Czech University of Life Sciences Prague

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# Reconstruction of the Disturbance Regime in the Mountain Spruce Forest

A Thesis
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Master of Science Degree

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# ZADÁNÍ DIPLOMOVÉ PRÁCE

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**Metodika:**

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## Declaration

I hereby declare that this thesis is my own work under the supervision of Ing. Miroslav Svoboda, Ph.D. Where other sources of information have been used, they have been acknowledged.

In Prague, 27/04/2011 Bc. Markéta Reitschmiedová

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# Abstract

Steep slopes of Eastern Carpathians represent a unique opportunity to study natural dynamics of mountain spruce forests within the temperate zone of Europe. Natural disturbances are of the most influential factors on the dynamics and developmental patterns of forest ecosystems and they can be detected using the dendroecological methods. 271 Norway spruce (*Picea abies*) trees within a 12 ha study area in an old-growth spruce forest in the Calimani Mountains, Romania, were cored in order to analyze their radial growth patterns revealing disturbance-induced events such as release from suppression and gap recruitment. All the release events and gap origins detected in the tree-ring records were used for construction of two centuries long disturbance chronologies for individual 1 ha plots and compared with the age structure data. No evidence of stand replacing disturbances was found during the period covered by the investigation. The constructed disturbance chronology indicates that the greater part of the studied forest was affected by a higher-severity canopy disturbance about the year 1845 and that low-severity canopy disturbances occurred randomly at different time intervals in the whole studied area.

**Key words**: Forest dynamics; Norway spruce; Calimani Mountains; Disturbance chronology; Release events, Gap origin

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# 1. Introduction

To follow the path of sustainable forest management it’s necessary to understand the natural processes in forests. Growth, death and replacement are the basic processes of forest dynamics which are very often driven by events called disturbances (*e.g.* PICKETT and WHITE, 1985; OLIVER and LARSON, 1996; FRELICH, 2002). Norway spruce (*Picea abies*) is the dominant tree species in many mountain ranges within temperate Europe and therefore understanding disturbance regimes of spruce forests is the key question for managers of many mountain forest areas, especially nature reserves where ideas of nature-based forest management are applied.

The spruce forest dynamics and disturbance regime have been studied in particular in boreal forests because the area they cover is so vast that many stands not affected by man can be found there (*e.g.*: QUINGHONG *et* HYTTENBORG 1991, KUULUVAINEN 1994, KUULUVAINEN *et al.* 1998, DROBYSHEV 1999, DROBYSHEV 2001, SHULZE *et al.* 2005, DOLEZAL *et al.* 2006). However, only few studies (*e.g.*: CHERUBINI *et al.* 1996, JONÁŠOVÁ *et* PRACH 2004, HOLEKSA *et al.* 2006, SVOBODA *et* POUSKA 2008, KATHKE *et* BRUELHEIDE 2010, SVOBODA *et al.* 2010) focus on this issue within European temperate forests. Such studies can help to solve current management problems related to European mountain spruce forests therefore there still is a need to conduct research particularly in those spruce stands whose dynamics is driven by natural forces and not human activities. The Carpathian mountain spruce forests are considered to be the least human-influenced among Europe (HOLEKSA *et al.* 2006).

While studying disturbance regime in a mountain spruce forest some questions should be answered, *e.g.*: how frequent and severe are the disturbances which have been influencing the forest?; what is the size of a disturbed forest area?; are larger extensive disturbances natural in mountain spruce forests?; how do the disturbances influence the structural and compositional heterogeneity of the forest?; what disturbance agents play the major role in such dynamics?; is it wind, bark beetle, fungi or their combination?; does occurrence of disturbance events differ according to habitat conditions?, *etc.*

This thesis aims to answer some of the above mentioned questions with help of literature survey while the main objective of it is to reconstruct historic patterns of natural disturbance regime of an old-growth spruce forest stand in Calimani Mountains, Romania.

# 2. Literature survey

Some parts of the chapter 2.1. were taken and translated from my bachelor's thesis (REITSCHMIEDOVÁ, 2009).

## 2.1. Natural forest and its dynamics

There are many terms used to describe the level of human intervention in the forest or its absence (KORPEĽ, 1989; VEEN *et al*., 2010).

MÍCHAL (1983) explains the term "natural forest" as the total concept for three states of forest ecosystems with different level of human influence: (1) intact (virgin, pristine or old-growth) stands which weren't influenced by human activities at all; stands influenced in past could be called old-growth only if there are no more visible marks of the intervention, (2) natural stands which are influenced irrelevantly and they keep the species, age and spatial structure very similar to old-growth stands, (3) close to nature stands, that is a wide range of forest stands with more or less natural species composition but spatial and age structure less differentiated than in an old-growth forest. Such stands would spontaneously develop towards an old-growth state without further human intervention.

Natural forest dynamics is influenced primarily by climatic and soil conditions, historical development of a given area, properties of dominant tree species and not least by disturbances (KORPEĽ, 1989; LORIMER and FRELICH, 1989; KUULUVAINEN, 1994; KUULUVAINEN *et al*., 1998). These driving forces create a complex effect that leads to small or large scale differentiation in tree growth stages as well as to development of temporary tree-less stages in the course of spontaneous forest succession (VEEN *et al.*, 2010).

### 2.1.1. Disturbances

PICKETT and WHITE (1985) defined a disturbance as "any relatively discrete event in space and time that disrupts ecosystem, community, or population structure and changes resources, substrate, or the physical environment". Such events strongly control species composition and structure of forest (*e.g.* OLIVER and LARSON, 1996; FRELICH, 2002). SPLECHTNA *et al.* (2005) have pointed out that according to the definition of PICKETT and WHITE (1985) a death of a single tree is also considered to be a disturbance, as it's an event disrupting structure of a forest, no matter what was the cause of the death. Therefore a consideration of the spatial scale is necessary because such a single-tree disturbance may have relevancy at the stand scale but not at the landscape scale. Disturbances are difficult to characterize because the causal factors of them are both endogenous and exogenous, and disturbances differ in size, frequency, intensity[1] and severity[2], as well as in structure that is left after them (PICKETT and WHITE, 1985; OLIVER and LARSON, 1996; TURNER *et al.*, 1998; FRELICH, 2002).

A disturbance regime is a word collocation used to express what types of disturbances and their combinations influence a given forest landscape in time (FRELICH, 2002; SPLECHTNA and GRATZER, 2005).

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[1] FRELICH (2002) describes disturbance intensity as "the amount of energy released by the physical processes" during the event.

[2] Severity is explained by FRELICH (2002) as "the amount of mortality that occurs among tree and plant populations in a disturbed area". It is closely related to intensity since more intense disturbances generally are more severe (TURNER *et al.*, 1998).

#### 2.1.1.1. Disturbance rate

Generally speaking the disturbance rate is dependent on size, intensity, frequency and disturbance interactions, as well as on species composition, health condition, spatial and age structure of the disturbed stand (PICKETT and WHITE, 1985; OLIVER and LARSON, 1996).

Based on the impact of a disturbance, in particular tree and plant populations' mortality in a disturbed area, FRELICH (2002) distinguishes between three types of disturbances: (1) low-severity, during which single trees or small groups of trees are eliminated from the stand, (2) moderate-severity, *e.g.*: windstorms removing the upper canopy but leaving seedlings, and finally (3) high severity disturbance that kills most of the understory and overstory layers. OLIVER and LARSON (1996) use rougher division expressing the amount of removed overstory: major (stand replacing) and minor (*i.e.* those which leave some trees alive) disturbances.

A general rule says that typical representatives of frequently disturbed forest stands are trees younger than in undisturbed areas (PICKETT and WHITE, 1985; FRELICH, 2002).

#### 2.1.1.2. Post-disturbance succession

Species dynamics after a disturbance is a secondary succession involving three main processes: changes in population size, extinction and immigration. Patch turnover of disturbed areas is very high, that means these places change very quickly (KOVÁŘ, 2008).

How will a disturbed stand develop depends on the rate of damage. After a minor disturbance, which leaves some overstory alive, successful regeneration depends on sufficient amount of fertile trees, their regular mast years and suitable soil properties for germination and growth of seedlings as well as on biotic residuals (buried seeds, roots able to reestablish vegetatively, etc.) (KORPEĽ *et al.*, 1991; TURNER *et al.*, 1998). Biotic residuals are low after a stand replacing (major) disturbance therefore the rate of the stand recovery will be slower and distance to seed sources is crucial (TURNER *et al.*, 1998).

Patterns of stand development after a disturbance could be generalized in four stages: (1) Stand initiation stage, during which the released growing space is reoccupied by new plants represented by high number of species; factors as timing of seed arrival, presence of soil-stored seeds or conditions for germination are fundamental for the colonization; the plants able to colonize open sites are often called "pioneer" or early-successional species; (2) Stem exclusion stage, patterned with high competition rate; new individuals can't invade successfully and the established plants with competitive advantage expand into other plants' growing space and eliminate them; (3) Understory reinitiation stage, in which shade tolerant species appear in the forest understory and live under the closed canopy until more light reaches them through some canopy opening caused by exclusion of an overtopping tree; (4) Old growth stage, stands often can't reach this stage due to repeated disturbances but if they do, they have heterogeneous structure caused by the understory trees growing to the overstory and overstory trees dying from various agents (OLIVER and LARSON, 1996).

### 2.1.2. Dynamics of mountain spruce forests

Large-scale disturbances in combination with small-scale gap disturbances are viewed in recent studies (*e.g.*: FISHER *et al.*, 2002; KULAKOWSKI and BEBI, 2004; HOLEKSA *et al.*, 2006) as a natural part of European mountain spruce forest dynamics. These processes strongly contribute to structural heterogeneity of the stands (TURNER *et al.*, 1998; SVOBODA *et al.*, 2010).

