Czech University of Life Sciences Prague

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Department of Ecology

Reconstruction of the disturbance regime of the Carpathian spruce mountain forests using dendroecological methods

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Declaration

I certify that work presented in this thesis is, to the best of my knowledge and belief, original, except as acknowledged in the text, and that the material has not been submitted, either in whole or in part, for a degree at this or any other university.

Prague, 26th of April Kristýna Svobodová

CZECH UNIVERSITY OF LIFE SCIENCES PRAGUE

Department of Ecology

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DIPLOMA THESIS ASSIGNMENT

Svobodová Kristýna

Thesis title

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Objectives of thesis

The aim of the thesis is to describe dynamics of mountaine spruce forests in the Carpathians and to answer the question if the broad scale disturbances are typical of this forest type.

Methodology

1. Plot establishment in the mountaine spruce forests
2. Tree layer characterization
3. Extraction of increment cores
4. Processing of increment cores using dendrochronological methods
5. Statistical analyses

Harmonogram zpracování

summer 2011: plot establishment in the mountaine spruce forests, tree layer characterization, extraction of increment cores

autumn 2011, winter 2011/12: processing of increment cores using dendrochronological methods, statistical analyses

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The proposed extent of the thesis

30-40 pages

Keywords

disturbance, Romania, spruce bark beetle, spruce, windthrow

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Abstract

The natural forest disturbances as wind-throw and insect outbreaks are the main shaping agent of forest stand structure in mountain spruce-dominated forest of the Eastern Carpathians. This study presents the reconstruction of history of forest stand structure in the Nature Reserve Codrul Secular Giumalau. 200 cores were extracted within eight plots representing 18 ha of the study area and used for construction of tree-ring chronologies. The changes in radial growth representing release in forest structure as well as the gap-originated individuals were detected. Disturbance chronologies covering past 190 years for particular plots are compared and discussed in temporal and spatial scale. Several scenarios can be driven from obtained data. No large stand-replacing disturbance in study area during available chronologies was occurred. Rather the low-severity disturbances occurred randomly in different temporal scale over the studied period. However the signs which could be associated with the large-scale disturbance event placed just before obtained data were recognized within study as well.

Key words: forest dynamics, *Picea abies*, Giumalau Mountains, dendroecology, disturbance chronology

Abstrakt

Vítr a napadení kůrovcem jsou hlavními přírodními činiteli, kteří formují strukturu horského smrkového lesa ve východních Karpatech. Předkládaná práce se zabývá rekonstrukcí historie lesa na studijní ploše v přírodní rezervaci Codrul Secular Giumalau v rumunských Karpatech. Dynamika lesa byla sledována na ploše o přibližné rozloze 18 ha. Za účelem zjištění změn v radiálním růstu stromů bylo odebráno 200 vývrtů. Pomocí dendroekologických metod byly zjištěny události uvolnění a původ jedinců v porostní mezeře. Studovaná data pokrývají období 190 let a může z nich být odvozeno několik variant vývoje porostu. Zjištěná data nepoukazují na výskyt velkého narušení během popisovaného období. Dynamika studovaného porostu je převážně ovlivněna nepravidelnými, slabými až středně silnými narušeními porostu, vyvolanými patrně větrem. Další možný scénář je výskyt události způsobující velké narušení lesního porostu, která se odehrála před studovaným obdobím.

Klíčová slova: dynamika lesa, *Picea abies*, pohoří Giumalau, dendroekologie, chronologie narušení

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Content

1 Introduction

The sustainable way of life is frequently discussed topic at the present. The sustainable forestry practices may contribute to implement this issue. The forest management going along the natural processes should be necessarily based on understanding of natural forest dynamics. The biological legacies, processes of regeneration and death of trees are the basic elements of natural forest ecosystem. They play the essential role in biological diversity. The key drivers of natural forest dynamics are disturbances. Fire, windstorms and insects outbreaks strongly affect forest structure and composition (e.g. Frelich 2002, Oliver and Larson 1996, Pickett and White 1985).

There are several studies focused on disturbance regimes and their influence on forest ecosystems. The forest dynamics in view of disturbance regimes were firstly studied in North America (Fraver and White 2005a, Frelich and Lorimer 1991, Frelich 2002). The role of natural disturbances as a shaping agent of European mountain forest ecosystems has received recently little attention. Now there are several studies focused on understanding of forest dynamics influenced by disturbances (Panayotov et al. 2011, Splechtna et al. 2005, Svoboda et al. 2011, Szewczyk et al. 2011, Zielonka et al. 2009, Zielonka and Malcher 2009). Findings from these studies may clarify the process of forest dynamics and thus contribute with new implementation to sustainable forestry.

There are scarce remnants of natural forest within Europe, because of intensive use of land. Thanks to inaccessible placement small isolated stands were preserved from harvesting (e.g. Cogbill 2000). Forests in Carpathians Mountains are among the best preserved natural forests in Europe (Splechtna et al. 2005) and these serve us unique opportunity to study natural processes.

The aim of this study was to reconstruct the history of spruce-dominated forest stand at the research area in the Nature Reserve Codrul Secular Giumalau, in the Eastern Carpathians. The dendroecological methods based on the detection of changes in radial growth in tree-ring chronologies were used for reconstruction of past living conditions of forest stand. The emphasis was placed on the investigation of disturbance regime and questions related with this process. For instance: has been the study area affected by large-scale disturbance event?, or has been the study forest rather shaped by frequent small-scale disturbances?, what could be the possible disturbance agent affecting the forest stand?, could human or animals play any role in past forest development?

2 Literature survey

2.1 Natural forest dynamic

Forest is a system of biotic and abiotic components. It is influenced by physical and biological factors, which change its composition and structure. Natural succession and disturbances are placed between two main elements. Specific type of natural forest has a specific character of dynamics, which is caused by different scale of disturbance events among various forests stands. For example taiga forest in northern Europe is often influenced by large-scale fires (Zackrisson 1977), while deciduous forests of central and western Europe is generally disturbed by small-scale windthrows (Falinski 1986).

2.1.1 Concepts of forest dynamics

There are several concepts of classification of natural forest dynamics. Different interpretation of time and spatial scale has caused the overlap in terminology.

Gap dynamics is currently one of the key issues in forest ecology. Gap is simply the surface under the canopy opening. It is created by mortality of individual or multiple trees and subsequent fall from the cohort. The source of death (e.g. insect, disease or meteorological factors) and gap formation affect spatial character as well as the potential process of regeneration (McCarthy 2001). The gaps provide vital resources such as sunlight and growing space and may offer the chance for suppressed understory trees to recruit into the canopy (Speer 2010) and beginning of new regeneration as well. The gap dynamics concept is based on regeneration of intolerant species within the canopy openings. In general, Watt (1925, 1947) is considered as the founder of the 'gap mosaic' concept. He described the gap as the essential mechanism for the regeneration of the plant community in general and the forest in particular (Glončák 2009).

Leibundgut (1959) described how the natural forests go through a number of stages. He made a distinction between the regeneration of the forest, with and without large-scale disturbance. This concept converges to the principle of two dimensional cycles which are well known in our latitude (Korpeľ 1989, Míchal 1999). The principle of small development cycle ('malý vývojový cyklus' in Czech) overlaps with the concept of gap dynamics. It is entirely about regeneration of forest stand with maintenance of environmental conditions (Korpeľ 1989).

Natural disturbances as a fire, windthrow and an insect outbreak play the essential role in the beginning of the large development cycle ('velký vývojový cyklus' in Czech). The succession starts with establishment of pioneer species. Following transitional stage is characterized by increasing amount of species which tolerate shade conditions. Next stage consists only from shade-tolerant species, in the terms of Clements (1916), Tansley (1935) and Watt (1947) is called climax (Vera 2000). This stage continues unless it is interrupted by a large disturbance event. This type of forest dynamics is typical for the boreal forest. However the large-scale disturbances do not occur regularly and forests regenerate within the small development cycle as well. Conversely the small development cycle is typical for temperate forest, but large disturbances occur there from time to time as well (Glončák 2009).

There are other approaches combining the spatial and temporal scale differently. For instance van der Maarel (1988) distinguished so-called *patch dynamics*, which is characterized by mosaic areas of patches. These could be results of slight disturbance influencing relatively stable ecosystems. *Cyclic succession* affects larger territory than in the case of *patch dynamics* and it includes a short period of climax stage. The last term from van der Maarel (1988) is *regeneration succession*. It has a similar range and sources as *cyclic succession*, but the duration of climax stage is much longer compared to the time required for regeneration.

Frelich (2002) presented a different approach. He focused on study of forest dynamics in case studies from the forests in the Lake States of the USA (Minnesota, Wisconsin and Michigan). The large primary forest remnants in this area present a unique opportunity to study and compare long-term dynamics of near-boreal, *Pinus* and *Tsuga*-hardwood forest. The comparability of these forests and forests from the other temperate zones may be possible to generalize and thus the obtained knowledge applied more widely. In the following text I am going to focus on the system presented by Frelich (2002). It is worldwide established at the present. Frelich (2002) distinguished two basic terms: *the stand development* and *the succession*. He defines the stand development as the major change in the stand structure over the time. It is possible to recognize similarities among stages of stand development cycle described by Frelich (2002) and large development cycle.

Stand development

Frelich (2002) develops and slightly changes Oliver's (1981) findings of four basic stand development stages following large stand replacing disturbances:

1. Initiation

   This stage follows immediately the major disturbance as stand replacing wind, large fire, insect outbreaks or overgrowth of certain kind of herbivores. Formed open space is occupied by regeneration from seeds (e.g. *Betula papyrifera*, *Populus* after fire), stump sprouts (e.g. *Quercus* after fire), roots sprouts (e.g. *Populus* after browsing by ungulates), or advance regeneration (e.g. *Acer saccharum* or other shade-tolerant species after a tornado).

2. Stem exclusion

   There is one dense dominant cohort within this phase, where the new saplings are not able to reach the dominant canopy. Trees compete intensively for the same set of resources as light, moisture and nutrients. Species differ between the ability to survive low levels of these supplies and consequently density-dependent self-thinning occurs and becomes major reason of mortality. In respect to scarce resources in multi-species cohort, from development patterns and interactions of species become competitive advantages as inherent faster growth or initial superior crown position. The range of diameters of breast height (further more DBH) is similar. Crowns are small, so when one tree dies other trees are able to fill place after the previous by expanding their branches.

   The duration of this period varies among specific forest. For example from 100 up to 150 years can last this stage in northern hardwoods, but just 20 to 40 years in some *Populus* and *Pinus banksiana* stands.

3. Demographic transition

During this period one stand cohort develops into more cohorts. A high range of mortality occurs at one time caused by senescence of trees. Reasons of species death change mostly from density-dependent self-thinning to density-independent occasions as senescence or blowdown due to weakened wood caused by rot or disease.

Crowns are not large enough in this phase, thus the new space originated from disturbance event form gaps in the canopy and therefore higher amount of sunlight can reach the forest floor. These gaps enable mid-tolerant species such as *Tilia*, *Fraxinus pennsylvanica* or *Pinus strobus* to enter the canopy. In the case of pioneer species establishment of stand within initiation stage, shade-tolerant species (e.g. *Acer saccharum*, *Tsuga*, *Fagus*, *Picea* or *Abies*) may begin entering the canopy during this stage.

The stand is becoming more similar to an old growth forest as a large rotten log on the forest floor and uneven canopy layer. A range of DBH contains larger sizes of remnants of the old forest stand and at the same time there is a new peak in the small size classes of trees growing within gaps.

This stage lasts from moment when a new younger tree gets into the canopy of original cohort settled during initiation stage until time when these individuals do not have significant presence.

4. Multi-aged stage

This phase is characterized by uneven age stand, with many age and size classes. Changes in species composition continue as well as gap formation and their consequent filling by new regeneration. Just few remnants of old original cohort are present. Mortality takes place only in a range of single trees and it is caused by density-independent incident. The DBH distribution varies from high amount of small trees, sharp decline until middle-age trees, where the curve becomes flatter, followed by next steep drop is in the largest size classes. It goes naturally along with mortality phenomenon. The rate of mortality is high in young stands filling gaps (because of self-thinning), low for middle-age stands and again increased for mature trees on the score of senescence.

