lifespan of the main tree species. The specific dynamic features of Öserdö can be explained by its small area, the past management and also the wind throw in 2004 all of which shaped the processes of gap dynamics in this reserve.

Tree size (dbh) was the main factor determining whether a tree acted as a gap maker or not, which is a straightforward consequence of the multi-layered character of the canopy. Death of large trees in the dominant canopy layer usually creates gaps, while the death of smaller suppressed individuals does not. However, in general deciduous trees were more effective as gap makers than coniferous trees. The reasons behind these findings are compound. On the one hand, deciduous trees of a given size have wider canopies than coniferous trees of the same size. On the other hand, in this mixed deciduous forest type the dense canopy of deciduous trees (mostly beech) usually forms an almost closed dominant layer. On the other hand, the narrower canopies of large fir trees form a sparse emergent layer, hence their death does not necessarily result in the opening of a detectable canopy gap. Another aspect of the relationship between tree size and gap creation is that even if the death of a sizable tree can create a relatively small gap, it can be closed so quickly that we cannot detect the gap by using a series of aerial photos taken in every ten years. The role of well developed sub-canopy layer also seems to be important as it gradually infills areas with a degrading canopy.

In Öserdö more small seedlings were established in old gaps, but the density of saplings up to 0.5 m in height was similar to densities in young gaps, which suggested that seedling survival was less successful in old gaps, perhaps because of competition from ground vegetation. However, a range of other factors, notably light availability, localized deer browsing and uneven seed fall, may have been involved. Deer browsing was overwhelming in the area. An extremely high proportion of seedlings were damaged. No young trees were found in the 1-2-m height class, and trees higher than 2 m were found only in old gaps where they had grown beyond the reach of browsing game at a time of lower browsing pressure. It is necessary to consider that these large herbivores use a much larger area than the Reserve itself. The negative effects of high browsing pressure could be reduced on a landscape scale.

The investigation of developmental phases showed that the phases can be characterised by the size, number and proportion of gaps but these characteristics are not enough to clearly
distinguish the phases. Important field information e.g. on regeneration is needed for determination.

Based on the results of the investigations in the Börzsöny we can say that the microclimate – affected by the topography – can have an influence on the severity of ice storm, e.g., by affecting the thickness of deposited ice. Therefore, the importance of specific elevations in the development of ice damage can be understood. Slope steepness can increase the severity of damage because individual trees are more likely to have less stability on steeper slopes and also the development of the ‘domino-effect’ is more likely. The relationships between aspect and the severity of disturbance need more careful consideration, since tree species composition and aspect are strongly related. Species-specific sensitivity – including that of beech – to ice damage was shown by several authors. Initial stand density, thinning regime and tree slenderness are related characteristics. An apparent inconsistency exists between the findings that i) high stand density enhances the development of high height:dbh ratios, and ii) intensive thinning increases the susceptibility to disturbances. Although high initial stand density and lack of early thinning increase susceptibility by giving rise to high slenderness, thinning not only assists in the development of tall trees with small root system, but also increases susceptibility if intensive thinning taking place not long before the disturbance event.

Reliability of predictions can be limited. It is not sure that data of all important explanatory variables were used. Moreover, the study site had been disturbed two times (in 1996, 1999) before the ice break in 2001 and the effects of the former disturbances can influence the development of the later one.

Publications

*Scientific papers*


**Conference presentations**


Reports, manuscripts


Kenderes, K., Král, K., Vrška, T. & Standovár, T. Natural gap dynamics in a Central European mixed beech-spruce-fir virgin forest (Žofín, Czech Republic). Accepted manuscript (major revision), Êcoscience