KUULUVAINEN (1994) describe the origin of a tree fall gap as an elimination of individual trees or smaller groups of them by small-scale perturbations caused by autogenic (competition) or allogenic factors (wind, snow, mammals, insects or fungi). These events contribute to natural processes as mortality in consequence of senescence or self-thinning of young stands. A "gap" or a "gap phase" and the subsequent regeneration was initially mentioned by WATT (1947) in his study from temperate beech (*Fagus sylvatica*) forests and later it was studied in detail in boreal forests by different authors (*e.g.*: LIU and HYTTEBORN, 1991; KUULUVAINEN, 1994; DROBYSHEV, 1999; VEPAKOMMA, 2008). Since studies focused on processes of gap formation and closure require mature forests with no or negligible human influence, papers about gap dynamics are mostly based on studies from boreal forests. There is just a few of them from European temporal forests (*e.g.*: SPLECHTNA and GRATZER, 2005; KATHKE, 2010). Physical[3] and biological[4] conditions in boreal coniferous forests differ considerably from temperate coniferous forests (KUULUVAINEN, 1994), however, studies from boreal forests provide great source of information about general patterns of gap dynamics.

Under natural conditions, the average age of Norway spruce (*Picea abies*) is 200-300 years, exceptionally up to 600 years (ELLENBERG, 1988; MUSIL and HAMERNÍK, 2007). Spruce trees in a stand usually start to propagate seeds when they are about 60 years old but they become fertile sooner on extreme sites. Mast years repeat every 4-5 years. Production of seeds decreases with altitude and lower annual temperature (MUSIL and HAMERNÍK, 2007; OLIVER and LARSON, 1996). Spruce seeds are equipped with a wing 2-5 times longer than the seed itself therefore they are able to fly dozens of meters (MUSIL and HAMERNÍK, 2007). Production of light seeds modified in favour of wind propagation is characteristic for plants adapted to disturbances (FRELICH, 2002).

An interesting feature of Norway spruce is its ability to partly behave as a pioneer tree species even though it is not natural for it (MUSIL and HAMERNÍK, 2007). Its another important trait is the potency of spruce saplings to survive several decades in suppression (*i.e.* under the closed canopy) and respond to canopy openings with increased growth (MCCARTHY, 2001). The latter mentioned feature of Norway spruce is used for identifying disturbances in the tree-ring record (see the chapter 2.2. Dendrochronology).

Regeneration of spruce is positively linked to the presence of coarse woody debris. Fallen logs and decayed stumps are called ‘nurse logs’ since the major proportion of spruce seedlings and saplings grow on such sites (SVOBODA *et al.*, 2010).

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[3] One of the remarkable differences concerning different physical conditions of boreal and temperate forests is the fact that in boreal forests trees cast long shadows due to low predominant sun, narrow tree crowns and many snags remained standing after death caused by fungal or insect attack. Tree regeneration in gaps isn’t then influenced by availability of light as forth as in temporal forests and gaps provide primarily growing space as well as enhance water and nutrients availability (KUULUVAINEN, 1994).

[4] For example different growth habits of trees should be mentioned: in contrast to trees growing in temperate forests, those of boreal forests have more rigid architecture and fill neighbouring canopy gaps slower (KUULUVAINEN, 1994).

Typical components of natural disturbance regimes driving dynamics of mountain spruce forests are: wind, snow and bark-beetle. The following text doesn't consider anthropogenic disturbances, as clear-cutting, air pollution or soil acidification, because this thesis is focused on natural processes in mountain spruce forests.

All the three above mentioned disturbance agents create canopy gaps, selectively removing trees and thereby making resources available to surviving neighbours but they also can appear as large-scale disturbances killing most of the overstory (TURNER *et al.*, 1998; KULAKOWSKI and BEBI, 2004; HOLEKSA *et al.*, 2006; SVOBODA *et al.*, 2010).

#### 2.1.2.1. Wind

Wind is a natural and common disturbance in mountain spruce forests. Morphology of trees growing on windward slopes and other places exposed to frequent scuds is modified according to the direction and intensity of wind. Branches usually grow in the shape of a flag at the leeward side of a tree and roots are stronger there. Stems exposed to intense wind are thicker and their wood is denser (OLIVER and LARSON, 1996; MUSIL and HAMERNÍK, 2007). Damage risk depends on terrain configuration, stand stability and not least on age, height and health condition of a tree itself. Wind can damage a tree in a three different ways: (1) it can kill it, in mountain spruce forests this generally happens by uprooting the tree (if the ground is frozen or the tree is rotten, the stem usually breaks), (2) it can injure the tree by harming just a part of it, *e.g.*: breaking branches or the tree top, or (3) it can increase the risk of tree-damage during next windstorm by killing or injuring the surrounding trees (OLIVER and LARSON, 1996; FRELICH, 2002; VICENA *et al.*, 2004).

According to studies conducted in the Šumava Mountains (VICENA *et al.*, 2004) even a stabile stand is not able to resist wind velocity higher than 30 $m.s^{-1}$. Repeated wind gusts have the most destructive impact on a forest stand, as they destabilize the edges of the stand and domino effect usually follows. Trees growing on forest stand edges are typically more resistant against wind and they serve as a protection of the rest of the stand therefore their elimination is threatening for inner trees. On the other hand a windstorm can eliminate only the instable individuals and enhance the stability of the rest of the stand for next windstorms (OLIVER and LARSON, 1996). Wind with the same velocity can cause worse damages in wintertime when branches are encumbered with snow than in periods without snow pack (HOLUŠA, 2004). Larger trees are more susceptible to wind damages because (1) larger diameter of their stems decreases their elasticity, (2) their wood is often affected by rottenness and (3) wind velocity is higher in the upper part of the canopy where crowns of larger trees are placed (FRELICH, 2002).

Spruce stands growing in lower altitudes, on long and gradual slopes with quite stable site conditions, bear up against wind disturbances of the same intensity worse than more resistant stands growing on extreme, specific sites (*e.g.*: rocky cliffs and sites close to the timber line (KORPEĽ, 1989).

Windstorms are not only destructive forces but they contribute to successful natural regeneration processes in mountain spruce forests by providing high amounts of dead wood. Branches and logs protect seedlings (especially rowan seedlings) against browsing by hoofed game (JONÁŠOVÁ and PRACH, 2004) and rotten logs provide favourable conditions for growth of spruce seedlings and other trees, as well as shrubs, herbs, ferns and bryophytes (ZIELONKA and PIĄTEK, 2004). Pit-and-mound topography created by windthrows increases the structural complexity of the forest floor and maintains plant diversity (ULANOVA, 2000). Lying wood serves as natural protection against erosion (ŠANTRŮČKOVÁ, 2008). Windthrows can positively influence the soil properties: uprooted trees expose soil surface, it subsequently warms up and that enhances microbial activity enriching forest soil by more organic matter (OLIVER and LARSON, 1996).

There's a strong relationship between windthrows and bark beetle occurrence since wind disturbances create favourable conditions for beetle reproduction (see the chapter below).

### 2.1.2.2. Bark beetle

Spruce bark beetle (*Ips typographus*) is considered to be a major biotic disturbance agent in European spruce forests. Reports of its occurrence have been preserved since the 17th century (SKUHRAVÝ, 2002). Its life cycle is almost entirely bound to *Picea abies* and it usually appears in less dense stands older than 60 years (very suitable are dry and warm localities) where it firstly attacks freshly fallen trees and windthrows as well as weakened trees. Windthrows and snowbreaks create a good source of food for the bark beetle and thus are the most frequent causes of *Ips typographus* outbreaks (JONÁŠOVÁ and PRACH, 2004; LIEUTIER *et al*., 2004; ØKLAND and BJØRNSTAD, 2006).

During a population outbreak it is able to attack healthy trees with help of powerful aggregation pheromones, a specific agent evolved to overcome the protection system of a tree. Males are polygamic; they usually copulate with 2-3 females. Males bite into the phloem, which serves as feed, and bite a nuptial chamber into which they lure females. After copulation females excavate mother galleries in which they lay eggs. One mother gallery usually contains about 50 eggs but this number depends on many factors (*e.g*. the amount of feed). Each hatched larvae feeds on the tree tissue and produces its own larvae gallery near one another. The resulting networks of tracks are called galleries (Figure 2-1.) and they firstly appear just bellow the green part of a crown (SKUHRAVÝ, 2002). The infested tree isn't apparent at first glance but upon closer examination, it has dry, reddish-brown dust in the bark crevices. The ability to develop sudden outbreaks is connected with its high reproduction capability. Hundreds of thousands of beetles can develop in just one tree (SKUHRAVÝ, 2002; ØKLAND and BJØRNSTAD, 2006; LIEUTIER *et al*., 2004). Because beetles must attack healthy trees with higher population density, their multiplication rapidity is reduced to a point when they are not able to maintain the population level any more and it leads to an outbreak decline (LIEUTIER *et al*., 2004).

Figure 2-1. The underside of bark from a *Picea abies* tree shows the tracks of *Ips typographus*. Photo by Markéta Reitschmiedová, 2011.

#### 2.1.2.3. Snow

In comparison with previous two disturbance agents (wind and bark beetle) there hasn't been paid so much attention to processes in forests dynamics driven by snow. However avalanches are often an important force in mountain areas because they can affect dozens to hundreds hectares of a forest landscape. Not only stands by the tree line are endangered because avalanches can appear in lower altitudes too. Most susceptible are steep slopes with scarce or no tree cover and places under these slopes. The most effective protection against avalanche genesis provide stands with dense canopy and stems not further than 25 m from each other (KULAKOWSKI and BEBI, 2004; BEBI *et al.*, 2009). Avalanches, as well as other disturbances, increase landscape heterogeneity and probability of other disturbances' emergence, but they also contribute to soil erosion. The answer of forest stands to this type of disturbance, similarly to windstorms, differs according to height, elasticity and position of every single tree and, of course, according to size, intensity and frequency of the events. If the pressure of an avalanche is high enough, it can cause breakage or uprooting of a tree. The most dangerous are powder snow avalanches because the pressure has effect on the whole tree, including its crown. Small and elastic trees have generally better chance for survival as they often bend and lean against the snow pack under them. Spruce stands often disturbed by avalanches grow slower and are typically shorter with stems of smaller diameter (BEBI *et al.*, 2009). As I mentioned before, when branches are encumbered with snow they are more susceptible to damages by wind (HOLUŠA, 2004).