This phase of development goes on until a next large disturbance event. In case of high frequency of disturbances this stage is not reached every time. The proportion of stands within each stage depends on disturbance regime of particular area.

Multi-aged phase was referred by Oliver (1981) as an 'old growth', but Frelich (2002) modified the term for this stage in order to avoid confusion with other political definitions of old growth stand, which are sometimes used incorrectly.

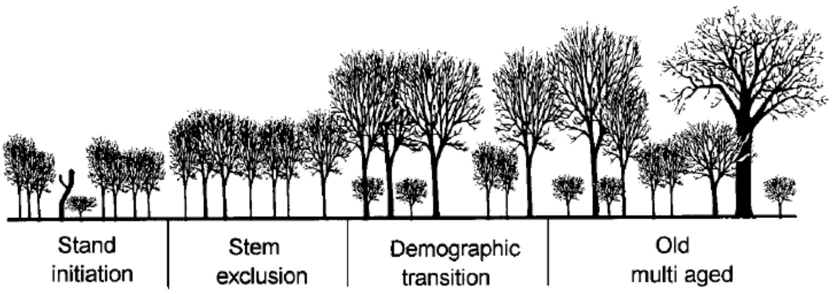

Figure 1 Four basic stages of stand development (Frelich 2002).

<u>Succession</u>

There is an additional process of forest dynamic called a succession. Succession is a sequence of changes in species composition in time. Frelich (2002) also differentiates idea of succession with lesser extent than stand replacement and call it fluctuation. The convergence of succession and stand development is questionable. This issue has been debated since beginning of ecology as science (e.g. Clements 1916, Moss et al. 1910, Tansley 1935). It is necessary to take into account coherence between succession and disturbance event variants in its magnitude, frequency and severity. Disturbances inherently may reverse the successional process (Norkko et al. 2005). Clements (1916) presented that the secondary succession takes place after forest destruction for example, by fire, tidal waves, animals or human activity (Glončák 2009). Frelich (2002) represents different idea, that after severe disturbances there is a new stand development sequence, but the beginning of succession does not come in all cases. Predicting of successional development has been focused in several studies (e.g. Clements 1936, Gleason 1927, Watt 1947). Frelich (2002) classified the prediction of succession direction into five basic theoretical models: cyclic, parallel, convergent, divergent and individualistic. Generally field work shows presence of elements from different models and therefore it is difficult to predict succession direction.

The basic concepts of forest dynamics were introduced above. The great influence during development of forest characteristics have the local conditions which differ across the world. But it is necessary to note the overlapping of particular concepts, which is usually caused by the time and spatial variation.

2.1.2 Disturbances

Disturbance simply means event usually discrete in time which affect ecological conditions in forest and change microclimatic and other physical condition of forest environment (Picket and White 1985).

We can classify disturbances according the origin into two main groups such as **natural** and **human**. A human influence for long term history changed the natural forest to the form as we know it from present time (Perlin 1988). These anthropogenic activities contain the hunting, the grazing of domestic herbivores, the clearing forest stands for agriculture and industry, the logging for firewood or other purposes of human needs, extraction of litter for fertilizing, planting monocultures and non-native species due to fast grow and better suitability of wood etc. Approximately for the last 4000-5000 years humans have affected landscape composition and its dynamics. There were megaherbivories before humans who were probably also significantly changing forest structure by browsing and grazing (Vera 2000). If we compare large extinct herbivores with the domestic grazers today, the smaller grazers are more picky in diet, so the influence of species composition differ, however several key factors such as the large old trees and openings of forest stands stayed (Nilsson 1997, Peterken 1996).

There are two different views of animals and human influence on forest dynamics. Clements (1916) believed that the destruction of climax stage by human or animal influence can result in numerous sub-climaxes. He presented the idea that the grassland have developed everywhere where burning and grazing occurred. And that the disappearance of influence will initiate the development of a series of stages with different vegetation which will eventually again result in the climax. Controversially Tansley (1935) presented concept that the animals are continuously present and therefore continuously active factor. They follow the development of vegetation and do not play determining role in the succession. In his view the catastrophes are responsible for changes in the vegetation (Vera 2000).

The range of forest cover has been changing with human population, industry, way of farming, development of technology for managing land etc. The biggest change within landscape character has happened during the last century. The development has enabled to easily utilize larger area of land and remaining forest stands were started to be managed. Many signs of old forest stand as a dead wood, old trees, naturally grazed areas and natural disturbances as fire were during this period removed or suppressed. It had consequently a large negative impact on biodiversity. For example a lot of species adopted to open grazed forest disappeared. On the other side there are many exotic species which have become naturalised (Bengtsson et al. 2000). Generally increasing population lead to more intensive cultivation practices and natural or near-natural forest is becoming more and more valuable (Stanner and Bourdeau 1995).

The subject of this study known as natural disturbances is described in the following chapter.

2.2 Natural disturbances

Natural disturbances significantly influence not just temporal forest stand function, but the forest ecosystem as a complex within long-term scale (Whittaker 1975). By affecting forest structure, composition and availability of resources, disturbance events are the key factors of forest dynamics (Laska 2001, Oliver and Larson 1996). Disturbances serve conditions for colonization, living and mortality of tree species. Specific species respond to disturbance events differently. Thus the disturbances play an essential role in their coexistence. And consequently forest dynamics cannot be explained without knowing relations between disturbance and response of the species and other important characteristics of the disturbance regime (Splechtna and Gratzer 2005).

2.2.1 Terms associated with natural disturbances

The **disturbance regime** is characterized by variability in frequency, severity and spatial extent of the event. It determines the proportion of stands in each stage of development, which were mentioned earlier.

It is necessary to distinguish the conception of **intensity** and **severity**. Intensity is amount of energy released during disturbance. Severity covers amount of tree and plant mortality. Generally there is a high correlation between them (Frelich 2002).

Spatial scale of natural disturbances ranges from involving individual trees to groups of overstory trees and in the end to large-scale mortality events described as stand-replacement disturbances (Franklin et al. 2007). Large-scale stand destruction occurring within Europe can be caused by strong wind, fire and insects. Forest fires are usually limited to the boreal forest in range of Fennoscandia (e.g. Niklasson and Granström 2000), whereas western and central European forests are mostly influenced by windstorms (e.g. Quine and Bell 1998). Moderate disturbances are often caused by insect outbreaks, when only group of trees is destroyed instead of large stands. These events are usually activated by patch scale windthrows increased by dry and hot summer weather (Grodzki et al. 2006).

2.2.2 Natural disturbances influencing temperate and boreal forest

Wind, fire, insect outbreaks and land-slides are included among the most frequent types of disturbances affecting mountain spruce forest stands. There are several existing studies focused on windthrow and bark beetle (*Ips typographus*) outbreaks in European temperate forest, which help us to understand natural forest dynamics in this region (e.g. Splechtna et al. 2005, Svoboda et al. 2011, Zielonka et al. 2010).

2.2.2.1 <u>Wind</u>

Wind-created gaps are a primary disturbance regime of many forest types (Franklin et al. 2007). In the temperate forest of central Europe blowdown is the most common disturbance shaping the forest (Ulanova 2000).

Disturbances caused by wind differ temporally and spatially from small-scale affecting individuals to large-scale events (Pickett and White 1985). After larger disturbance the number of surviving trees and rate of natural regeneration is mostly lower than in case of insect outbreak, which is the second most common agent in the case of mountain spruce forests (Jonášová et al. 2010).

Ulanova (2000) describes dependence between various scales wind disturbance and different type of vegetation dynamics in case study of south boreal spruce forest of Central Forest Reserve in Russia. There three spatial sizes of blowndown in the study are distinguished: *landscape, forest community* and *fallen tree ecosystem* and linked with three types of dynamics, *secondary succession, gap-phase dynamics* and *micro-succession.*

Frelich (2002) describes the main regularities of wind as a disturbance agent caused by topography. Generally there is the highest wind speed if the direction of blow is at the right angle to ridge on the top. In case of midslope the wind reaches the highest speed at an acute angle. Lastly, the highest speed in valley is from parallel direction. Consequently the extent of damage and wind direction is connected. Frelich and Lorimer (1991b) also found that larger trees are more likely to topple down in comparison with smaller ones.

2.2.2.2 Fire

The fire frequency, intensity, seasonality and type depend on local weather condition such as wind speed, air humidity, temperature and in addition climate, forest structure and composition (Dale et al. 2001). Severity is influenced by an amount of fuel present in stand and linked to weather condition (Frelich 2002). We can recognize the crown and surface fire. These are characterized by different procedure, extent, biological legacies etc.

Some of forest types are adapted to regime of fire disturbances. In these forest types fire is sort of periodic feature. Mediterranean ecosystems are highly influenced by wildfires and adaptation of species is known from several studies (e.g. Bond and van Wilgen 1996). The regeneration is characterized by a big amount of persisting individuals. The sprouters regenerating sexually are able to resprout just after the fire. Species reproducing by seeds regenerate from aerial or soil-stored seeds. These are usually enhanced by fire because they are accumulated in the soil and their germination is triggered by heat. In California forest ecosystem high amount of fire recruiters is present and in case of lack of fire for longer than usual period, there is a low possibility for population to expand and hence potential extinction (Keeley and Fotheringham 2000).

2.2.2.3 Mammalian herbivores and insect

There are several biotic factors which influence forest dynamic and can even change the process of succession (Ostfeld et al. 1997).

Herbivores such as *Odocoileus virginianus* native species from America, *Alces alces* or *Cervus elaphus* in Europe attack forest stands by browsing in winter or by grazing during summer, rodents such as mice, squealer or rabbits also eat seeds and small trees. But these influences do not have such as strong damaging effect to be able to kill adult trees, or it has to continue for long period to cause some changes in future composition, as it was described by Watson (1983) in Scotland, when *Cervus elaphus* has precluded recruitment of new *Pinus sylvestris* the late 1700s.

There are several species of insect which attack forest of different species structure. For example *Dendroctonus ponderosae* aggressively attacks stands in western North America (Jenkins et al. 2007) or *Choristoneura fumiferana* defoliates and kills *Abies* and *Picea glauca* in boreal forest of eastern Canada (Frelich 2002). Bark beetle is commonly source of disturbance event in European forest where *Picea abies* is frequently present (Figure 2). Insect outbreaks are often triggered by the windthrow and high spring and summer temperature occurring at the same time (e.g. Aakala et al. 2011, Wermelinger 2004), weaker trees are easier prey. Beetles usually spread within newly fallen trees (Schmid 1981), rarely they also attack over mature trees. Local population can increase to epidemic scale and kill from individuals to small groups and thus create canopy gaps (Hebertson and Jenkins 2007, Veblen et al. 1991b). Consequently they can attack standing living trees by account of lack of food.

Figure 2 Affected area by bark beetle in Bavarian National Park. Photo by Kristýna Svobodová, 2011.

2.2.2.4 Land slides

The movements of soil, rock and associated plants are triggered by weather events as snowmelt, intense rainfall, long-term processes as erosion and nonclimate factors such as earthquakes or volcanism. The probability is enhanced by slope steepness, character of soil, parent rock, vegetation cover and hydrological factors. Landslides in forest cause removal of fertile soil and vegetation from steep hill-side and destruction of forest environment of gentler areas where deposition stay (Dale et al. 2001).

2.2.2.5 Disturbance interactions

The fundamental principles of main disturbance agents were described above, but it is necessary to emphasize the convergence and interaction between different disturbance agents.

