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# The true response of *Fagus sylvatica* L. to disturbances: A basis for the empirical inference of release criteria for temperate forests

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ABSTRACT

Because of some arbitrary decisions in recent dendrochronological research on forest disturbance histories, describing the actual growth responses of trees to disturbance events is still an issue of great importance. This is even more important in temperate beech-dominated old-growth forests driven by fine-scale disturbances, where a majority of growth pulses occur close to the arbitrary threshold of release detection. Recognizing this limitation, we provide a new empirically-based release detection criterion on the basis of actual reactions of trees to independently dated disturbance events interconnecting three data sets – tree censuses, dendrochronology and historical aerial photographs. The growth response of *Fagus sylvatica* L. was studied in detail in relation to the canopy position of surviving trees as well as regional climate responses, using 280 increment cores extracted in 8 old-growth forests in the Czech Republic.

Cluster and bootstrap analysis resulted in distinguishing 2 ecoregions with site-specific growth patterns and plasticity. A boundary line (BL) method was applied to the identification and quantification of release, providing a new curve for *F. sylvatica* regionally valid in the mountainous regions of Central Europe. During the period investigated (1970s–1990s) 7% of trees experienced no reaction, despite clear evidence of canopy disturbances in both aerial photographs and tree censuses. 25% of growth changes were attributed to regional-scale environmental factors, in particular climate and air pollution. The magnitude of the growth response varied significantly among canopy positions, with subcanopy trees released from suppression experiencing the most intense growth rates, and individuals under permanent suppression showing a negligible response. Considering these differences we empirically inferred new criteria, subdivided into two categories according to disturbance intensity. Pulses falling within the 25–63% of the boundary line are classified as weak releases while pulses exceeding 63% of the BL are identified as major. Still, our results imply relatively high uncertainty in the detection of disturbance using dendrochronology, which can be troubled particularly in spatial analysis of past disturbances. We believe that our empirically-derived criteria represent a substantial contribution to further dendroecology research, with broad applicability to a wide range of beech-dominated temperate forests.



## 1. Introduction

Natural disturbances are regarded as one of the main driving forces of forest dynamics (Pickett and White, 1985). Their importance in forest ecosystems has been widely studied in relation to influences on forest structure, species diversity as well as soil complexity (Runkle, 1989; Franklin et al., 2002; Gravel et al., 2010; Phillips et al., 2005). Detecting the response of surviving trees in the form of abrupt and sustained radial growth pulses, the so-called release, has been an issue of crucial dendroecological importance and numerous techniques have been developed, particularly in the USA (e.g. Canham, 1985; Lorimer and Frelich, 1989; Nowacki and Abrams, 1997; Black and Abrams, 2003; Fraver and White, 2005; Druckenbrod et al., 2013). As yet, the criteria of radial increment that is considered a release have been conventionally derived subjectively, obscuring both the validity of results and comparability among studies. Because of this,

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arbitrary decisions in dendrochronological data processing steps can fundamentally change the view of forest disturbance history (Rubino and McCarthy, 2004).

The change in radial growth that exceeds a predefined threshold is one example of an arbitrary decision, since we do not know what proportion of false releases (e.g. responses of trees to short-term pulses of climate) was included in the calculation of disturbance history, or – on the other hand – what proportion of actual disturbances was omitted due to a weak response. Determining the lower release criterion limit is likely even more important in forests with dynamics mostly driven by fine-scale disturbances, where the growth pulses of surviving trees are frequently close to the usual threshold of release detection (e.g. Šamonil et al., 2009), or there are even a few trees with no response in growth throughout their life (Šamonil et al., 2013). *Fagus sylvatica*, classified as shade tolerant, small-gap specialist, responds positively to even small light level fluctuations or year-to-year climate variability (e.g. Dittmar et al., 2003; Piovesan et al., 2003), and these changes might be easily confused with reactions to canopy gaps.

Considerable differences in radial growth responses among various canopy positions have been repeatedly recognized (Poage and Peart, 1993; Nowacki and Abrams, 1997; Black and Abrams, 2003; Stan and Daniels, 2010; York et al., 2010). Nevertheless, trees undergo various canopy positions over their lifespan and not all of them are dendrochronologically relevant, resulting in interpretative difficulties (Lorimer and Frelich, 1989). Moreover, results are not easily transmittable between regions and forest types. The challenge, therefore, is to elucidate empirically-based criterion for the detection of release for *F. sylvatica* and describe the structure of its actual and false growth responses to disturbances, all in relation to the social status of surviving trees and to regional climate responses. To meet this objective we interconnect three different independent data sets that supplement each other: dendrochronology, repeated tree censuses, and aerial photographs.