## 2.2. Dendrochronology

Dendrochronology is the scientific method which utilizes accurate tree-ring dating and measurement to reconstruct past processes and environment. There are many sub-disciplines of dendrochronology as dendroecology, dendroclimatology, dendrohydrology or dendroarcheology (BAILLIE, 1995; RUBINO and MCCARTHY, 2004).

Most of the tree species growing in the temperate zone put on one ring of new wood each year (BAILLIE, 1995), but the growth rate of each stem is subject to different influences as climate, site conditions, competition or other intra- and interspecific interactions, etc. (HENRY and SWAN, 1974).

### 2.2.1. Dendroecological methods used to assess disturbance events

The sub-field of dendroecology involves the use of dendrochronological methods to gain more information about ecological phenomena, such as forest stand dynamics. To understand the interactions of a tree or a forest stand and its environment a number of techniques have been developed (HENRY and SWAN, 1974; LORIMER and FRELICH, 1989; D'AMATO and ORWIG, 2008). With respect to the aim of this thesis, the following text is focused on those dendroecological methods that are used for identifying disturbances in the tree-ring record.

Data on stand age structure can help us to determine dates of stand-replacing disturbances but this is appropriate only in areas with predominant even-aged stands. For uneven-aged stands of shade-tolerant tree species some other data should also be used since disturbance is not a precondition for germination of such species (LORIMER and FRELICH, 1989). Combination of stand age structure data with a good knowledge of the studied area could serve as a valuable predisposition for indication of stand disturbance history based on dendroecological analysis (BLACK and ABRAMS, 2003).

For temperate zone forests FRELICH (2002) considers tree-ring evidence to be a universal tool for fine resolution of temporal and spatial disturbance processes. Other methods, as fossil evidence, historical records or constructing succession model based on tree gaps analysis, can be used to investigate stand history but they have their limitations.

Growth releases identification is one of the most essential dendroecological approaches for reconstructing and evaluating disturbance history of a stand (LORIMER and FRELICH, 1989; FRELICH, 2002; BLACK and ABRAMS, 2003). It gives us the possibility to identify a disturbance occurred in the stand with an accuracy of a few years (MOTTA *et al.*, 1999). However, FRAVER and WHITE (2005) mention numerous obstacles connected with growth releases detection: (1) effects of weather have to be filtered out since radial growth of trees varies with temperature and precipitation, (2) different tree species have dissimilar pattern of disturbance-related response; age, diameter and prior growth rate are also significant factors worth consideration, (3) type, magnitude, and duration of the disturbance strongly influence a tree's response.

There are many release-detection methods applied in order to reconstruct historical disturbances. The great variety of them is caused by obstacles noticed above. Visual assessment of radial-growth releases was a widely used method earlier but recently it is rarely applied and if it is, a good knowledge of the autecology, sensitivity, and range of growth anomalies expected for a given species is necessary (RUBINO and MCCARTHY, 2004; FRAVER and WHITE, 2005). HENRY and SWAN (1974) used for the first time method of release detection based on the percent-increase of tree-rings radial growth. They examined cores, taken from different tree species growing on the 8.1 ha plot established in an old-growth forest of south-western New Hampshire, for major suppressions or releases in growth. Each recorded release and suppression had to be noticeable in at least four consecutive tree-rings. Release had to exceed the previous rate 2.5 times or more whereas decrease of 0.4 or less of the previous rate was recorded as suppression. This new method of reconstructing forest history was successfully introduced and, as FRAVER and WHITE (2005) present, is currently the most widely used one.

The following text aims to provide a brief overview of the most commonly used dendroecological techniques with respect to historical reconstruction of disturbance regimes.

#### 2.2.1.1. Release events

Each individual of any tree species growing in suitable conditions will increase in size until one or more factors necessary for growth becomes limiting, it is killed by an exogenous force or dies of senescence. If there is a lack of sunlight, nutrients, water, carbon dioxide, oxygen or there are not suitable temperatures, the tree dies or its growth rate decreases. Due to competition for growing space often linked to competition for resources some individuals have an advantage and those which don't, become suppressed (OLIVER and LARSON, 1996). Suppressed saplings of shade tolerant tree-species able to germinate and grow in the understory are a typical phenomenon of many forests (PICKETT and WHITE, 1985). A release from suppression occurs after removal of one or more overtopping canopy trees. When the solar radiation reaches the forest floor the previously suppressed tree responds with an extraordinary, swift and sustained increase in radial growth. Moreover, such reaction could be observed among overstory trees when one or more closest competing individuals are eliminated (FRELICH, 2002), but as LORIMER and FRELICH (1989) explain, the understory trees typically show much greater disturbance-induced increases in growth since the overstory trees grow in better light conditions and the difference in growth before and after the release isn't so obvious. Some methods take this fact into account, identify the canopy accession[5] date and then apply different criteria to the understory and overstory phases of the tree (BLACK and ABRAMS, 2003). For suppressed shade-tolerant species a small-scale disturbance is a great, and sometimes the only, opportunity to attain canopy status (LORIMER and FRELICH, 1989; D'AMATO and ORWIG, 2008).

#### 2.2.1.2. Criteria for release identification

There's a wide range of release criteria in the literature. A very important one is a minimum growth-change threshold criterion. It must be defined in order to identify a release event in tree-ring series. Such threshold has to be sensitive enough to discern growth responses induced by disturbances of old trees (NOWACKI and ABRAMS, 1997).

Nowadays scientists use their own criteria tailored to the particular forest types, in contrast to former methodologies that used fixed thresholds (LORIMER and FRELICH, 1989; BLACK and ABRAMS, 2003; SPLECHTNA *et al.*, 2005). An example of forest-type-specific criteria can provide the methodology proposed by LORIMER and FRELICH (1989) for developing a disturbance chronology from tree-ring data obtained in dense temperate forest stands. This method, considering canopy accession dates of existing trees to be the basis

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[5] In this thesis canopy is considered to be the sum of all trees' foliage exposed to direct sunlight, including small trees in gaps (sensu Lorimer and Frelich, 1989). Therefore the canopy accession date means the time when an understory tree was released from supression by gap formation or a seedling grew in an existing gap.

for disturbance chronology construction, defines a release as an average growth increase of at least 50% and more. Another example might be the method designed again in dense temperate forest stands of North America and proposed by NOWACKI and ABRAMS (1997) that uses 25 % as the minimum growth-response threshold. The latter mentioned authors argued that using higher threshold as release criteria caused researchers to miss disturbance-related releases in older or canopy trees due to the fact that such trees respond for shorter periods at lower magnitudes. Moderate and major releases are often distinguished from each other. In the case of the above mentioned methodology proposed by LORIMER and FRELICH (1989) a moderate release is the one which is equal to or exceeds 50% and simultaneously doesn't extravagate 100%, while a major release must be equal to or exceed 100%. As another example can serve one of the methods used in the study of BLACK and ABRAMS (2003), in which we find the definition of a moderate and major release as any change in growth exceeding the threshold of 25 and 50%, respectively.

Another aspect of a release is the time span in which it occurs. According to FRELICH (2002) the increase in growth must be explicit for at least 15 years to screen out short-period climatic effects. This criterion is used in several studies but in some other ones the time span is slightly adjusted to fulfil the specific aim of the study (BLACK and ABRAMS, 2003). FRELICH (2002) also highlights 15 years of slow growth as a pre-release criterion.

#### 2.2.1.3. Radial-growth averaging

For the purpose of this thesis the radial-growth averaging technique *sensu* NOWACKI and ABRAMS (1997) was used to derive releases and consequently past canopy disturbances from the tree-ring data. NOWACKI and ABRAMS (1997) introduced the value %GC (percent growth change) which shows the change in average annual increment between preceding and subsequent time spans with a length of ten years. It can be expressed numerically by the %GC formula = ((M2-M1) / M1) * 100, where M1 represents the average annual ring width over the previous 10 years, and M2 is the average width of annual rings per decade following the year for which the calculation is performed. A plot showing %GC and the minimum established threshold is constructed after calculating this value for the tree-rings in the series. As I have already mentioned in the previous chapter, they used 25% as a minimum threshold for detecting a release to reflect growth responses induced by canopy disturbances. NOWACKI and ABRAMS (1997) developed this technique while studying tree-ring chronologies in mixed-oak forests but as they present it can be used in much wider range of forest types.

#### 2.2.1.4. Boundary line

BLACK and ABRAMS (2003) came up with a boundary-line method which is considered more precise than expressing a release as a percentage of post-disturbance growth exceeding a given threshold (FRAVER and WHITE, 2005). For their study BLACK and ABRAMS (2003) had chosen an old-growth hemlock forest in central Pennsylvania with a view to evaluate past disturbance regimes. They redefined release criteria using prior growth rates for prediction of maximum possible growth response to canopy openings. The construction of a boundary line leads to a negative exponential curve representing the species-specific threshold for defining releases. The growth values from the tree-ring series are then compared with the curve and those events falling within 20–100% of the boundary are considered to be releases.