There is a complex system of dependencies among disturbance agents, extent of events, severity, forest environment etc. Several studies handle with this topic (e.g. Dale et al. 2001, Franklin et al. 2007, Jenkins et al. 2007, Mayers and van Lear 1997). However there is a very small part of interactions introduced in following text. For example high importance for fire severity has amount of burnable fuel which is created by windthrow. Blowdown is also caused by presence of canopy gaps which are edible for grazing new regeneration by deer. Interaction among disturbance events is connected with specific biological legacies remaining after them. Fire as well as wind usually injures live trees and thus they are more predisposed for attack of insect. And conversely insect create burnable fuel of all sizes by killing or weakening trees (Frelich 2002). The coherence between wind and bark beetle infestation is the most important process in European spruce forests and there are many studies at the present time dealing with this issue (e.g. Jonášová and Prach 2004, Panayotov et al. 2011, Svoboda et al. 2011). Bark beetle outbreaks are often trigged by the windthrow and warm spring and summer weather. Beetles preferentially attack newly fallen or weaker trees, which may be caused by recent windthrow. Population can spread from individuals to groups of trees. Consequently they can attack standing living trees by account of lack of food.

Several studies tried to evaluate an importance of future climate change and its impact on forest dynamics (e.g. Dale et al. 2001, Jönsson et al. 2004, 2007, Kellomäki and Väisänen 1997). In the case of confirmation of predicted climate change as a rise of occurrence of large-scale windthrows combined with high temperature during spring and summer, we can expect increase in frequency and severity of windstorms and insect outbreaks.

2.2.3 Biological legacies

Biological legacies are defined as the organisms, organically derived structures and biological features persisting from pre-disturbance stage of ecosystem. First of all legacies notably influence recovery processes in ecosystem, they occur in variant types depending on kind of disturbing event (Franklin et al. 2000), as a living logs, intact thickets, large living trees, snags etc (Figure 3). But not only disturbance agent is important for describing remnants, but also spatial gradient of events is correlated with extent of remaining intact forest and proportion of heterogeneity.

Tree and moderate scale disturbances leave usually large part of forest intact and forest matrix stays generally still dominant in the post disturbance environment. They tend to create and maintain structural heterogeneity and provide conditions for new cohort establishment and release of remaining trees. Compared to stand scale events, they destroy a major part of forest cover and shift the forest matrix to an open space as a post-disturbance environment. There are provided conditions for establishment more or less homogenous post-disturbances tree population structure of a stand, as for example abundant coarse woody debris (Fajvan and Seymour 1993).

When more types of disturbances of different scale occur simultaneously it is possible to observe open and intact canopy conditions in the same time (Franklin et al. 2007).

Figure 3 The example of biological legacies in the Nature Reserve Codrul Secular Giumalau. Photo by Kristýna Svobodová, 2011.

2.3 Dendrochronology

There are various methods of studying natural disturbances and reconstructing past disturbance dynamics (e.g. historical records, early land surveys, paleoecology and dendroecology), however in boreal and temperate forests dendrochronology seems to be the most efficient (e.g. Frelich 2002, Splechtna et al. 2005).

Dendroarchaeology, dendroclimatology, dendrogeomorphology, dendrochemistry and dendroecology are included within dendrochronological subfields (Speer 2010). Yet there is unquestionable overlapping among certain sections.

Dendrochronology provides new findings which are recognized from tree-ring structure. This technique is based on identification of events in tree-ring series most likely caused by disturbance of forest ecosystem. The tree is used as a tool for environmental monitoring. The wood structure serves long-term records of many phenomena from life of tree.

Therefore the extent of reached data is bordered by tree lifetime (Speer 2010). The tree-rings are able to offer "vast potential" for research of natural disturbances especially in case of the long tree-ring series obtained from old-growth stands with minimum anthropogenic influence (Nowacki and Abrams 1997).

2.3.1 Dendroecology

Combining ecology and study of tree-ring structure helps us to understand the forest dynamics and interaction of many natural factors (Speer 2010).

It can provide high spatial and temporal resolution. However since there is a need of large amount of samples, the majority of dendrological studies is mostly applied just for smaller areas (e.g. Fraver and White 2005a, Henry and Swan 1974, Panayotov et al. 2011, Svoboda et al. 2011, Szewczyk et al. 2011). According to our knowledge only Frelich and Lorimer (1991) present dendrochronological research of canopy-gap disturbances in regard to landscape scale. They provide insight to the questions as rotation period, agent and spatial patterns of disturbances.

One of the essential approaches for reconstruction history of forest stand is based on detection increases in radial growth in tree-ring structure, so-called release events (Frelich 2002, Lorimer and Frelich 1989). Releases may be caused from changes in an environment of individual such as more availability of sunlight or water supply following a disturbance that removes surrounding competitors (Kienast and Schweingruber 1986, Pickett and White 1985).

There are several methods dealing with release detection. Their great variety is caused mainly by character of criteria used to identify a release event. Rubino and McCarthy (2004) present literature review of twenty-eight different objective or quantitative release methods. According to the release criteria they distinguished five main groups of methods. Firstly, *the statistic release methods* use a single measurement when the ring width greater than fixed critical value is considered as a release event. This value is derived from identifying growth rates for known periods of release and/or suppression. The application of this method is, according to the authors, not suitable for intermediate shade-tolerant and shade-tolerant species, as they do not take into account the changes in radial growth as a reaction to release in stand structure highly vary during their life time.

Second type represents *detrending or standardization methods* based on application standardized or detrended tree-ring series to identify sustained increases in growth rates.

Other group of methods use the *mean growth rate* as a detection of growth release. Release events are identify by an exceeding the mean annual growth rate.

The *radial-averaging or running mean methods* are at the present time the most commonly used. These methods are based on comparison of radial mean growth over the years before and after the specific year for which we identify occurrence of release event. Running comparison approach investigated by Nowacki and Abrams (1997) was used during my study and therefore it will be introduced in chapter focused on methodology.

Lastly, the *event response methods* are similar to running mean technique, however for comparison of growth rates are used rates over a given time period and growth in a given year.

Methods mentioned above dealing with natural disturbances and subsequent forest dynamics are focused on growth release from suppressed canopy. But these methods do not consider individuals which are already in gap at the time of the earliest ring on their tree-ring series. The principle of release methods is based on the fact that a sapling was recruited from overstory (Frelich 2002). Lorimer et al. (1988) investigated a method dealing with gap status of trees during their juvenile stage. This technique is based on given threshold of mean radial growth width between individuals growing in gap and those living under the canopy.

To reconstruct past disturbance chronology in our study I followed methods introduced above: detection of abrupt release in radial growth indicating death of canopy trees and fast growth during juvenile stage indicating establishment in prior gap. Applied methods will be introduced in details in the following chapter.

3 Methodology

3.1 Study area

The extensive remnants of old-growth spruce forests are still present in Carpathians, therefore there is a great worth for research of mountain spruce forests dynamics (e.g. Holeksa et al. 2006).

The study was conducted in an old-growth spruce-dominated forest of the Nature Reserve Codrul Secular Giumalau, in the Eastern Carpathians, Suceava County, Northeastern Romania (Figure 4). The Reserve was established in 1941 and the total area is 309.5 ha. The geographic coordinates of the Reserve are 47°26´ N and 25°29´ E and the altitude ranges from 1200 to 1650 m a.s.l.. The northern and southern slopes dominate with the slope from 20° up to 40° (Giurgiu 2001).

Figure 4 The location of the Nature Reserve Codrul Secular Giumalau (http://www.romaniatourism.com/romania-maps/physical-map.html).

The research in the Codrul Secular Giumalau Nature Reserve included also study of the soil formation processes and the study of soil variability through spatial scales (project GACR P504/10/1644). Following data collected in the field in 2010 and 2011 represent part of this study, however not published yet. Approximately 50 % of the evaluated soil profiles were classified according to the World reference base for soil resources 2006 (Michéli et al. 2006) as Entic Podzols. Albic Podzols (Michéli et al. 2006) – soils with mutually clearly separated eluvial and iluvial horizons as a result of advanced podzolization process – were distinguished in 13 % of the cases. On the other side, soils with the predominance of weathering process and low level of soil leaching were recognized as Cambisols Dystric (Michéli et al. 2006). Hyperskeletic Leptosols, Lithic Leptosols, Gleysols or Stagnosols (Michéle et al. 2006) were rarely represented, associated predominantly with the sharp rocky ridges or water-affected sites, respectively. The parent rock represents mainly slate and limestone.

The character of a climate is, in winter, governed by the inflow of polar-continental air masses arriving from the east. The oceanic air masses from the west predominate during the other seasons. The mean annual temperature varies from 3.2°C to 3.9°C and mean annual precipitation range from 750 to 810 mm (Giurgiu 2001).

The forest composition of research area consists predominantly from *Picea abies*, rarely accompanied by young individuals of *Sorbus aucuparia*. The understory differs considerably with a character of forest stand. There were mainly present *Vaccinium myrtillus*, *Calamagrostis villosa* and *Luzula sylvatica*.

The characteristic forest structure is shown in Figure 5. There are evident snow and wind influences, because number of damaged trees and uprooting individuals were observed. The top layer of canopy rarely reaches 30 m.

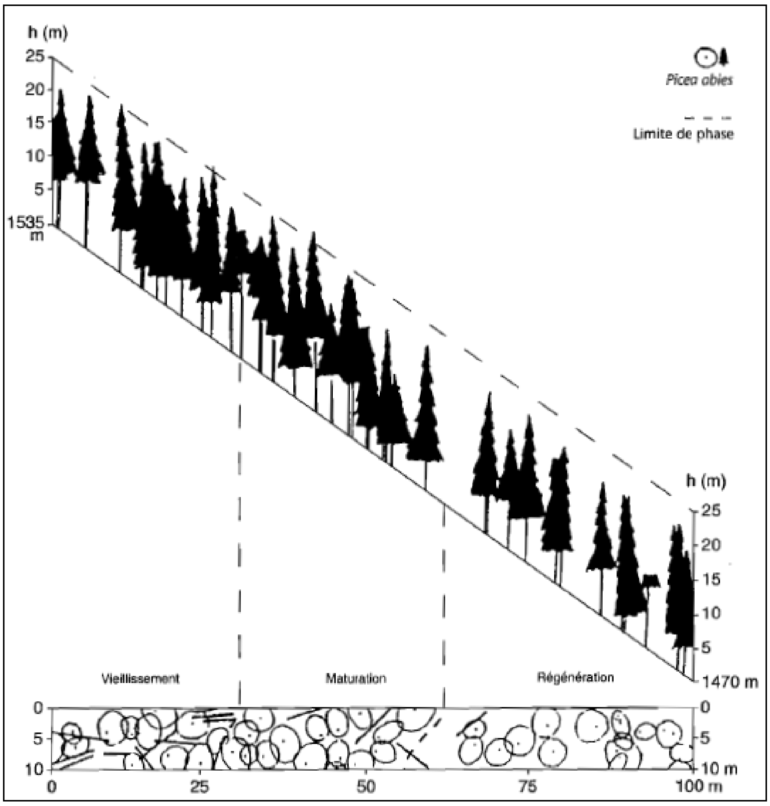

Figure 5 The forest structure typical for higher elevation stands in the Nature Reserve Codrul Secular Giumalau (Giurgiu 2001).

3.2 Data collection

The collection of samplings and records from study area was made during field work in August 2011.

By Geographic Information System grid of plots 141.4 m × 141.4 m was established. Buffer zones 35 m wide were set along inner edge and consequently the midpoints (Figure 6) of circle plots were determinate by random selection in new formed squares (70 m × 70 m). These points in the field were founded by GPS. There were two sizes of plots, 500 m^2 (diameter 12.62 m) and 1000 m^2 (diameter 17.84 m). The extent was selected according to character of stand structure. The selection was done due to the effectiveness of the field work. The time duration spent on homogenous plots with simple structure was by this process reduced. Therefore it was possible to spend more time working on heterogeneous and more difficult plots. In the case of plots used for this thesis only one plot with diameter 12.62 m from eight total was chosen. The circular shape is advantage because of the easy way of setting up the borders if the central point is known and also it can be clearly define if the tree should be included in plot or not (Speer 2010).