We attempted to address the following specific objectives: (i) to compare plasticity in the radial growth of *F. sylvatica* among localities to develop region-specific boundary line curves; (ii) to elucidate the effect of regional-scale climatic variability on growth reaction; (iii) to evaluate the magnitude of responses in relation to the different canopy positions of surviving trees; and (iv) to infer new empirically-based criterion for the detection of release applicable in the Central European region.

## 2. Materials and methods

### 2.1. Study sites

The survey took place in 8 beech-dominated mountain forest reserves (Fig. 1, Table 1) in four biogeographical regions of the Czech Republic: the Carpathians, Sumava Mountains (Mts.), Novohradske Mts. and the Bohemian-Moravian Highlands. The Carpathians, located in the eastern part of the country, included three sites – the Salajka, Mionsi and Razula forest reserves. The Sumava Mts., situated close to the Czech-Austrian border, also included three sites – the Boubínský prales (hereafter Boubin), Milešický prales (hereafter Milesice) and Stozec. The Žofínský prales (hereafter Zofin) belongs to the Novohradske Mts., while the Polom site is the only representant of Bohemian-Moravian Highlands in the central part of the Czech Republic.

As well-preserved remnants of old-growth forests, these sites have been under strict protection for decades at least. Neither Zofin nor Boubin has ever been logged, and they are among the oldest continuously protected reserves in Europe (since 1838 and 1858). Cambisols or Podzols predominate on sedimentary, metamorphic or magmatic rocks in all localities, while rare spring areas are occupied mainly by Gleysols (e.g. Šamonil et al., 2011). The tree layer is dominated by *F. sylvatica* L., followed by *Abies alba* Mill. and *Picea abies* (L.) Karsten; other tree species are accessory. Plant communities can be mostly classified into *Galio odorati-Fagetum sylvaticae* and *Luzulo luzuloides-F. sylvaticae* (Chytrý, 2013).

Fine-scale disturbances are the main driving forces in the dynamics of the forest ecosystems studied here (Šamonil et al., 2013), resulting in a mosaic of forest patches with a mean patch size of about 700 $m^2$ (Král et al., 2014a). Severe disturbances affecting a significant proportion of canopy have been infrequent (examples include the Kyrill storm that hit Zofin in 2007, and strong storms at Boubin in 1870 and 2008).

### 2.2. The detection of disturbances

In contrast to conventional dendroecological studies focused on the identification of disturbance history on the basis of tree-ring records (e.g. Splechtna et al., 2005; Zielonka et al., 2010; Trotsiuk et al., 2012), we first detected past fine-scale disturbances events using independent tree census data and aerial photographs, and then studied the radial growth responses of surviving trees. Fig. 2 demonstrates the basic concept we used. Tree censuses were established in the 1970s (1950s in Mionsi) and repeated in the 1990s and 2000s. Each census contains the positions, dimensions, health status and tree species identity of all living and dead trees of DBH $\geqslant$ 10 cm within the site (see Král et al., 2014b). Repeated stem position maps provided information about the forest dynamics of every disturbed or undisturbed tree. Within each site we selected appropriate gaps according to following rules. First, we accepted only events recorded between two known surveys (the period from the 1970s–1990s in most cases). From this extensive data set we randomly chose past disturbances with gap-makers of DBH $\geqslant$ 40 cm within the whole area to represent the most variable habitats (excluding water-affected areas). In case of an unclear disturbance history (neighbouring events confusing the situation) or a lack of trees to sample we disregarded that gap and chose another one. The number of gaps assessed for each site is shown in Table 1.

In order to fill in the 20-year period between censuses, we used historical aerial photographs. The precision of disturbance detection was determined by the at-least 1-year and maximally 13-year "windows" between aerial images (Table S1) due to the insufficient quality and coverage of some images. In our approach, canopy gaps were examined visually on screen using time series of photogrammetric point clouds, appropriate canopy-level orthophotos and tree census maps, from both perspective and profiles and thus the timing of gap opening was established (Fig. 2A and B).

### 2.3. Processing the time series of aerial photographs

Archived stereo-pairs of aerial photographs in a nominal scale ranging from 1: 11,000 to 1: 31,000 provided by Military Geographic and Hydrometeorologic Office and by State Administration of Land Surveying and Cadastre were scanned on a Vexcel Ultrascan5000 photogrammetric scanner at 15 or 20 μm; the resulting digital images thus had a nominal ground pixel size between 0.17 and 0.47 m (for details see Table S1 in Supplementary material providing parameters of particular historical aerial photographs).

Stereo models were built in ERDAS IMAGINE Photogrammetry 2014 (Hexagon Geospatial) by establishing their interior and exterior orientation. Thereafter, image matching and extraction of photogrammetric 3D points were conducted using the enhanced Automated Terrain Extraction (eATE) algorithm, which is designed for generating high resolution terrain information. We customized