The boundary line doesn't have to be only species-specific but even stand-specific criterion for evaluation of releases since it depends on prior growth rates and percent growth change of the trees sampled from the stand. This fact gives the approach a high level of flexibility and precision (BLACK and ABRAMS, 2003; BLACK and ABRAMS, 2004). However, for comparisons of disturbance histories among multiple stands application of a universal boundary line for a given species is acceptable (BLACK and ABRAMS, 2003).

#### 2.2.1.5. Cross-dating

Cross-dating is a very important procedure in dendrochronological studies that makes it possible to obtain absolutely dated tree-ring chronologies (TESSIER *et al.*, 1997). For studies focused on reconstruction of stand disturbance history it is fundamental to point out the factual years of annual rings formation. Extreme growth conditions are quite rare and reflected in the ring-width patterns, and therefore usable for cross-dating. According to the occurrence of wider or narrower tree-rings, we can deduce the extreme conditions and these tree-rings of significantly bigger or smaller dimension are of great importance for potential linkages (YAMAGUCHI, 1990, SCHWEINGRUBER *et al.*, 1990). SCHWEINGRUBER *et al.* (1990) began to use the term “a pointer year” for the calendar years in which the width of tree-rings varies significantly from other years. The pointer years are used for creating the summation of conspicuous cross-dated rings of more tree-ring series and thus for feedback control for possible counting errors or errors brought about by absent or false rings (YAMAGUCHI, 1990, SCHWEINGRUBER *et al.*, 1990). However, the identification of pointer years was used much earlier in the graphical method called skeleton plotting (DOUGLASS, 1939) as well as in several other methods developed since then. YAMAGUCHI (1990) proposes a quick and simple visual method for cross-dating of increment cores obtained from living trees. By assigning exact calendar years to narrow tree-rings (so called marker rings) it is possible to create an exact chronology against which difficult cores can be dated.

Nowadays there are many computer-based tools used in the field of dendrochronology. For instance the department of Lamont-Doherty Earth Observatory at Colombia University called Tree-Ring Lab offers a commonly used program COFECHA which serves for a tree-ring chronology quality control analysis. It can be found at their web page http://www.ldeo.columbia.edu/res/fac/trl/public/publicSoftware.html, as well as many other programmes for dendrochronoligical analysis, and is free of charge.

However, BUNN (2010) notes that successful cross-dating is primarily dependent on the experience of the analyst and his correct judgement. He warns against displacement of an experienced dendrochronologist by statistical programs because human expertise is not replaceable by a computer. Computer-based tools are a welcome aid in cross-dating, but should serve only as an additional technique.

#### 2.2.1.6. Analysis of early growth rates

Some trees don't show any release from suppression due to their origin in a canopy gap (FRELICH, 2002). COATES (2002) studied many tree species' regeneration over a wide range of gap sizes in Canadian mixed temperate and as he presents the regeneration was abundant. If conditions are suitable, the tree individuals grow further, until they achieve the overstory level of trees. However, even the seedlings that won't be suppressed during their lifetime may be delayed in reaching the upper layers of canopy due to gradual release of growing space and resources, (especially light) under trees that died and remained standing, *e.g.* after a bark beetle attack (RENTCH *et al.*, 2010).

Objective methods for classifying so called gap origin trees have been developed and one of the most commonly used was proposed by LORIMER *et al.* (1988). It allows us to determine the gap status of a tree even though it is already mature. The technique is based on growth averaging over five consecutive years at 4 cm DBH and comparing this mean radial growth value with value obtained in the same way from samples of samplings from the open and closed canopy.

# 3. Methods

## 3.1. Study area

The Carpathians are of great value for research on mountain spruce forest dynamics since there still are extensive remnants of old-growth spruce forests. Grazing and forestry has apparently influenced forests in other European mountains (CHERUBINI *et al.*, 1996; BIRIS and VEEN, 2005; HOLEKSA *et al.*, 2006).

The study was conducted in the Calimani Mountains, the highest volcanic complex of the Romanian Carpathians. The chosen location is a part of the Calimani National Park and is quite inaccessible due to steep slopes so it can be assumed that the dynamics of the forest results from natural processes with very low anthropogenic influence.

During an inventory of virgin forests in Romania, conducted in the period 2001-2004 by the Royal Dutch Society for Nature Conservation in co-operation with Romanian Forest Research and Management Institute (BIRIS and VEEN, 2005), were the forests in the Calimani Mountains classified as virgin spruce (*Picea abies*) forests. However, there was a sulphur mine close to our study site active between 1972 and 1992. According to POPA and KERN (2009) were the main effects on the surrounding forest ecosystems: (1) dust pollution and (2) nitrogen deposition. Sulphur emissions were negligible as the sulphur extraction from the ore was not carried out on site.

There occur two important weather phenomena in these mountains with heterogeneous relief: (1) Foehn wind and (2) a temperature inversion which favours development of forest vegetation at higher altitudes. The timberline altitude is about 1780 m and the tree line is up to 1860 m (POPA and KERN, 2009; CENUŞĂ, 2010). Average annual temperature varies from 2.4 to 4.0 °C. The annual amount of precipitation is highly variable, between 580 and 1650 mm, the richest month is July (200 mm) and the poorest is November (33.5 mm). Snow lies in the Calimani Mountains for 139-208 days, and the contribution of precipitation from snow is between 97 and 502 mm. In this massif, the height and duration of snow cover plays a vital role in maintaining and developing population of *Pinus cembra*, which has a metabolism adapted to short growing season (CENUŞĂ, 2010).

Dominant soils in the whole study area were described during the terrain survey as Albic and Entic Podzols that create a multifarious mosaic in each plot. Cambisols occur very rarely at lower altitudes. Stony and exposed sites are represented by Lithic, Hyperskeletic or other Leptosols. At wet, mostly by lateral water runoff influenced sites, typically Stagnosols, seldom Gleysols occur.

As found during the field research, the tree layer of the studied forest is composed of *Picea abies* rarely accompanied by *Pinus cembra* and *Sorbus aucuparia*. The understory comprises *Vaccinium myrtillus*, *Calamagrostis villosa*, *Luzula sylvatica*, *Avenella flexuosa* and *Rubus idaeus*.

## 3.2. Research plots

A grid of forty 1 ha plots (100 x 100 m) was established and twelve of them were used for the purpose of this thesis. The altitude of these twelve plots ranges from 1565 to 1636 m. A sub-plot of circular shape with 30 m in diameter was randomly placed in each plot avoiding stream corridors and larger groups of rocks.

| Plot | Sub-plot centre elevation (m a.s.l.) | Sub-plot centre coordinates | |
|---|---|---|---|
| | | Latitude | Longitude |
| 2 | 1586 | 47°15’28.20" N | 25°06’45.63" E |
| 3 | 1582 | 47°15’23.18" N | 25°06’45.09" E |
| 4 | 1577 | 47°15’18.14" N | 25°06’46.45" E |
| 5 | 1607 | 47°15’29.25" N | 25°06’49.20" E |
| 9 | 1590 | 47°15’23.48" N | 25°06’48.37" E |
| 10 | 1617 | 47°15’17.87" N | 25°06’49.14" E |
| 11 | 1625 | 47°15’28.59" N | 25°06’52.77" E |
| 12 | 1636 | 47°15’23.70" N | 25°06’52.34" E |
| 19 | 1590 | 47°15’19.06" N | 25°06’52.38" E |
| 20 | 1610 | 47°15’29.38" N | 25°06’55.60" E |
| 21 | 1610 | 47°15’24.23" N | 25°06’55.61" E |
| 22 | 1630 | 47°15’19.75" N | 25°06’54.83" E |

Table 3-1. Elevation and geographic coordinates of the sub-plot centres. Data were obtained from a GPS unit.

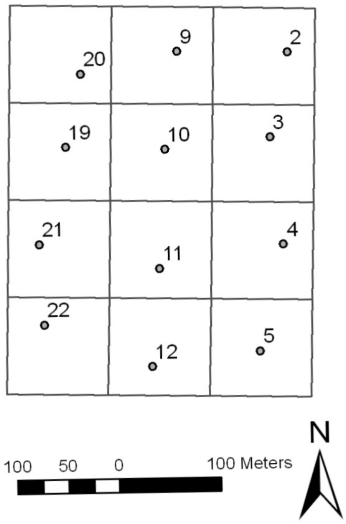

Figure 3-1. Grid of 12 plots used for the purpose of this thesis

## 3.3. Data collection

### 3.3.1. Sampling and core processing

Within each sub-plot every living and dead tree with diameter at breast height (DBH) ≥ 5 cm was identified, labelled with a number and its DBH was measured and recorded. Microsite type was defined and recorded for each tree individual. Three microsites were distinguished: (1) dead wood, (2) pit and (3) mound. Any other microsite wasn't specified and was recorded as "other".

15 – 25 randomly selected non-suppressed canopy trees (i.e. trees that were not overtopped by other trees) were cored at 1 m height. The number of cored trees on the sub-plot varied according to the level of stand heterogeneity: if the stand seemed homogenous, fewer trees were sampled and vice versa. Sampling was conducted from that side, which was perpendicular to the slope fall line. In the case there was no slope, the core was extracted on the side where the tree appeared to have the largest increment. If the crown was asymmetric, the tree was cored on the side of the densest part of the crown. A total of 217 cores were obtained from the 12 sub-plots. Surrounding of each sub-plot was explored and 3-6 more cores were extracted from old trees within the same one hectare plot as the sub-plot. The choice was subjective with the aim to find the oldest trees within the particular plot. The cores from these trees were meant to serve as reference samples for identifying potential disturbance events.

Altogether 271 samples were obtained in the whole research area and used for the purpose of this thesis. Pith was reached in 84 % of the samples, while the remaining 16 % were less than 8 mm from the pith. When an incomplete core was excluded, *i.e.* it was too rotten to distinguish tree-rings, the closest tree of the same or similar DBH and height was chosen. The cores were then transported to the Czech Republic in straws, air-dried, stuck onto a grooved wooden holder, shaved with a razor blade to prepare a flat surface with well visible tree-rings.