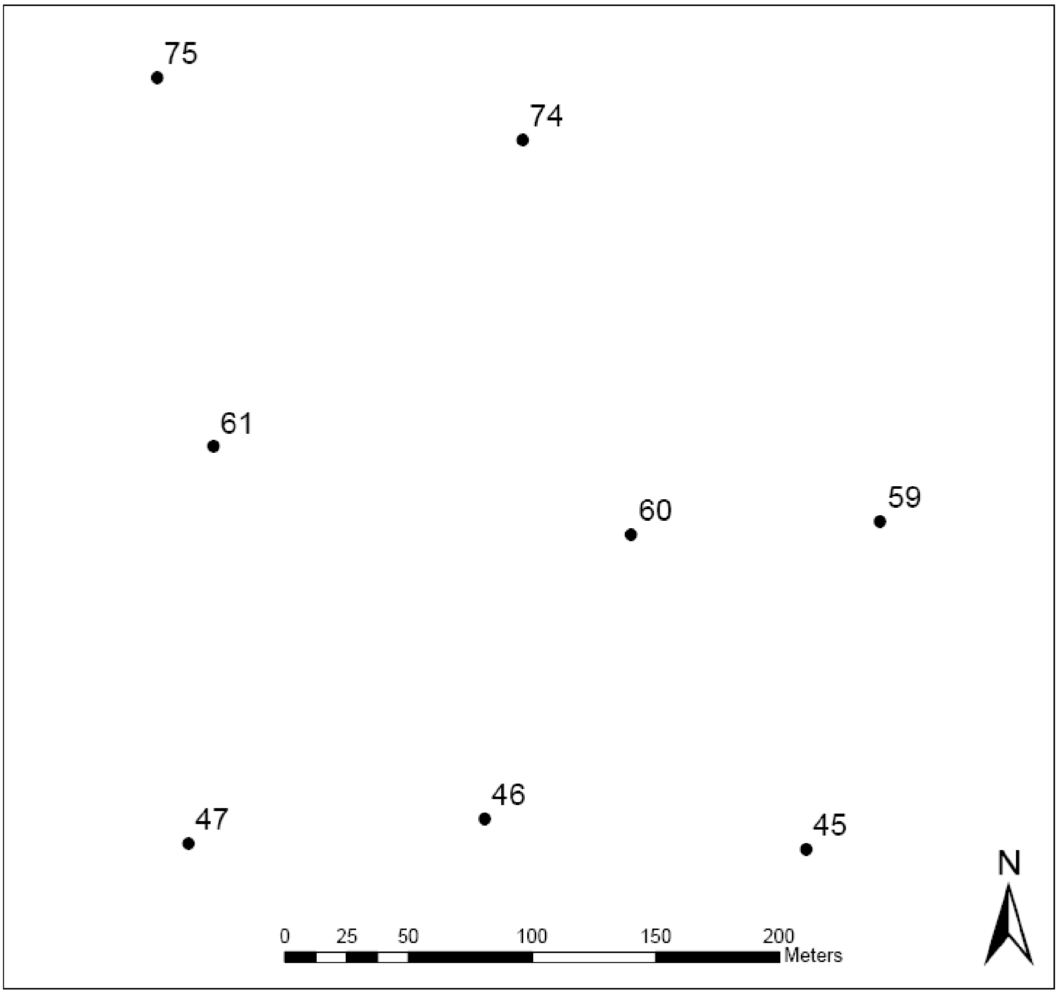

Figure 6 The placement of particular plots.

ID of plot	Area (m^2)	Slope (°)	Aspect (°)	Altitude (m a.s.l.)
45	1000	35	230	1499
46	1000	37	225	1447
47	1000	28	256	1400
59	1000	22	290	1525
60	1000	21	290	1501
61	1000	25	275	1397
74	500	23	232	1444
75	1000	28	217	1455

Table 1 The overview of studied plots and their basic characteristics.

To describe research area additional characteristics were listed. In every particular plot unique name of plot, topography character as hillform and landform, slope, aspect and altitude were recorded. Farther a natural regeneration divided into three groups according to height ((1) 0.5–1.3 m, (2) 1.3–2.5 m and (3) >2.5 m) and other four subgroups according to a placement of saplings on dead wood, mound or pit and other sites was recorded. An amount of dead wood, its placement and stage of decomposition was noted as well. All trees with diameter larger than 10 cm at DBH was numbered and their DBH measured, in addition, release or suppression of living individuals were assessed as well as their canopy accession or sublevel position. In the case of dead trees approximate height and stage of decay was noted. Height and proportion of crown of five randomly chosen non-suppressed individuals were noted as well.

The main task within the field work was to obtain the cores from trees. Twenty-five non-suppressed individuals were randomly selected for that purpose. The most precise age estimation is obtained from cores taken as close to the point of germination as possible, controversially heart rot due to root diseases, basal injury or browsing by animals can influence tree at the base rather than at higher level (Speer 2010). Regardless the mentioned aspects and better accessibility cores were taken by the increment borer at 1 m above ground coupled with parallel direction to the contour to avoid reaction wood. The emphasis was placed on reaching the pith. In the case of failure the pith, we suppose to be at least not further than 1 cm from the pith. Just after extraction cores were placed into labelled plastic straws to protect samplings during transfer and storing until reaching laboratory.

Afterwards dry cores were fixed on prefabricated wooden mount in the laboratory. Once the glue was dry the cores were sanded and polished until to smooth surface with clearly recognizable tree rings.

3.3 Sample processing

Tree-ring widths were measured in direction from bark side of the tree by a timetable sliding-stage device interconnected with computer program Past 32, accuracy was set at 0.01 mm. In the case of missing pith the distance to the pith was estimated by a pith indicator consisting from concentric circles. Subsequently absent rings were calculated.

The curvature of specific set of circles is assigned to curvature of tree-rings and the distance to the pith estimated. Consequently the number of missing tree-rings is derived from the estimated distance and mean width of the oldest five present tree-rings (Brumelis et al. 2005). As a next step crossdating method to confirm correctness of dating tree-ring was used.

3.3.1 Crossdating

Precise crossdating is the most important part of dendrochronological analysis and every effort should be in conformity with this fact.

The principle of crossdating is the basic element of tree-ring structure study. It is a tool to obtain exact year of growth of every annual ring, way to prevent wrong allocation of tree-ring series due to inaccurate measuring, false or absent tree-ring (Speer 2010).

The growth of tree and consequently the tree-ring width depends on life condition of particular individual. According to presence of narrow or wide ring we can derive the unsuitable condition such as large dry period or extreme temperature. The term "pointer year" represents a calendar year when the tree width differs significantly from the others. It is possible to set exact chronology series against which we can compare and modify inconvenient cores by determination of pointer year (Schweingruber et al. 1990).

The best correlating tree-ring series were chosen from all samples by Past 32. These were therefore used for compilation of the mean tree-ring series, which was applied as a reference row during statistical confirmation in software COFECHA (Holmes 1983).

3.4 Dendrochronological analyses

3.4.1 Growth release

The approach based on an assessment of release events in tree-ring series is a unique technique to identify both local and stand replacing disturbances at a high temporal resolution. A detection of release within tree-ring series is defined as pulse in percent growth change which exceeds given threshold for certain period (Black and Abrams 2003). There is an assumption that the magnitude of percent growth change corresponds to the severity of canopy disturbances. However the relationship between percent growth change and disturbance magnitude is complicated by number of variables. Significant variables affecting radial growth are for example crown size and position, prior growth change, type of forest structure meant as age, diameter, species and climatic conditions (Nowacki and Abrams 1997).

In other words, the smaller understory trees grow slower and their potential of release is greater whereas larger overstory trees grow faster and their potential is lower (Lorimer and Frelich 1989). The explanation for this behaviour is that overstory trees generally receive suitable amount of light, nutrients, water and space, and thus they are growing near their optimum (Black and Abrams 2004). Variation among species exists due to physiological differences, generally shade-tolerant species release more vigour than less tolerant (Lorimer and Frelich 1989, Nowacki and Abrams 1997, Orwig and Abrams 1994), and thus the threshold for release detection should vary between species. Finally climate can affect the radial growth character in different ways. For instance when short-term climate shifts follow disturbance event, then the growth release could be reduced during unfavourable climatic conditions such as drought or enhanced by favourable climatic event as longer growing season as usual (Black and Abrams 2004, Rentch et al. 2004).

For my study I followed method investigated by Black and Abrams (2003). They developed new release criteria which is based on finding that radial growth rate was the most fundamental predictor of percent-growth change pulse within their study of *Tsuga canadensis* in central Pennsylvania, simply that young, small and suppressed trees with slow radial growth were found to be more capable of large pulses in percent-growth change compared to their larger, dominant counterparts. This method, so called boundary line, characterizes growth release by the comparison of *average prior growth* and *percentage growth change*. The line represents extent of release which is potentially physically possible for given prior growth. Small, slow-growing, understory trees tend to reach the boundary line with large pulses in percent-growth change and dominant, fast-growing, overstory individuals are able to reach the boundary with just modest pulses. This should serve a better comparison of release events among individuals of different size, age and canopy levels.

Another advantage of this method is that by setting sufficiently stringent threshold for release is possible to block the effects of even the most extreme moderate–length climate events (Black and Abrams 2003), otherwise pulses caused by climate could be falsely counted as releases.

There is a requirement of large number of tree-ring measurements for estimation specific boundary line. For this study a regional boundary line from 2000 samples of *Picea abies* collected in research area Giumalau was developed.

In order to apply boundary line the determination of following values was essential. Firstly percent growth change for each ring in each tree-ring series according to Nowacki and Abrams (1997) was calculated.

$$\%GC = \frac{M2 - M1}{M1} * 100.$$

- where *M1* is preceding 10 years mean growth, and *M2* is subsequent 10 years mean growth.

This running comparison of sequential 10-years ring-width method shows sustained growth increase caused most likely by canopy disturbances and neutralizes short-term and long-term growth trends affected by climate.

Therefore the average prior growth over the 10 years was calculated, for each ring in every series as well. Figure 7 shows determination of variables for year 1980.

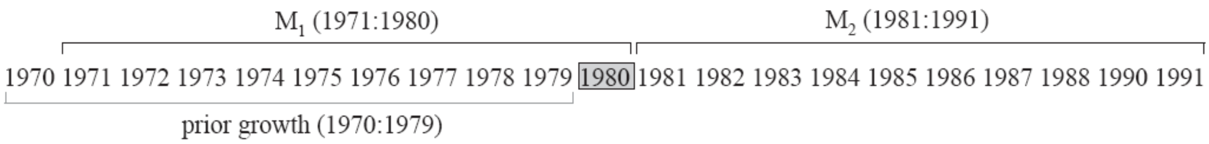

Figure 7 Graphic of calculations for prior growth chase and percent-growth chase formula (Black and Abrams 2004).

In order to estimate the maximum growth change for each release pulse similar method as Nowacki and Abrams (1997) was following. Only percentage growth change values higher than 50% were selected due to exclusion extreme climatic changes and mast years (Splechtna et al. 2005). In each case of exceeding this border just the maximum percent growth value of particular peak was recorded, thus each pulse was register only once. These recorded pulses were scaled relatively to developed boundary line. Pulses in range

100% - 50% of boundary line were defined as major releases and these between 49.9% and 20% as moderate ones (Black and Abrams 2003). Values lower than 20% were considered as reaction to climate conditions. The major release was considered as loss of overtopping canopy trees and moderate as partial removal of a canopy or death of neighbouring trees (Svoboda et al. 2011).