### 3.3.2. Natural regeneration

Natural regeneration was measured within each sub-plot by recording seedlings of all tree species and dividing them into 3 height categories: (1) 0.5 – 1.3 m, (2) 1.3 – 2.5 m and (3) > 2.5 m of DBH ≤ 5 cm. Four microsites were distinguished: (1) dead wood, (2) pit, (3) mound and (4) other.

### 3.4. Data analysis

Diameter size class distribution for all the sub-plots was prepared based on the recorded diameters of all the living trees with DBH ≥ 5 cm rooted in the particular sub-plot.

Rings of the cores were counted from pith to bark and their widths measured with 0.01 mm accuracy using TimeTable sliding-stage connected with a computer programme TSAP-Win™. Estimation of the distance to the pith based on average growth of five innermost tree-rings (DUNCAN, 1989) solved the absence of pith in the 16 % of cores. The cores were then visually cross-dated using the marker year approach, to ensure against counting error, or errors caused by missing or false rings (YAMAGUCHI, 1991). Identification of atypical rings and assigning them with a factual year was then confirmed using the program COFECHA (for further information see the chapter 2.2.5. Cross-dating).

The year at which each tree reached coring height was placed in 10-years periods (i.e. 1931–1940, 1941–1950, *etc.*) to reconstruct the recruitment history at each sub-plot and at the whole study area.

#### 3.4.1. Disturbance chronology

To describe the frequency and severity of past disturbances that occurred in the studied area a disturbance chronology compiled of all detected releases and gap origins was constructed for each study plot as well as for the whole study area (SPLECHTNA and GRATZER, 2005; SPLECHTNA *et al.*, 2005). The reference samples were plotted separately. The length of each study area's disturbance chronology was truncated when the number of living trees dropped below 15% since these data are of low informative value and would be misguiding (FRAVER *et al.* 2009). Each disturbance chronology was compared with the age structure of recruitment to 1 meter of height

The disturbance chronology is relatively expressed since it takes into account the number of trees from which the analysis is made (so called sampling depth).

#### 3.4.1.1. Determination of releases from suppression

To identify releases from suppression, a novel approach of NOWACKI and ABRAMS (1997) was used. This radial growth averaging technique enhances detection of abrupt and sustained radial-growth increases that have to extend over 10 years time span. Such criterion was chosen because it is sufficient to distinguish disturbance-induced growth responses of older trees and is effective in neutralizing short-term growth trends associated with climate, such as drought. The minimum threshold for disturbance recognition was determined to be large enough to screen out the "false" growth responses induced by side light that don't directly represent a gap-forming event (FRELICH, 2002). Therefore increases in ring width exceeding 50% were recorded as moderate releases while exceeding the 100% threshold indicated a major release (Figure 3-2.). The same thresholds were used in the study of MOTTA *et al.* (1999) focused on structure and stand development of three mountain spruce forests in Italy.

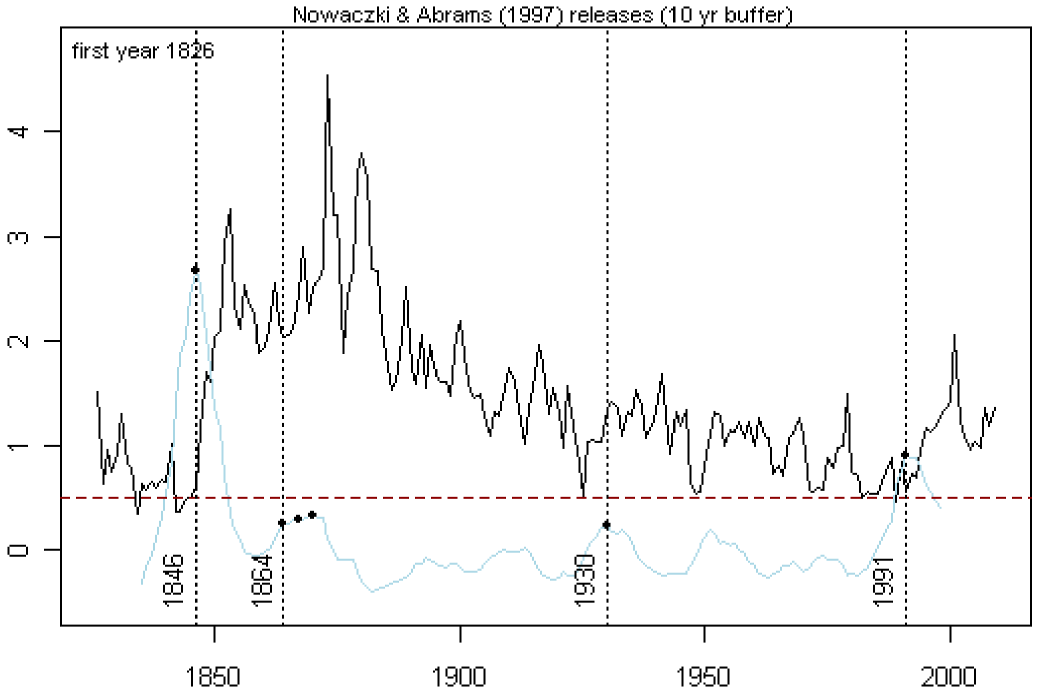

Figure 3-2. An example of a major release detected in the year 1846 and a moderate release detected in the year 1991. This graph expressing the radial increment in time of one of the old trees sampled in the vicinity of the sub-plot n. 21 was created with help of R Statistical Software.

### 3.4.1.2. Analysis of early growth rates

In many cases trees show no releases from suppression in their early growth rates because they were already in a gap at the time of the earliest ring on their increment core. Such information regarding a tree's past location relative to openings in the canopy is useful for reconstruction of the past forest structure and disturbance chronology, respectively (FRELICH, 2002). To determine the gap status of a tree at the time it was a sapling, a method proposed by LORIMER *et al.* (1988) was applied. Based on averaging and subsequent comparison of 5-year radial growth rates (starting at the point where the DBH of the tree was 4 cm) obtained from tree-ring data of existing samplings growing in gaps and in the understory, a gap origin criterion is derived for the particular site (LORIMER *et al.*, 1988; LORIMER and FRELICH, 1989; FRELICH, 2002).

The criterion for gap origin, derived from comparison of early growth rates of young trees growing under the open and closed canopy in the Calimani Mountains, was defined as 0.9 mm. The value was estimated based on intersection of upper and lower percentiles of growth rate distributions. Every tree exceeding this threshold with its mean early growth rate was considered a gap-originated.

### 3.4.1.3. Growth trends

If there wasn't evident a period of suppression with a subsequent release in the sample or the sampled tree didn't originate in a gap, it was evaluated using the so-called growth trend. Ambiguous or irregular radial increment patterns (Figure 3-3.) were excluded from further analysis while declining, nearly flat or parabolic radial increment patterns (Figure 3-4.) indicated a gap origin (LORIMER and FRELICH, 1989; FRELICH, 2002; D'AMATO and ORWIG, 2008).

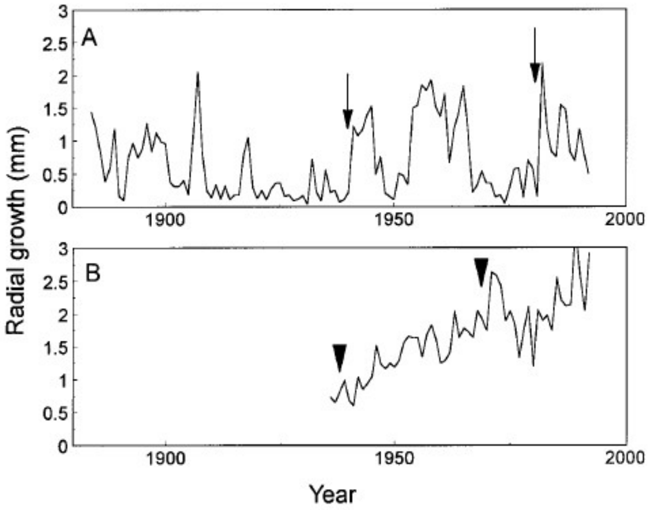

Figure 3-3. Exemplar radial increment patterns of irregular (A) and ambiguous (B) growth, taken from FRELICH (2002). Irregular patterns could be caused for instance by cycles of release and overtopping by injury and subsequent gradual recovery; such events are indicated by pointers in (A) while in (B) the triangles delimit the ambiguous zone.

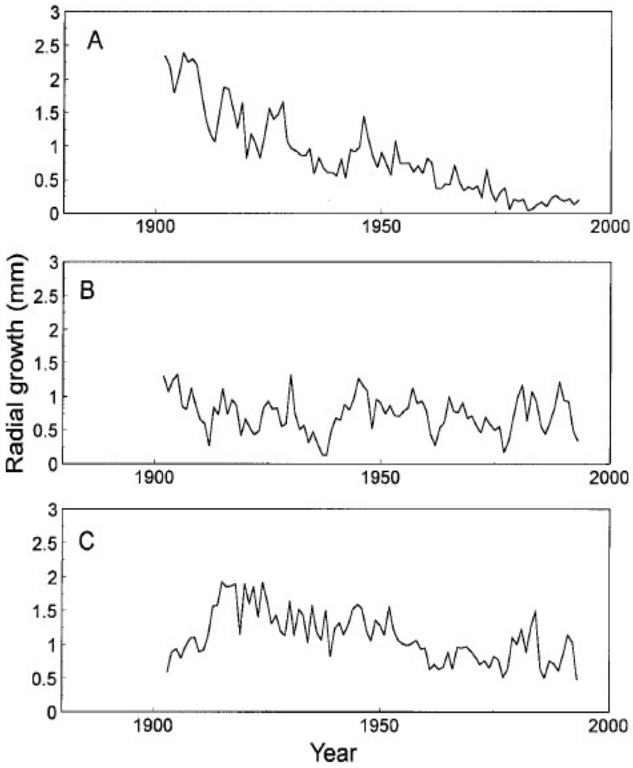

Figure 3-4. Exemplar radial increment patterns: declining (A), nearly flat (B) and parabolic (C), taken from FRELICH (2002).

# 4. Results

## 4.1. Structure of the forest

The forest structure is described based on the data gathered within the 12 sub-plots.

### 4.1.1. Trees with a DBH ≥ 5 cm

A total of 390 living and 181 dead trees with a DBH ≥ 5 cm were counted in the investigation area (12 ha). The total basal area of living trees was 38.73 $m^2$ per hectare whilst the total basal area of dead trees was 5.65 $m^2$ per hectare. At the time the research was conducted, the approximate ratio of number of living to dead trees with a DBH ≥ 5 cm in the whole study area was 2:1 while the total basal area of living trees was nearly 7 times higher than the one of dead trees. Absolutely dominant tree species was *Picea abies*, there were only 5 living individuals of *Sorbus aucuparia* (4 of them were found on the plot 19 and 1 was rooted on the plot 20) and 22 living individuals of *Pinus cembra* (again found only on the plots 19 and 20). DBH class distribution is presented only for all living *Picea abies* trees because none of the cores from *Sorbus aucuparia* or *Pinus cembra* were used for the purpose of this thesis.

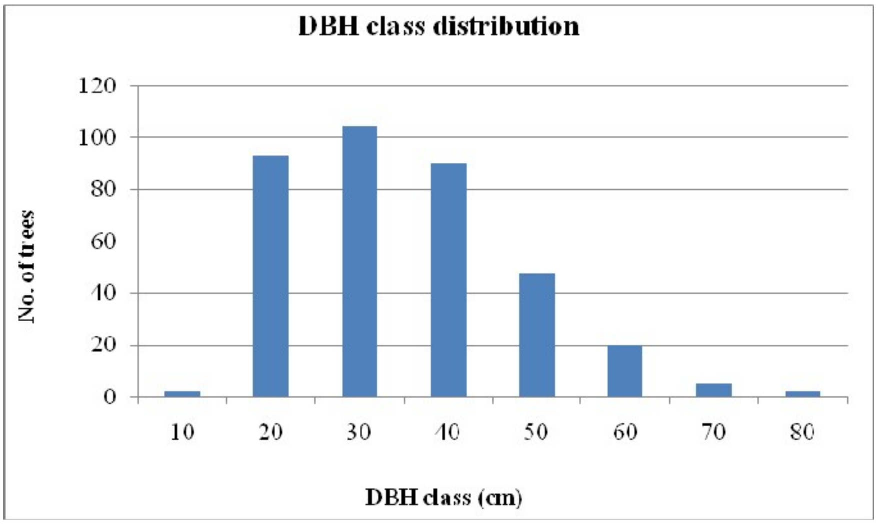

Figure 4-1. DBH class distribution of all living *Picea abies* trees recorded within the 12 sub-plots.

For a better understanding of the DBH structure among the sub-plots, the Table 4-1. shows more detailed numbers for individual sub-plots recalculated per 1 hectare. The dead trees characteristics are included in the table as well with the aim of comparison with the living trees characteristics.

| **Plot number** | | **Number of trees per ha** | **Stand basal area (m² per ha)** | **Maximum DBH (cm)** | **Average DBH (cm)** |
|---|---|---|---|---|---|
| **2** | Living | 481 | 49.26 | 62.5 | 34.4 |
| | Dead | 368 | 11.81 | 65.0 | 16.0 |
| **3** | Living | 396 | 58.44 | 71.5 | 40.7 |
| | Dead | 212 | 10.91 | 53.0 | 21.3 |
| **4** | Living | 495 | 58.03 | 55.5 | 36.7 |
| | Dead | 156 | 4.49 | 36.0 | 16.5 |
| **5** | Living | 622 | 51.25 | 51.5 | 30.8 |
| | Dead | 283 | 6.65 | 31.5 | 15.7 |
| **9** | Living | 382 | 40.83 | 61.5 | 35.1 |
| | Dead | 99 | 1.15 | 20.0 | 11.2 |
| **10** | Living | 198 | 11.18 | 42.5 | 25.5 |
| | Dead | 28 | 0.26 | 13.5 | 10.5 |
| **11** | Living | 594 | 38.10 | 54.0 | 26.0 |
| | Dead | 340 | 5.62 | 33.0 | 12.5 |
| **12** | Living | 354 | 28.52 | 52.0 | 29.9 |
| | Dead | 255 | 6.21 | 45.0 | 13.7 |
| **19** | Living | 792 | 39.88 | 42.0 | 24.0 |
| | Dead | 396 | 3.49 | 20.0 | 9.8 |
| **20** | Living | 292 | 38.83 | 56.5 | 22.6 |
| | Dead | 241 | 2.04 | 21.0 | 9.6 |
| **21** | Living | 184 | 21.68 | 55.0 | 38.0 |
| | Dead | 170 | 15.02 | 66.0 | 30.0 |
| **22** | Living | 226 | 28.78 | 65.5 | 38.3 |
| | Dead | 14 | 0.15 | 11.5 | 11.5 |

Table 4-1. The number and basic characteristics of living and dead trees on individual plots. The number of trees and stand basal area were recalculated per hectare.

A total of 217 trees from the 12 sub-plots were successfully aged, and are reported as ages at a coring height of 1 m above ground. The oldest tree from all the 12 sub-plots (and simultaneously the oldest tree sampled in the whole research area) was found on the plot 3 and it reached coring height in 1724, while the youngest tree with DBH ≥ 5 cm reached that height in 1990 and was rooted in the plot 22. The age class distribution along the timeline will be displayed, compared with the disturbance chronology and discussed later.

### 4.1.2. Seedlings and saplings with a DBH ≤ 5 cm

There was no regeneration of height ≥ 0.5 m found on the plots 2, 3 and 4. Norway spruce (*Picea abies*) was the only tree species regenerating on the 9 remaining plots. For the majority of seedlings and saplings recorded (91 individuals), no particular microsite was specified while 19 individuals grew on dead wood, 17 grew on a mound, and none was recruited in a pit. Table 4-2. shows the density of seedlings and saplings among each type of recorded microsites recalculated to number of individuals per 1 hectare. The pit microsite was excluded from the Table 4-2. since no regeneration was found there.

Figure 4-2. An example of seedlings growing on a decaying log. Photo by Miroslav Svoboda, 2010.

|  |  | Height (DBH) class |  |  |
|---|---|---|---|---|
| **Plot number** | **Microsite** | **0,5-1,3 m** | **1,3-2,5 m** | **> 2,5 m (≤ 5 cm)** |
| 5 | dead wood | - | - | - |
|  | mound | - | - | - |
|  | other | 184 | 57 | 57 |
| 9 | dead wood | 28 | 28 | - |
|  | mound | 14 | 28 | - |
|  | other | 42 | 28 | - |
| 10 | dead wood | 99 | 28 | - |
|  | mound | 57 | - | 14 |
|  | other | 198 | 156 | 42 |
| 11 | dead wood | - | - | - |
|  | mound | 28 | 28 | - |
|  | other | - | 28 | 28 |
| 12 | dead wood | - | - | - |
|  | mound | - | 28 | - |
|  | other | 57 | 184 | 42 |
| 19 | dead wood | - | - | - |
|  | mound | 14 | - | - |
|  | other | 14 | - | - |
| 20 | dead wood | 14 | 42 | - |
|  | mound | - | - | - |
|  | other | 42 | - | - |
| 21 | dead wood | 14 | - | - |
|  | mound | - | - | - |
|  | other | 42 | - | 14 |
| 22 | dead wood | - | 28 | - |
|  | mound | 28 | - | - |
|  | other | 14 | 42 | 14 |

Table 4-2. Regeneration density (individuals per ha) on the research plots.

## 4.2. Disturbance chronologies

Disturbance events were detected within every single sub-plot and also the additional trees, sampled in the vicinity of each sub-plot, revealed evidence of disturbance events.

The disturbance chronologies are presented for all the sub-plots together, compared with the reference samples and then the chronologies of individual sub-plots are displayed and commented in groups based on the similar patterns.

As mentioned before, the oldest tree from all the 12 sub-plots (and simultaneously the oldest tree sampled in the whole research area) was found on the plot 3 and reached the height of 1 m 286 years ago. Due to this fact it was possible to construct the disturbance chronologies for less than 3 centuries but finally they were truncated to less than 2 centuries because the bars expressing gap recruitment or release events with sampling depth lower than 15% of the total number of trees were excluded from all the chronologies since they are of low informative value and might be misguiding (FRAVER *et al.* 2009).

### 4.2.1. Summary of the 12 sub-plots

Of the 217 trees sampled in the 12 sub-plots, 120 individuals (47 % of the trees analyzed within all sub-plots) showed one or more release events, namely 58 moderate and 44 major release events were detected. More than one release was detected only for 14 trees. Rapid early growth rates exceeding the 0.9 mm threshold were identified for 180 trees (83 % of the trees analyzed within all sub-plots) and another 11 trees' radial growth patterns indicated gap recruitment thus all together 191 individuals were considered to be gap recruited. As already mentioned in the methods, all the gap recruitment and release events are included in the disturbance chronology displayed in the Figure 4-3. below. 4 cores were excluded from the analysis since they showed neither gap origin nor any single release and their growth pattern was ambiguous or irregular.