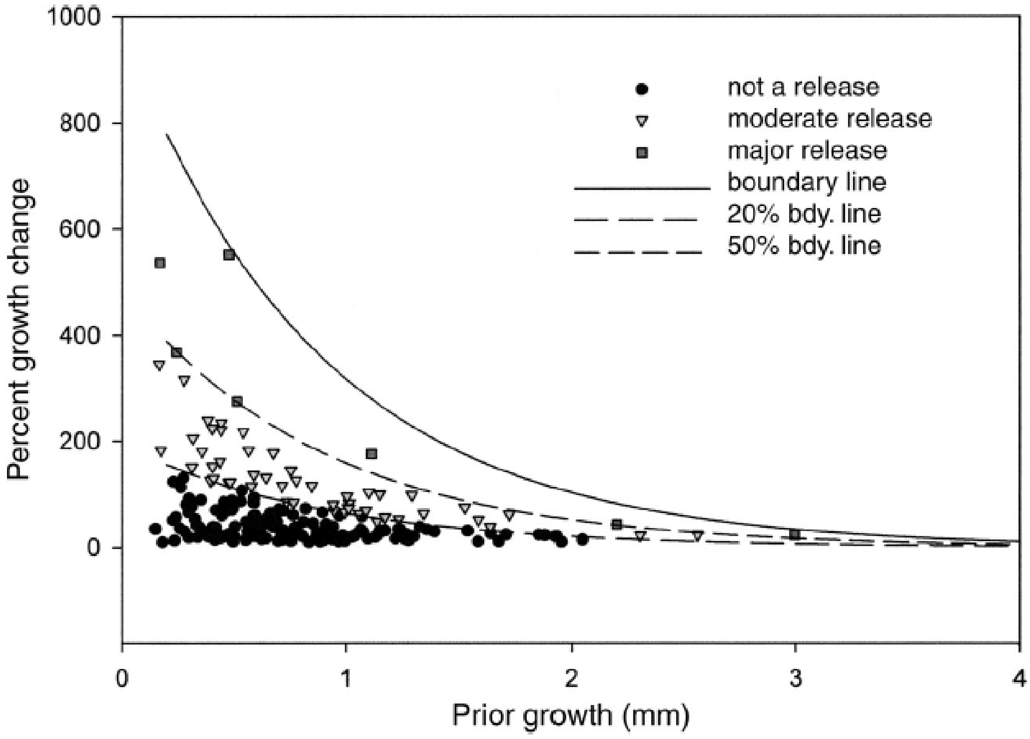

Figure 8 Example of boundary line developed for *Tsuga canadensis* in Pennsylvania by Black and Abrams (2003).

3.4.2 Gap recruited individuals

Gap is simply the surface under the canopy opening. It is created by mortality of individuals or multiple trees and subsequent fall from the cohort. The source of death (e.g. insect, disease or meteorological factors) and gap formation affect spatial character as well as the potential process of regeneration (McCarthy 2001). The gaps provide vital resources such as sunlight and growing space and may offer the chance for suppressed understory trees to recruit into the canopy (Speer 2010) and beginning of new regeneration as well.

The goal of methods dealing with detection of gap-originated individuals is to determine their placement during period when they are becoming from small sapling to mature tree.

However it is necessary to include the fact that gap-recruited trees are not in every case in gap since their germination, shade-tolerant species are able to live long time within shaded conditions and at the time when overcanopy is removed they start to grow faster. The separation of gap-originated trees and those developed under the closed canopy is given by threshold (Fraver and White 2005a) which is based on comparison of an average radial growth during early 5-years (ending where samples were 4 cm at DBH) of suppressed and non-suppressed saplings (Frelich 2002).

The threshold is typically set at the arbitrary value. For my study the threshold derived from regional conditions was determined. This was reached by collecting cores from given amount of saplings - which are currently placed in gap (large clear-cut close to the study area was chosen) and those with similar heights under the canopy (Svoboda 2011). Using logistic regression a mean growth rate of 1.06 mm as a boundary between suppressed individuals and those coming from gaps was determined (M. Svoboda, P. Janda, T.A. Nagel, S. Fraver, J. Rejzek, R. Bače unpubl. data). This value is simply the most probable border between two distributions. Thus the trees which show tree-ring width during early stage greater than this value are supposed to growth under open-canopy and these with slower growth as growing in shaded conditions.

3.4.3 Disturbance chronology

To reconstruct the history of forest stand I used obtained data from cores as growth releases and the amount of individuals growing during juvenile stage in gap. Data expressing growth release were sorted according "boundary line" into major and moderate. Growth releases and gap originated individuals were sorted into decades. The numbers of disturbance events were expressed proportionally to the depth of sample.

The variable "depth of sample" was included into graphs. This important value shows the amount of trees which were alive in particular decade. Thus, it is necessary to take into consideration this feature and reflect it within study of old history, when only few samples from overall sample depth were living. The values in diagram at that period could seem to be misleading, since the amount of trees affected by disturbance events has been expressed relatively to the depth of sample. Therefore the decades where the amounts of samples drop below five individuals were not displayed.

4 Results

4.1 Forest composition and structure

The main canopy of the stand was homogeneous and composed from shade-tolerant *Picea abies*. Only two living individuals of *Sorbus aucuparia* and one living individual of *Abies alba* were observed. However sampled trees were only *Picea abies*, because none of the tree individuals of other species reached 10 cm of DBH. The oldest recorded and simultaneously sampled individual from all eight plots was found on the plot 47 and it reached coring height approximately in 1720.

Data characterizing forest structure recorded during the local survey in August 2011 are available as well. I use these ones just to illustrate the form of present forest structure. Particular plots differed among their characteristics (Table 2). For instance plots placed in a higher level (altitude >1499 m a.s.l.) had a character more likely homogenous with one canopy layer, rich herb layer and frequent regeneration consisting from small individuals. On some of them the occasional signs of previous grazing such as for instance trees with several trunks growing from one root system (polycormons) were recognized (Figure 9). On the other side plots situated at the lower altitude, namely plots 46 and 47, had the old mature growth character with a high canopy layer and very scarce regeneration. Therefore the analysis for the whole research area together would not be representative. The common features of particular plots were identified and the forest chronologies were combined for several plots together.

Figure 9 Polycormons in the Nature Reserve Codrul Secular Giumalau. Photo by Vít Sedlák, 2011.

ID plot	Living individuals (N/ha)	Dead standing individuals (N/ha)	Regeneration (N/ha)	Mean DBH of living (cm)	Maximum DBH (cm)
45	350	280	140	32,62	64,9
46	390	180	390	41,60	70,2
47	480	100	330	36,60	81,5
59	350	60	3280	31,90	58,6
60	190	130	1000	39,90	60,0
61	380	80	1180	36,75	75,4
74	620	260	60	33,11	61,8
75	310	50	3370	28,21	86,0

Table 2 The characteristics of particular plots. The number of mapped living and dead individuals (DBH > 10 cm) and regeneration is recalculated per 1 hectare. The maximum and mean DBH of mapped living trees are presented as well.

The DBH of the most of trees is situated from 10 to 60 cm (Figure 10). It could express the heterogeneous forest structure with more than one main canopy layer. The lack of robust trees with DBH over 70 cm does not have to coincide with the lack of old tree.

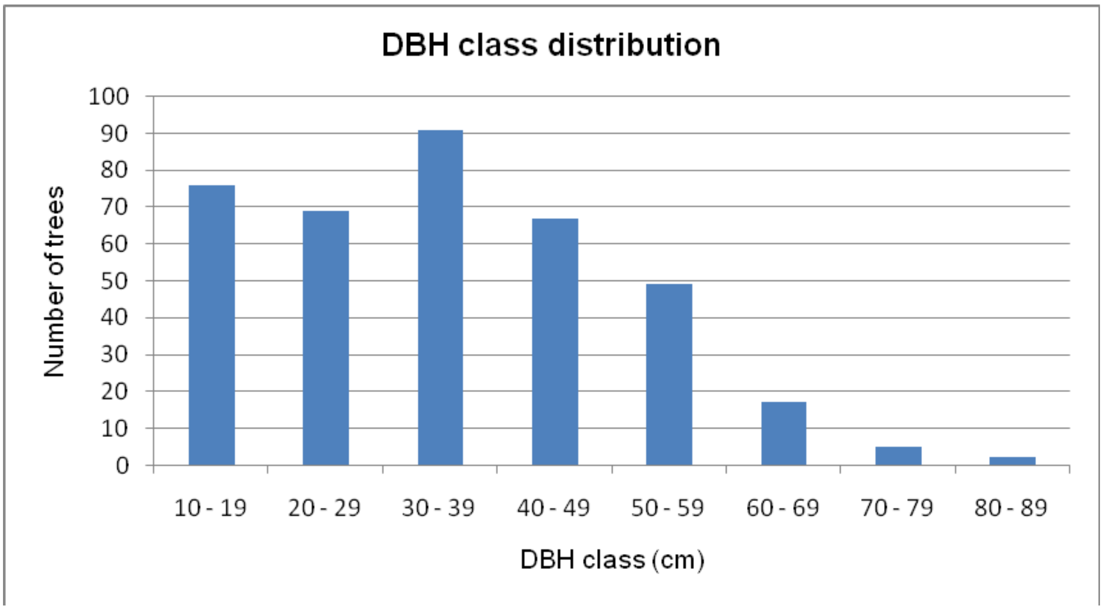

Figure 10 The DBH class distribution of all living and dead mapped trees (with DBH > 10 cm) within the eight study plots.

There was a great variation among regeneration present on particular plots (Figure 11). For instance on plot 74 only three individuals of *Picea abies* smaller than 1.3 m were detected. Controversially the most of young individuals was recorded on the plot 75, which is right neighbouring with mentioned plot 74.

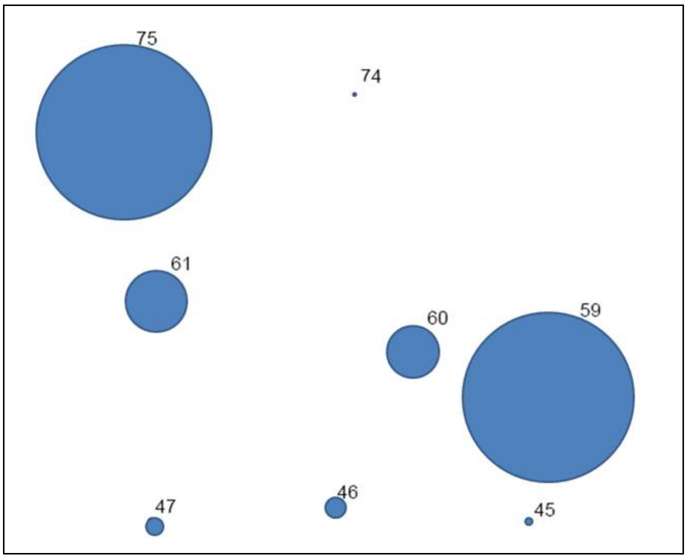

Figure 11 Relative expression of amount of regeneration in particular plots. The placement of plots is maintained according real state.

972 saplings were recorded in total. Only three individuals from this number were different species than *Picea abies*, as it was already mentioned above. Three types of microsites were distinguished (see the chapter 3.2. Data collection). For the majority of individuals no particular microsite was specified. The most common observed microsite was dead wood (DW). There were placed approximately 24% (229 saplings) of individuals, 92 grew on a mound and only one individual in a pit. Table 3 shows the amount of seedling and saplings among particular plot and an amount of individuals present in each type of recorded microsites recalculated for 1 hectare.

ID plot	*Picea abies* (N/ha)							*Sorbus Aucuparia* (N/ha)	*Abies alba* (N/ha)
	Individuals			Type of microsite					
	0.5 < 1.3	1.3 < 2.5	> 2.5	DW	mound	pith	other		
45	120	-	10	-	-	-	130	10	-
46	250	40	20	70	10	-	230	-	-
47	220	70	-	30	-	-	260	-	10
59	750	910	520	930	170	-	1080	-	-
60	460	180	-	200	160	-	280	-	-
61	490	130	60	380	120	-	180	-	-
74	60	-	-	-	-	-	600	-	-
75	1280	460	470	680	460	10	1060	10	-
Total	**3630**	**1790**	**1080**	**2290**	**920**	**10**	**3820**	**20**	**10**

Table 3 The overview of regeneration within particular plots. The individuals are sorted into class according the species, height in meters and distinguished microsite (see the chapter 3.2. Data collection). The last row contains the total numbers of individuals within specific class.