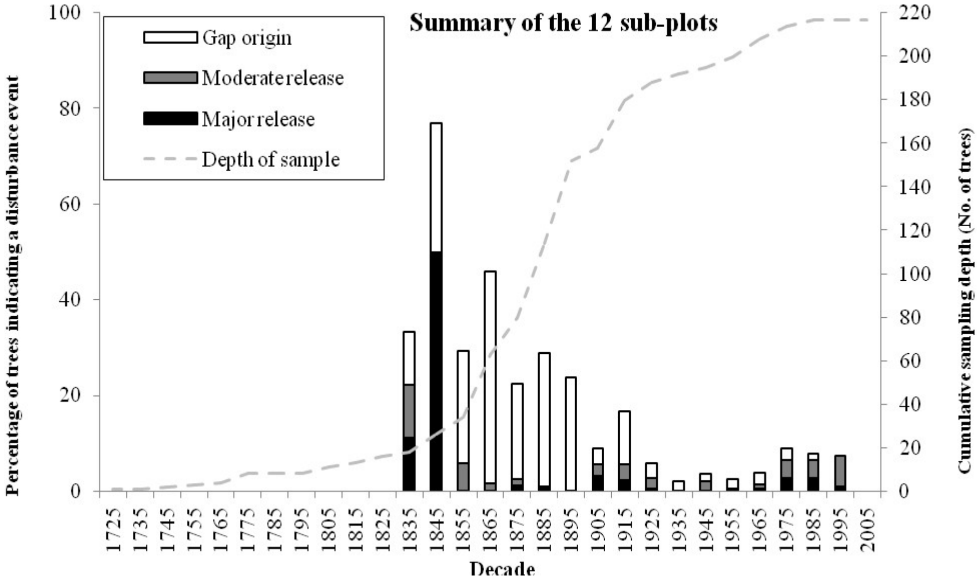

Figure 4-3. Disturbance chronology based on all release and gap-recruitment events in each decade for the whole study area (12 ha).

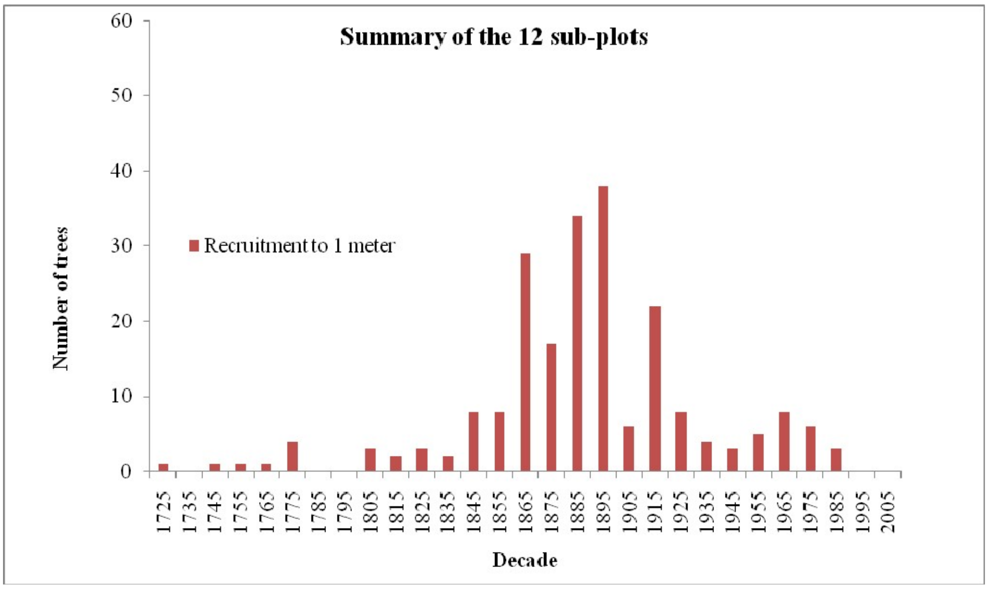

Figure 4-4. Recruitment to 1 m age structure for the whole study area (12 ha).

As shown in Figure 4-3., there is one distinct peak of major releases from suppression indicated in the study area. If we take into account the number of samples included in the analysis, the acme of designated release events is located between the years 1840 and 1849. The occurrence of releases from suppression is promptly followed by massive gap recruitment lasting over 6 decades. Releases slightly increased again during the beginning of the 20th century after a period of no or very low release frequency that had lasted for 5 decades. Considering the sample depth, another minor increase of release events occurred from 1970 to 1999.

For comparison with the disturbance chronology displayed above, Figure 4-4. shows the frequency of recruitment to 1 meter of height along the timeline for all the trees cored in the 12 sub-plots.

Occurrence of the period of massive gap recruitment following the previously commented peak of releases is supported by what is shown in the Figure 4-4.: The majority of sampled trees were recruited to 1 meter of height during the period of approximately 100 years, the recruitment was gradually increasing since 1840 for two decades with subsequent surge about 1860, persisting with more or less high intensity to 1929 and dropping to lower number for 3 decades since then.

### 4.2.2. Summary of the reference samples

The same type of disturbance chronology and the frequency of recruitment to 1 m of height along the timeline will be displayed for all the reference samples to be compared with the graph constructed for all the sub-plots. All 54 reference samples were successfully aged, and are reported as ages at a coring height of 1 m above ground. All of them were used for the construction of both chronology and age class distribution, none was excluded. Overall, 24 major and 22 moderate releases were detected from these samples. Only 8 trees were released from suppression more than once. Most of these trees sampled in the vicinity of each sub-plot were of a gap origin, namely 47 individuals (87%) and again, all of the releases and gap origins are considered in the Figure 4-4.

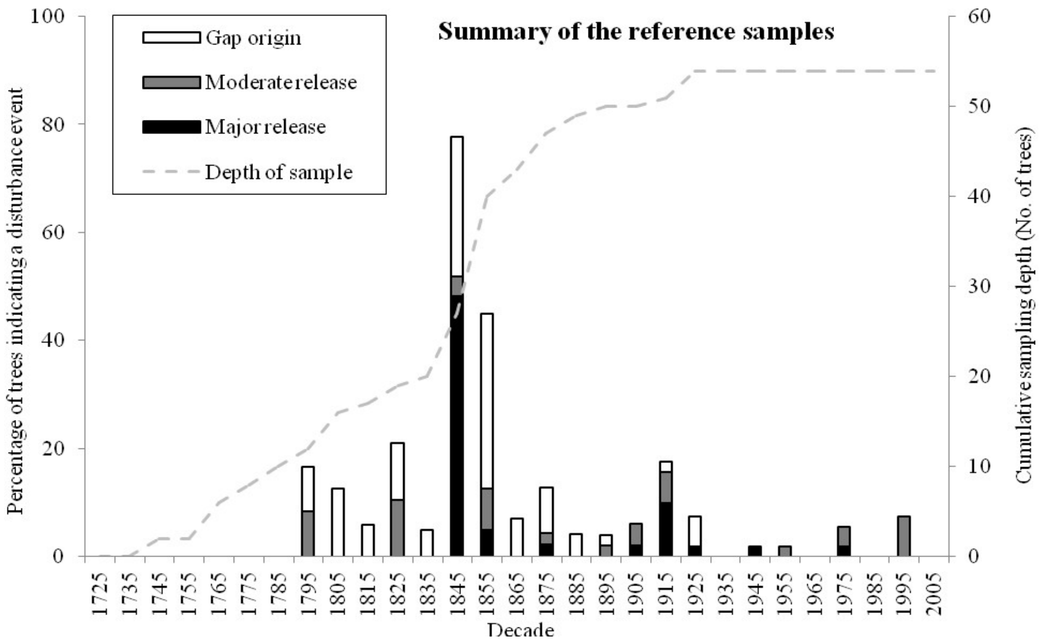

Figure 4-5. Disturbance chronology based on release and gap-recruitment events in each decade for the reference samples obtained in the whole study area (12 ha).

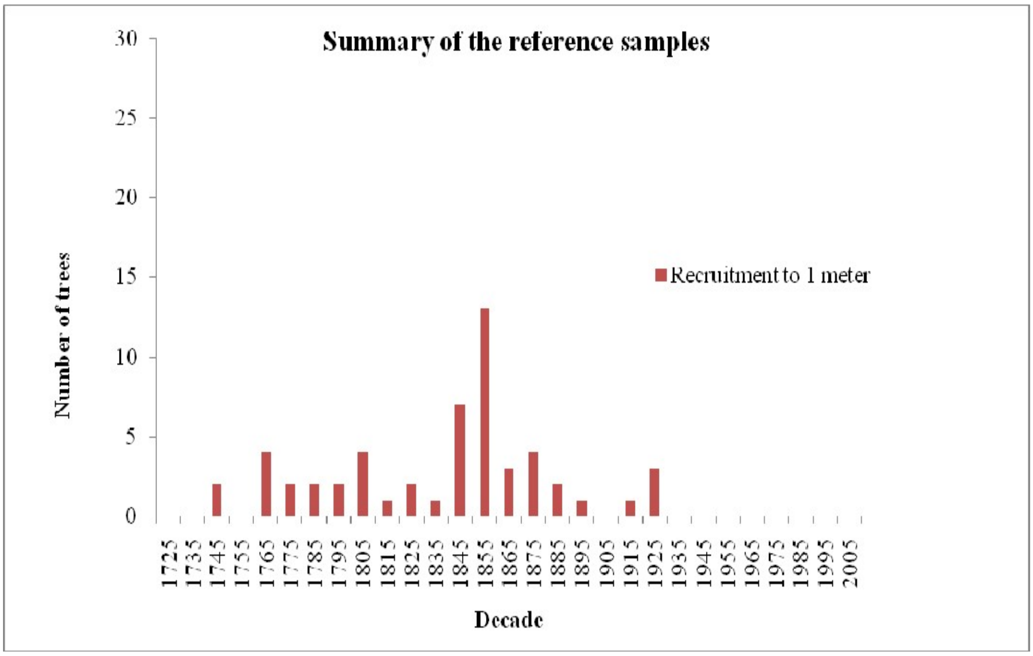

Figure 4-6. Recruitment to 1 m frequency along the time line for the reference samples obtained in the whole study area (12 ha).