4.2 Disturbance history

376 living and dead trees with a DBH ≥ 10 cm was mapped and described during the field work. 200 (72.5% from living individuals) trees were sampled. Dead standing trees were represented by 100 individuals.

Disturbance events were described within every single plot. Due to the heterogeneity of plots I will firstly present characteristics for all of plots together and consequently for groups of plots with similar development and character.

4.2.1 Summary of the eight plots

The oldest tree recruited to the coring height around 1720, so the possible time span for construction disturbance chronology could be over 290 years. However due to the exclusion of data of release events and gap recruited individuals during decades where the depth of sample was lower than five individuals, the period for disturbance chronologies reduced to 190 years. The analysed particular series has expressed the disturbance history since 1815. However time scale in the following graphs for all the plots together begins at the decade of the recruitment to the 1 m of the oldest tree. The depth of sample for all the plots together reached amount of five individuals in 1735. Since that the release events have been considered and described.

Figure 12 shows the temporal distribution of trees recruited to the coring height. The most of the trees have reached their height over the 100 years since the 1825. The chronology of recruited trees depicted a multiple age structure with pronounced peaks. The first significant peak occurred in 1825. During the following decades the amount of recruited trees was decreasing and again slightly increasing until the second peak in 1895.

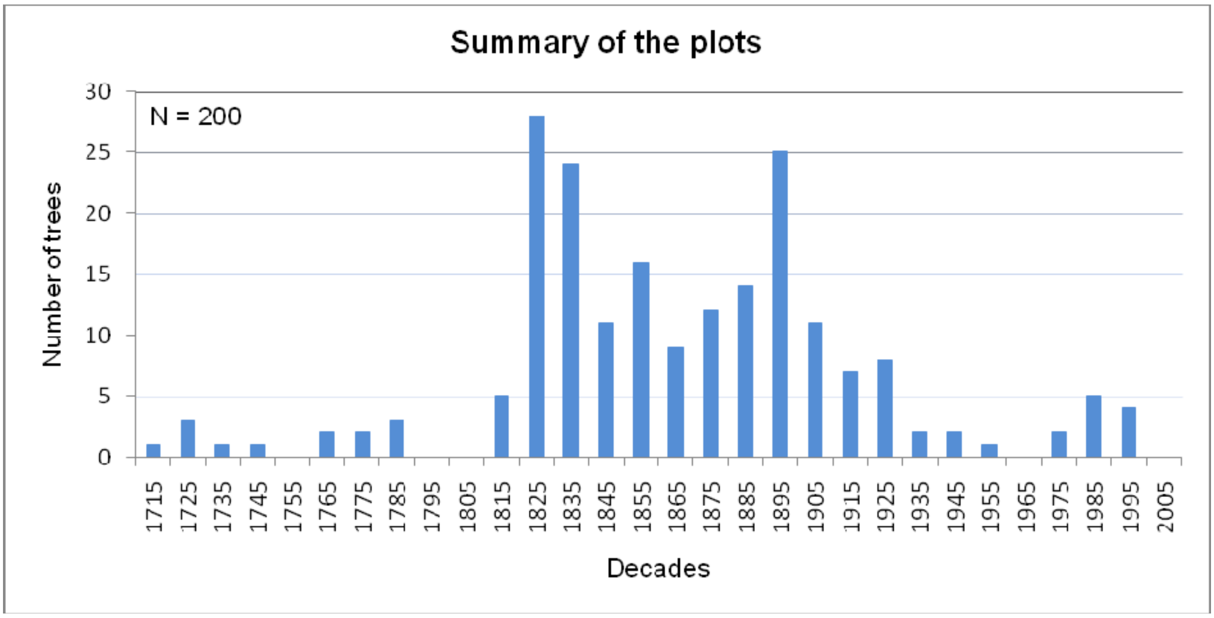

Figure 12 Number of trees recruited to the cored height 1 m in particular decades. *N* represents the number of sampled trees.

The gap-origin individuals and release events detected within all plots are included in the disturbance chronology displayed in the Figure 13. It is possible to recognize the slight temporal coincidence in trend of the gap-recruited individuals and trees recruited the coring height from Figure 12.

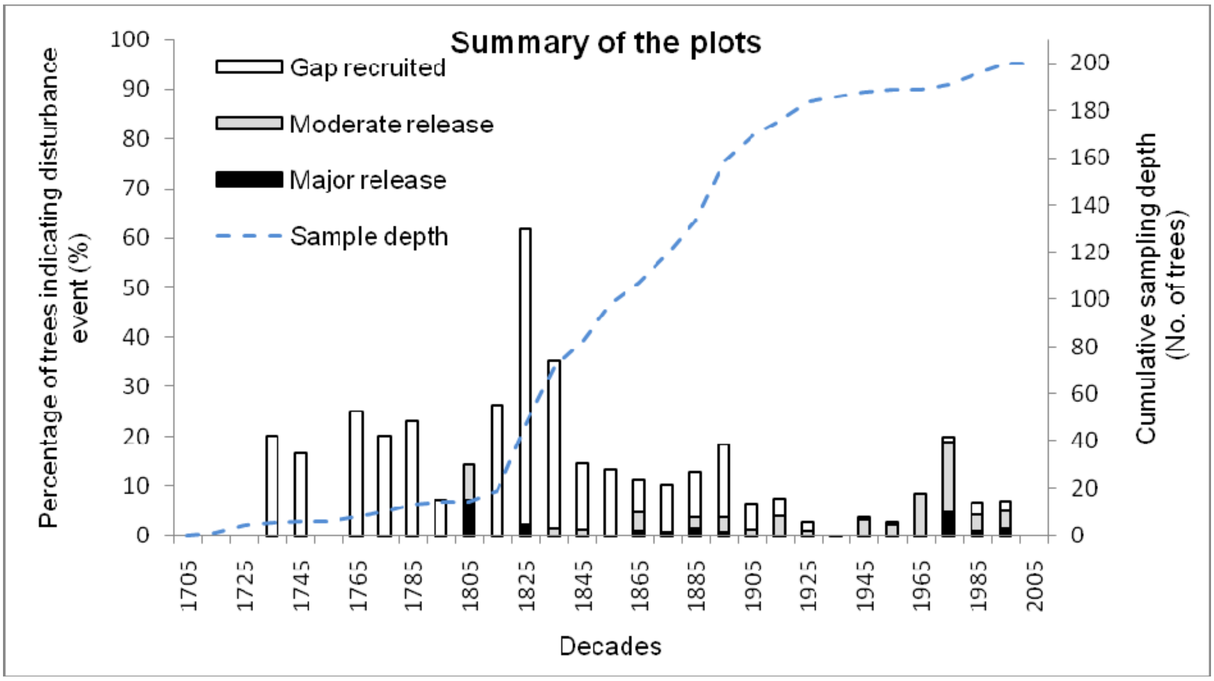

Figure 13 Disturbance chronology based on release and gap-recruitment events in each decade for the all of sampled plots together.

The distinctive release event has been detected during approximately four decades since the 1865. The releases in radial growth pattern were accompanied and followed by the gap-recruitment lasting over decades. The other pronounced release from suppression has occurred for several decades since 1960s. The major release was observed approximately on 5% and the moderate release on 15% of trees. This event has high importance if the depth of sample is considered.

There are also major release events detected before this period (Figure 13). However in that time the depth of sample did not exceed the amount of five individuals simultaneously within all of plots. And thus the disturbance chronologies were not analysed.

4.2.2 Groups of the plots

As it was mentioned above - the forest structure of specific plot is heterogeneous therefore there is a need to describe the disturbance history among particular plots in detail. Therefore I sorted eight studied plots into groups according to a significant common character in disturbance chronologies. The main feature for allocation of the plots into each group was the temporal scale of detected events. The groups of plots are described in the following text, only the most important and significant common patterns were described. The distributions of trees recruited into coring height according decades are also presented in order to compare and detect the coherence with disturbance chronologies.

4.2.2.1 Group 1

The plots 45, 47 and 59 were included into the first group. There has been observed a substantial number of gap-originated trees since 1840. This trend was continuing for several decades, the longest period is observed in plot 59, where the considerable gap-origin was present until 1919. This event coincides with the chronologies of recruitment into coring height. Thus the most of sampled trees recruited within this period. Beside that event, the significant amount of released individuals has been detected since 1960. The most of trees showing major as well as moderate release from suppression was found in plot 45 during 1970–1979 (Figure 14). There was coherence between these frequent releases and recruitment into 1 m.

In the case of this group consisting from plots 45, 47 and 59 is necessary to emphasize the spatial separation of plots, there is no common border between plot 47 and 45 together with 59 (Figure 6).

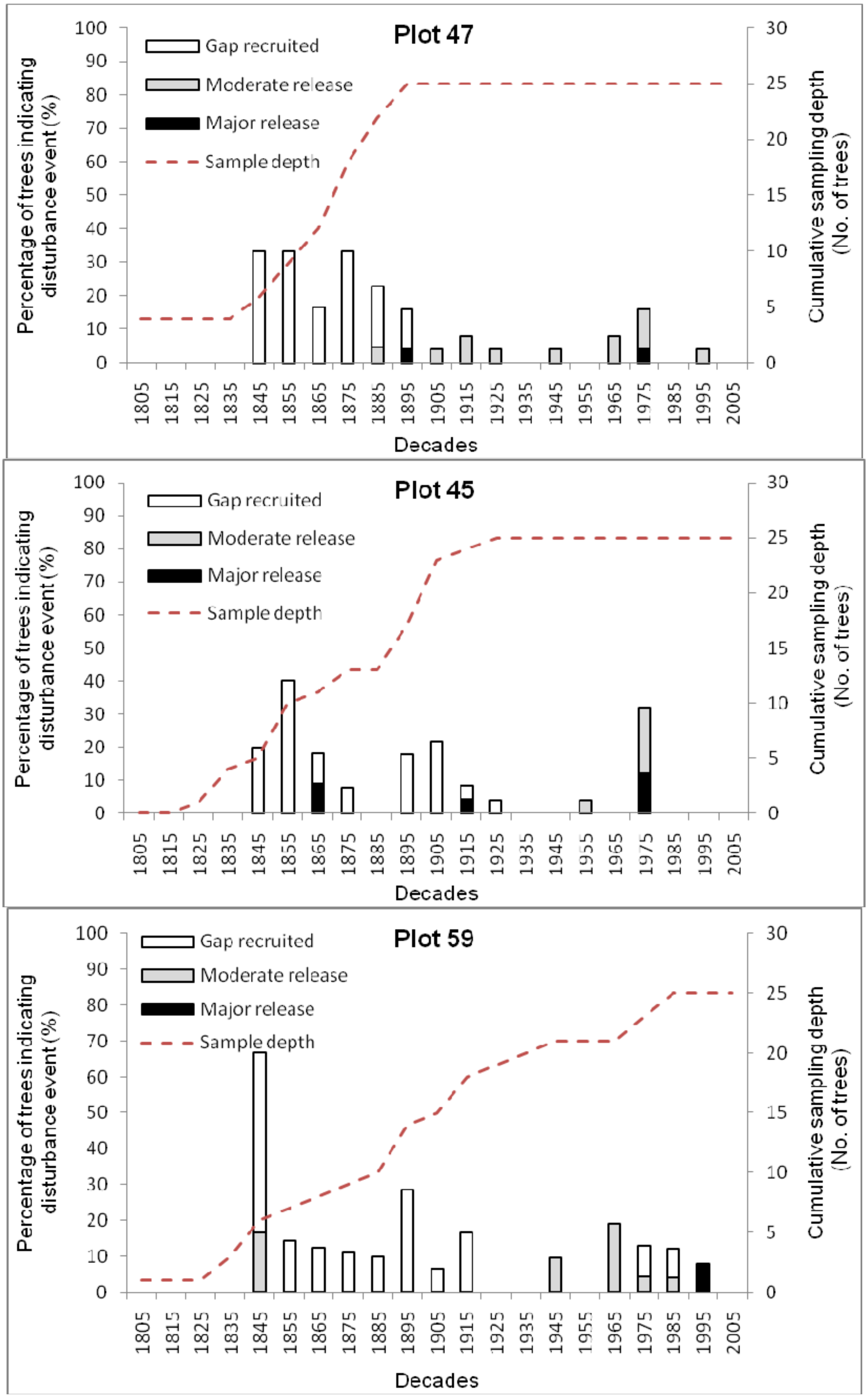

Figure 14 Disturbance chronologies of plots 47, 45 and 59.

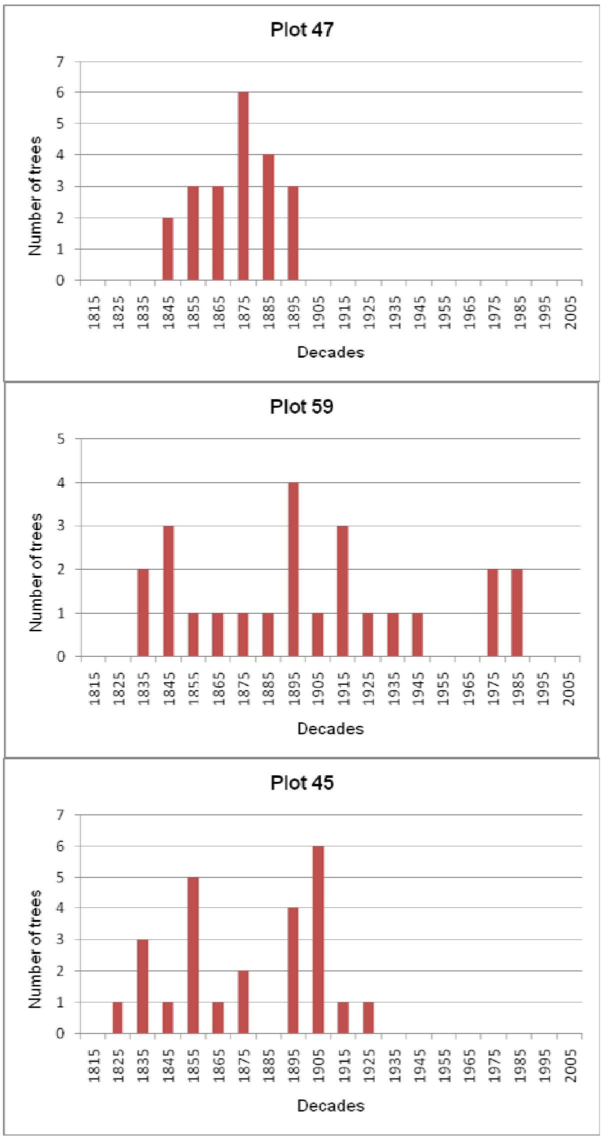

Figure 15 The recruitment into coring height during decades within plots from Group 1.

4.2.2.2 <u>Group 2</u>

Disturbance chronologies of plots 46, 60 and 61 represent Group 2. These plots are characterized by the similar disposition of amount of trees recruited to the coring height within decades (Figure 16). There is a major part of sampled trees approximately 200 years old at the time of data collection. The high amount of individuals recruited to the 1 m goes along the number of gap originated trees. This event has been observed for three decades since the 1810 in plot 61 and since 1820 within the other plots (Figure 17).

There has also been a minor occurrence of releases since 1960. The amount of trees where the release in growth is detected is significant if the depth of sample is considered. These releases are partially presented as major and moderate within plots 60 and 61, but they are presented only as moderate in plot 46. There is again no relation between these considerable releases and recruitment into 1 m.

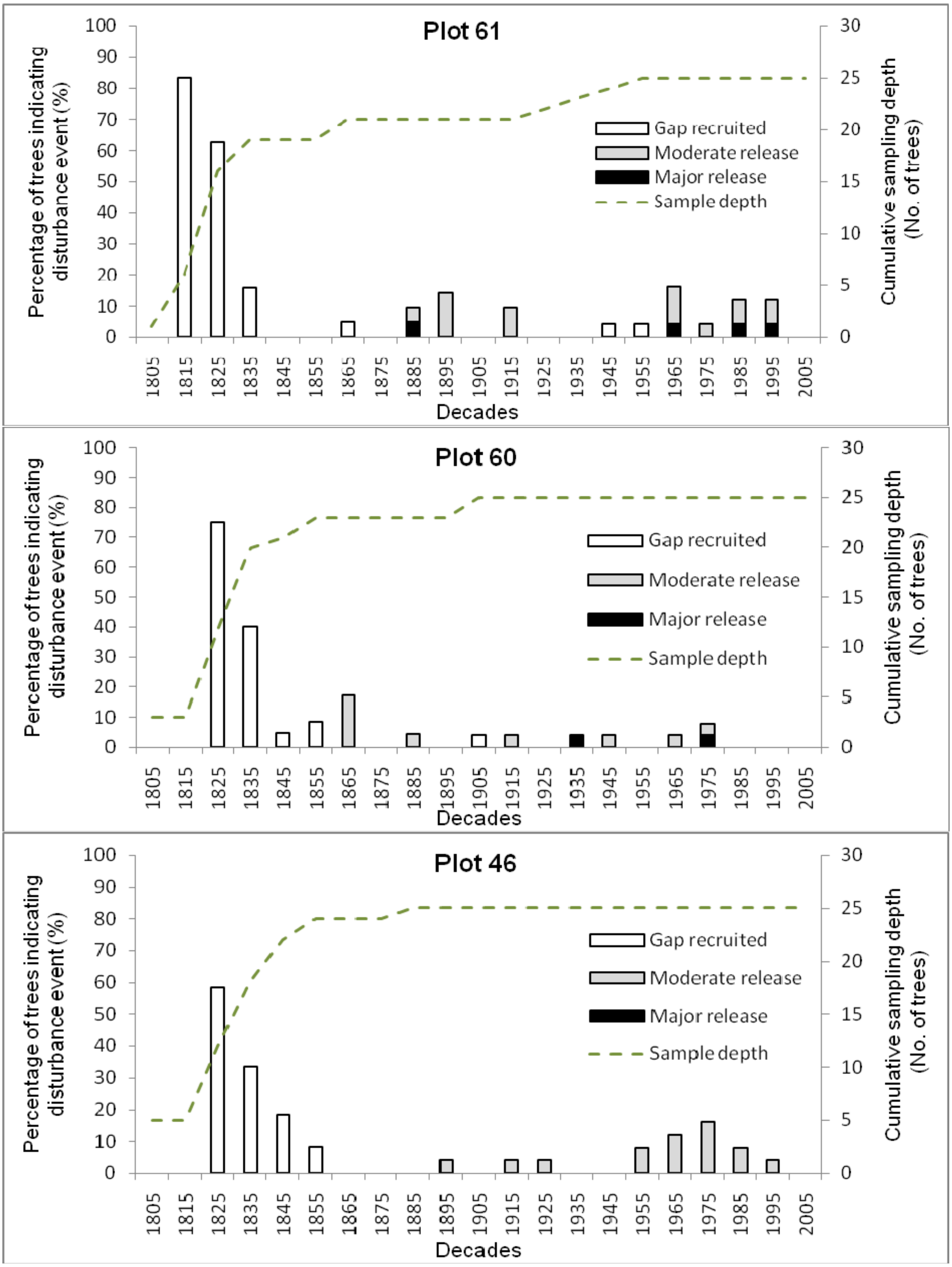

Figure 16 Disturbance chronologies of plots 46, 60 and 61.

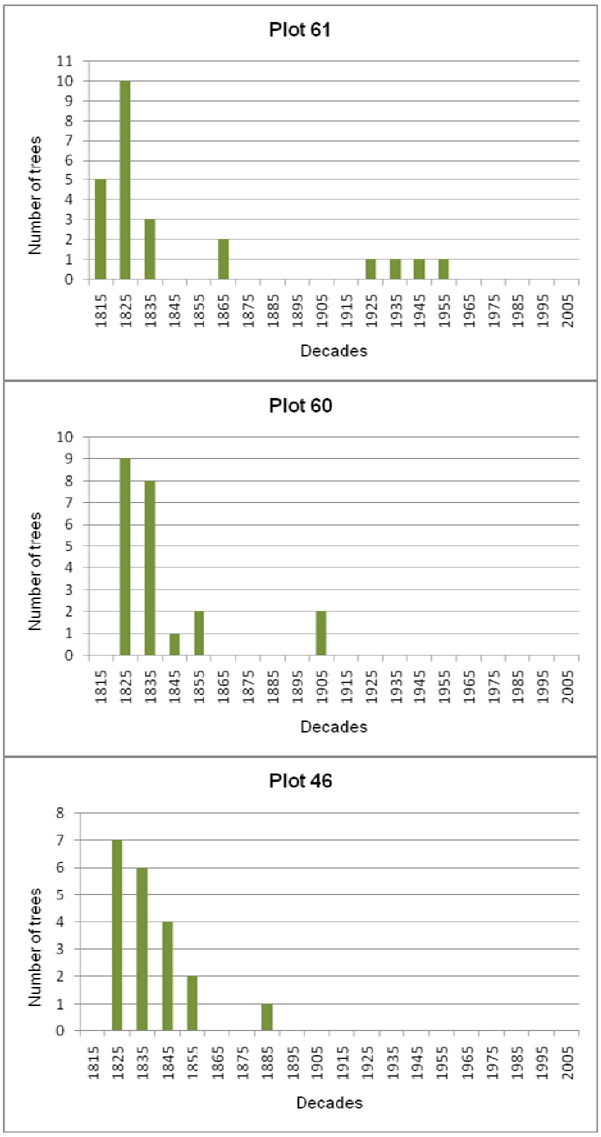

Figure 17 The recruitment into coring height during decades within plots from Group 2.

4.2.2.3 Group 3

Last two plots 74 and 75 were placed into the third group. The high amount of gap originated trees has occurred in both plots for three decades since 1870. However in plot 74 the amount of gap recruited trees accompanies and follows the major release detected from 1870 to 1889.

Within this group of plots there is a same pattern as in the first group recognized. A significant release event has been detected since 1970 as well. Approximately 25 % of trees showing major release and almost 40% less pronounced release are present in plot 75, thus around 65% sampled individuals were affected. Only moderate releases of 20% of trees were observed within plot 74 during this period.

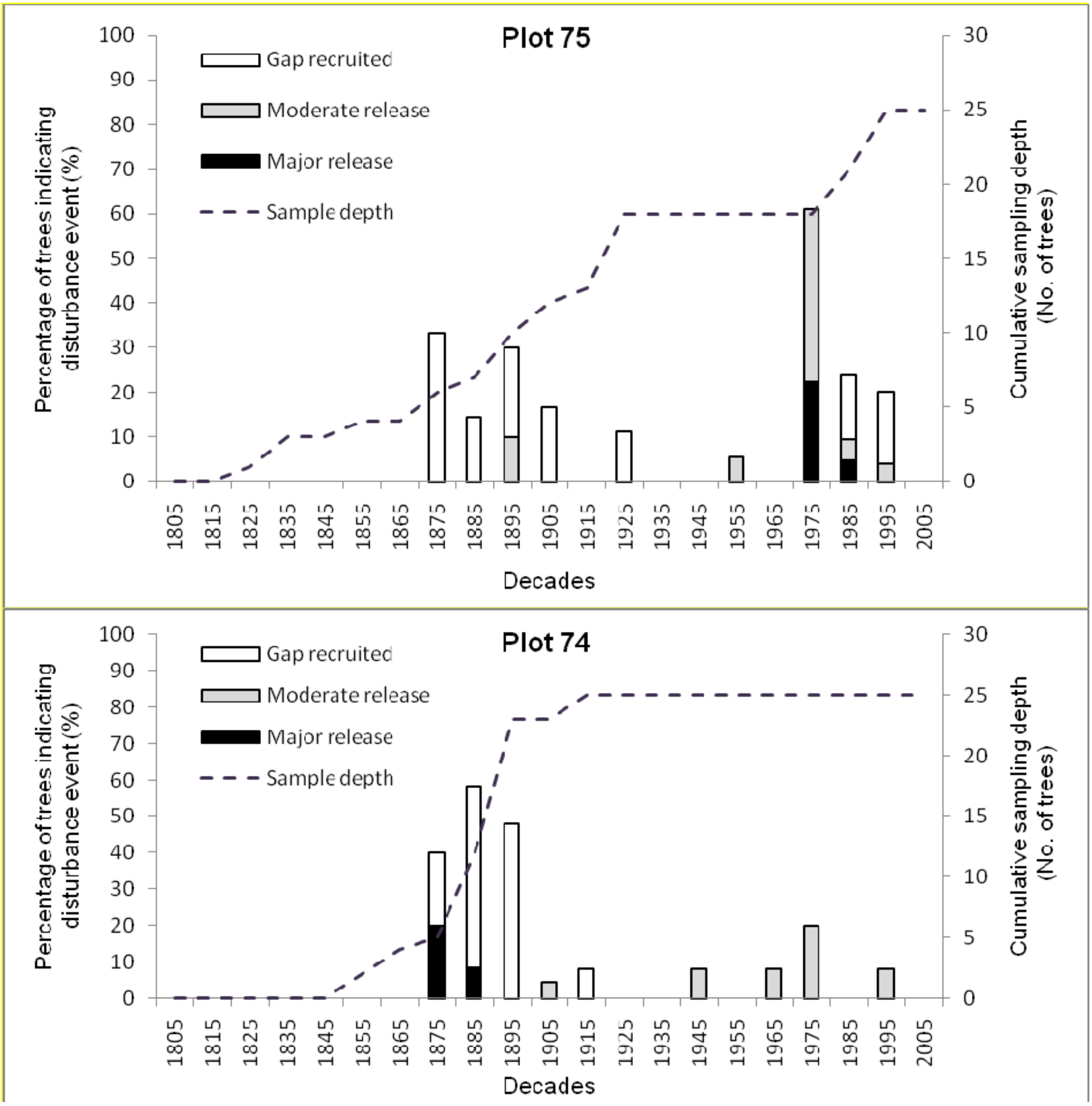

Figure 18 Disturbance chronologies of plots 75 and 74.

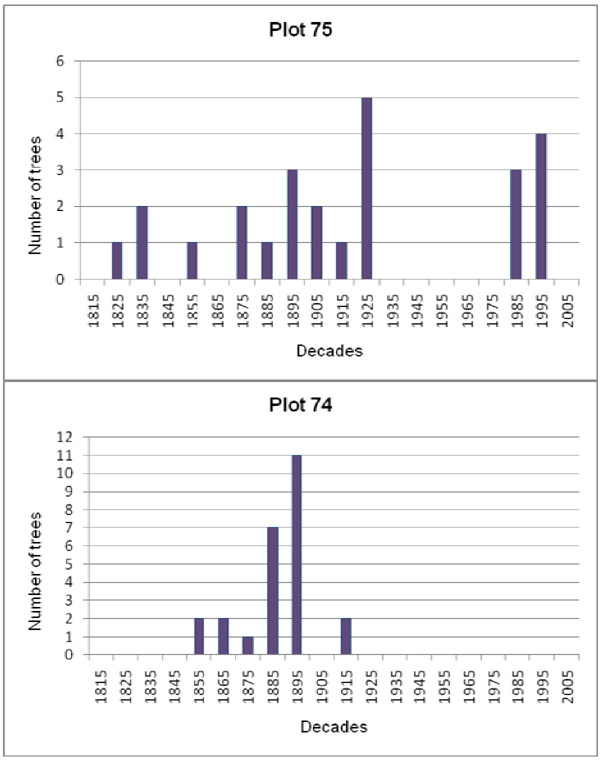

Figure 19 The recruitment into coring height during decades within plots from Group 3.

5 Discussion

5.1 The age structure and the disturbance chronology

Based on the chronology of trees recruited to the 1 m it is possible to express age structure of forest. However it is necessary to consider, that the determination of age from increments from 1 m above the ground is not as precise as it would be needed for accurate construction of forest stand structure. The suppressed shade-tolerant individuals of 10 cm DBH differ considerably from non-suppressed individuals in exact age. The significant difference between DBH distributions and age structure was in this study observed as well. The most of cored trees range from 10 to 60 cm DBH. However the span in age structure of the most individuals ranges only within 100 years.

The majority of sampled individuals within study area have been recruited to the coring height during 100 years since 1815 (Figure 12). There were only few trees presented before this period. Subsequently only scarce regeneration of single trees occurred. The trend of recruitment during mentioned 100 years was fluctuated. There were observed two distinct peaks in decades from 1820 and 1890. Therefore it is possible to present that the regeneration of analysed forest covering 18 ha stand is not constant in time. This finding does not go along with the statement that the recruitment in natural forests is continuous in time and the age structure is similar to rotated sigmoid curve (Fraver et al. 2008). However this finding is derived from data from my study area covering 18 ha and it is not possible to generalize it for whole forest cohort.

There are a several studies recorded the dominance of medium age classes in European natural spruce forests (Holeksa 1998, Svoboda et al. 2010). This phenomenon is based on establishment of young trees after the stand-replacing disturbances. In central Europe the source of such disturbances is attributed to large windthrows, massive bark beetle outbreaks or their interaction (Svoboda and Pouska 2008). However, within my study area there were no obvious signs of occurrence of large stand-replacing disturbance event derived from collected data that would affect whole area at one time.

There is numerous of potential scenarios of forest development in this study area. The variety of interactions among factors combined with the specific temporal and spatial pattern shape a history of forest stand structure. However I will present just the main possible scenarios developed from obtained disturbance chronologies.

There were not detected any clear signs of large disturbances within study plots, as was already mentioned. The occurrence of significant major release within disturbance chronologies is considered as that type of sign. However no distinct major releases within described chronologies were observed. Only numerous of releases limited usually to the single plots were detected. For instance, the plot 75 shows substantial major release during decade from 1970 (Figure 18). However none of neighbouring plots was considerably affected at the same time. These patterns suggest that not only large-scale disturbance can lead to uniformity of age structure. Time and spatial patterns play the essential role of forming the forest structure. Instead of one severe disturbance event, the numerous local disturbances sequential in timeline could be the reason of forest stand with roughly uniform age structure. For example, there is a distinct major release event covering approximately 5 % from 191 sampled individuals during 1970s. Major release of different size during this period was within plots 45, 47, 60 and 75 (Figure 14, 16, 18) detected. Figure 6 shows the location of particular plots and that the potential disturbance did not influence one large area but the numerous of patches.

These findings tend to approach gap-phase dynamics (Watt 1925, 1947). This kind of dynamics has been suggested as the process governing spruce-dominated mountain forests in central and south Europe (Splechtna et al. 2005, Szewczyk et al. 2011). These studies support the statement that rather low-severity disturbances forming small gaps with higher frequency are main factors shaping the long-term structure of old-growth natural forest.

However there is a large variability of possible historical development. For instance, the presence of nearly uniform age structure and the sharp increase in amount of recruited individuals in beginning of 1820 can signal the occurrence of large-scale disturbance event (Figure 12). This large disturbance had to take place before obtained data, because no significant major release in available disturbance chronologies was distinguished. During subsequent 100 years new stand was regenerating. The length of the period could be result by variability of forest character, local condition or small-scale disturbances as grazing by animals. In addition, heavy snow or ice in post-disturbance cohorts can affect new regeneration as well as sensitive individuals recently exposed to open condition and thus further delay stand development (Svoboda et al. 2011). On the other hand, the favourable weather conditions with the mast year could cause peaks in 1825 and 1895 (Figure 12). This type of mountain spruce-dominated forest dynamics would agree with studies in Tatra Mountains (Zielonka et al. 2010) and in ŠumavaNational Park (Svoboda et al. 2010). These studies present forest dynamics shaped by the occurrence of scarce large-scale disturbances rather than more frequent small disturbance events.

The influence of both small and large disturbances has been reported for mountain spruce-dominated forest as well (Panayotov et al. 2011, Svoboda and Pouska 2008, Zielonka and Malcher 2009). The clear distinction between forest dynamics leading by gaps formation or occasional stand-replacing disturbances is questionable. The character of forest response to similar disturbance essentially depends on stand structure (developmental stage) at the time of disturbance. Therefore it is linked with the history of the stand and legacies as variable of potential post-disturbance development. Specific disturbance event of higher-severity can damage only weaker cohorts more predisposed to be injured or died, which are not spatially connected.

There is great variation among disturbance regimes. Introduced study from the Nature Reserve Codrul Secular Giumalau contributes and supports studies mentioned above. They present that the mountain spruce forest is leading from low-severity high-frequency disturbances to large-scale infrequent disturbance events. In all cases the essential role of disturbances within natural forest dynamics is indisputable. However these statements are not in agreement with the traditional point of view that the forest dynamics is leading only by endogenous tree mortality caused by senescence or diseases (Leibundgut 1982, Korpeľ 1989, 1995).

5.2 The disturbance agents

The methods used during this study are not suitable for study of disturbance origination. Based on obtained data it is only possible to describe my results and compare them with other studies and general assumptions. Dendroecological studies from European mountain *Piceaabies* forests (Panayotov et al. 2011, Svoboda and Pouska 2008, Svoboda et al. 2011, Zielonka et al. 2010) suggest that windstorms, bark beetle and their interactions have played important role in natural forest dynamics. Thus the windthrows and subsequent bark beetle outbreaks could be probable agent of eventual stand-replacing disturbance occurred in the beginning of 19^{th} century in our study.

The low-severity winds and local bark-beetle outbreaks could be sources of smaller-scale disturbances. The senescence of forest stand accompanied by lower-severity disturbance can contribute to gaps creation in forest structure as well.

As was already mentioned in the upper part of study area the signs of grazing was observed, namely within plots 74 and 75. The grazing affecting regeneration and stability of stand structure can be also possible factor influencing the forest stand development as well as to enhance the disturbance severity. There were no transparent marks of logging in study area noticed. Nevertheless the past anthropogenic influence cannot be certainly excluded.

Unfortunately it is not possible to support or compare the results coming from this study with historical or other records. There are no historical data or photographs available as well as the present scientific papers dealing with the natural forest dynamics in the Nature Reserve Codrul Secular Giumalau. Thus the question concerning the character of past disturbance agents' remains unexplained.

6 Conclusion

This study shows that the forest stand dynamics in mountain spruce-dominated forest studied within approximately 18 ha in the Nature Reserve Codrul Secular Giumalau is obviously shaped by both types of disturbance regime. It is not possible to set up clear border between these types of regimes. The character of forest dynamics derived from this study is influenced by mixture of scarce stand-replacing large-scale disturbances and frequent small-scale disturbances. Based on my observation and existing study from similar natural conditions the possible disturbance agent of larger disturbances could be the wind and therefore bark beetle outbreaks. The smaller-scale disturbances creating gaps could be caused by death of individual trees caused by senescence, fungi, attack of insects or for instance combination of different agents such as low-severity wind and weakness of tree. Several indicators of possible grazing by herbivories were observed within study plots. This finding could also contribute to different forest structure development. Due to the lack of any historical records it is not possible to exclude the influence of human activity and existence of controlled pasture.

There is a clear and sharp regional variation in the severity and frequency of natural disturbances over the mountain spruce-dominated forest in central and south Europe. Thus the more complete description of the natural forest dynamics could lead to understanding of natural processes and bring new knowledge to forest management which goes along the needs of nature. Such knowledge helps to prepare better stage of forest stand for potential exogenous severe disturbances that may occur and to build stable forest stand.

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