As can be seen from the disturbance chronology displayed in the Figure 4-5. above, the reference samples show patterns similar to those presented in the disturbance chronology constructed for the samples gathered within the 12 sub-plots.

Again, there's a major release event detected about the year 1845 followed by massive regeneration and a slight increase of release events in the first 2 decades of the 20th century.

The Figure 4-6. reveals higher intensity of recruitment during the years 1840 – 1859. The majority of trees were recruited to 1 m in a continuous period lasting from 1760 to 1899 but this fact isn't comparable with the summary of the sub-plots since the reference samples were chosen subjectively.

However, there are some differences in the patterns of disturbance chronologies constructed for individual sub-plots and therefore the following text comments on single sub-plots grouped according to the patterns they have in common.

### 4.2.3. Groups of the sub-plots

I have decided to separate the sub-plots into 4 main groups. Each sub-plot is considered and commented in the text below but displayed only once based on its most significant pattern. The patterns that are not the main topic of the text considering each group are listed and commented at the end of this chapter (4.2.3.5. Other patterns). The age class distribution for each sub-plot is presented for the comparison with disturbance chronologies.

#### 4.2.3.1. Group 1

Disturbance chronologies of the sub-plots 3, 9 and 21 (Figure 4-8) were put into the first group since all of them show release events that happened within a 2-decades timeframe beginning in the year 1830 (sub-plots 9 and 21) or 1840 (sub-plot 3). There's especially high percentage of sampled trees showing a major release in the period of 1840-1849 in all three chronologies. Beside that, increased number of gap recruited trees especially in the decade starting with the year 1880 is obvious from the graph expressing the disturbance chronology for the sub-plot 3 and the same pattern but of lower intensity is evident in the disturbance chronology of the sub-plot 21.

The Figure 4-7. below confirms the high intensity recruitment since 1880, particularly in the plot 3.

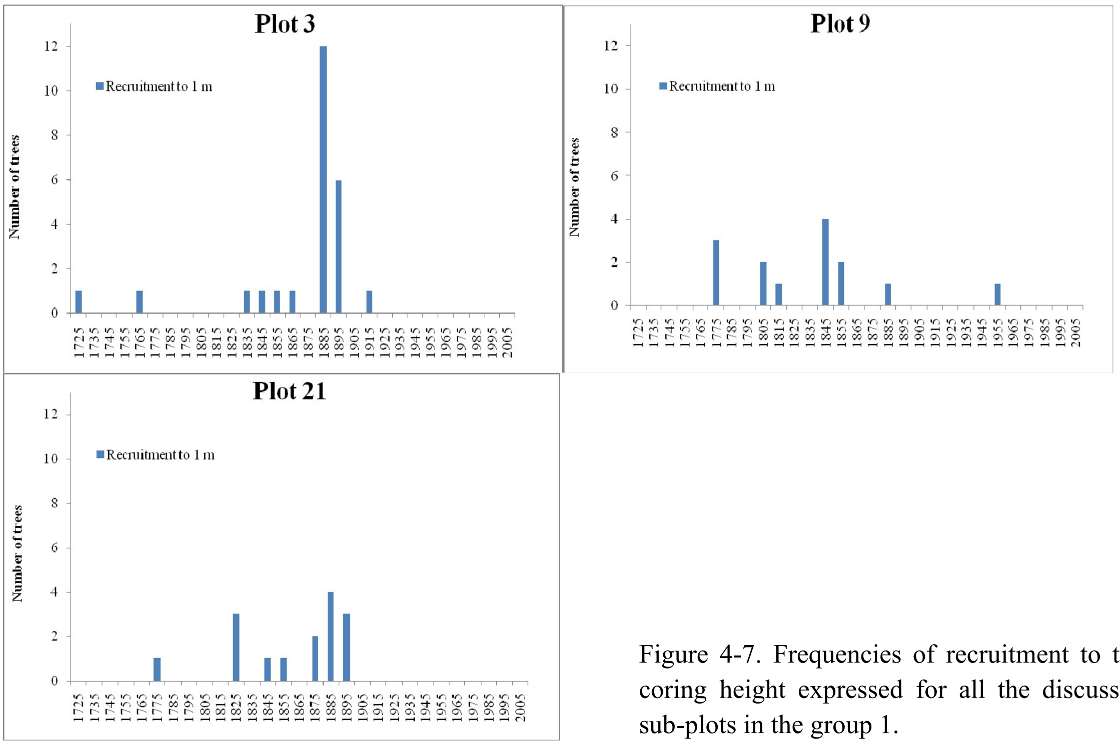

Figure 4-7. Frequencies of recruitment to the coring height expressed for all the discussed sub-plots in the group 1.

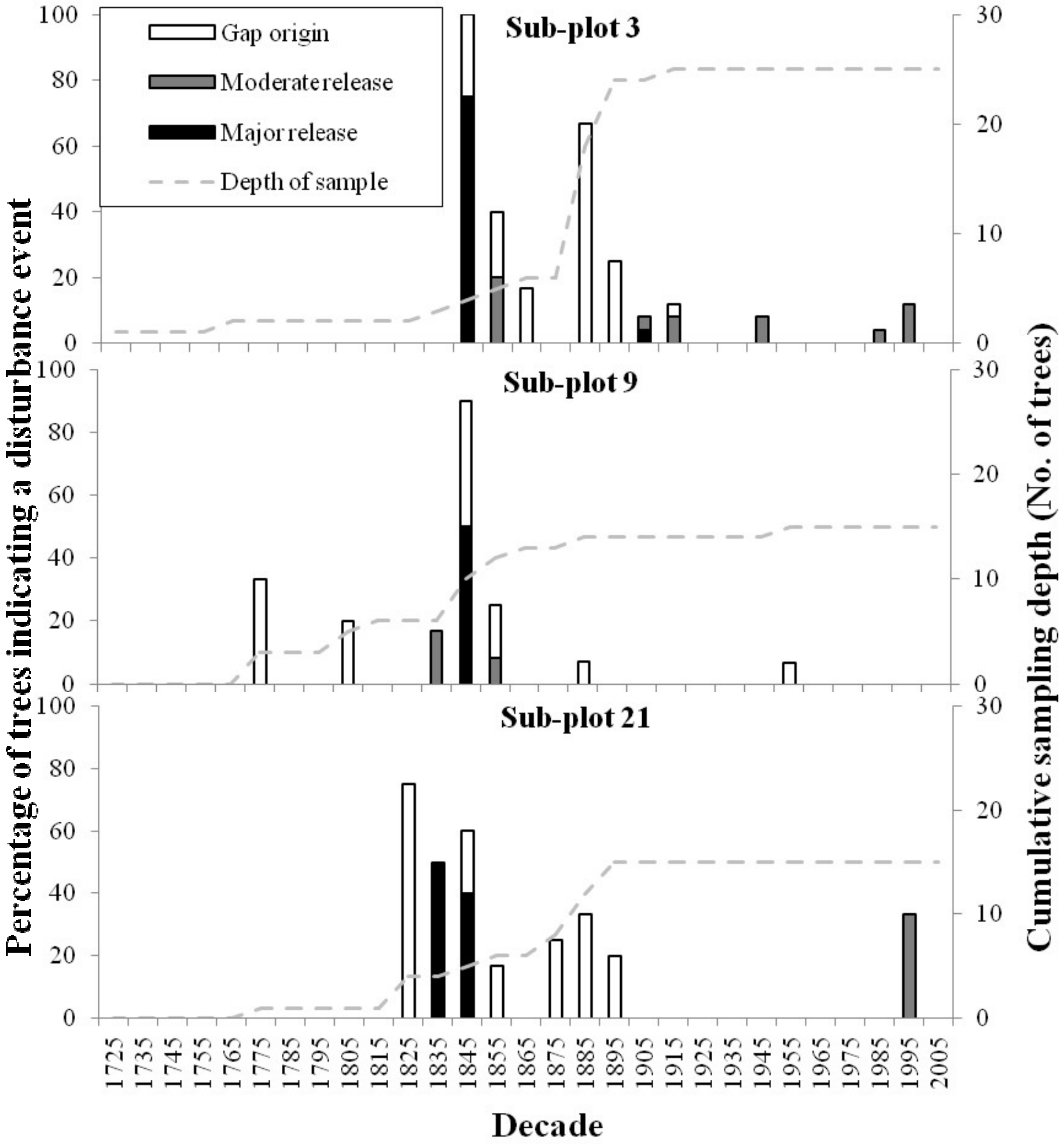

Figure 4-8. Disturbance chronologies of the sub-plots 3, 9 and 21 displayed together.

### 4.2.3.2. Group 2

The second group links together the sub-plots 2, 10, 19 and 20 since all of their disturbance chronologies revealed more intense gap recruitment beginning since 1860 (Figure 4-10). Continuance of this trend differes among the sub-plots. While the increased rate of gap recruitment persists only over 2 decades among the sub-plots 10 and 19, it lasts twice longer among the sub-plots 2 and 20. The sub-plot 10 isn't as representative for this group as the other sub-plots since the number of the sampled trees within it was only 15 and the cores obtained from these trees revealed quite different patterns (Figure 4-9. and Figure 4-10.). In this case the reference samples gathered close to this sub-plot within the plot 10 should also be mentioned: Of the 6 trees cored, 3 show the same pattern that links the plots 2, 19 and 20 thus the sub-plot 10 is also included.

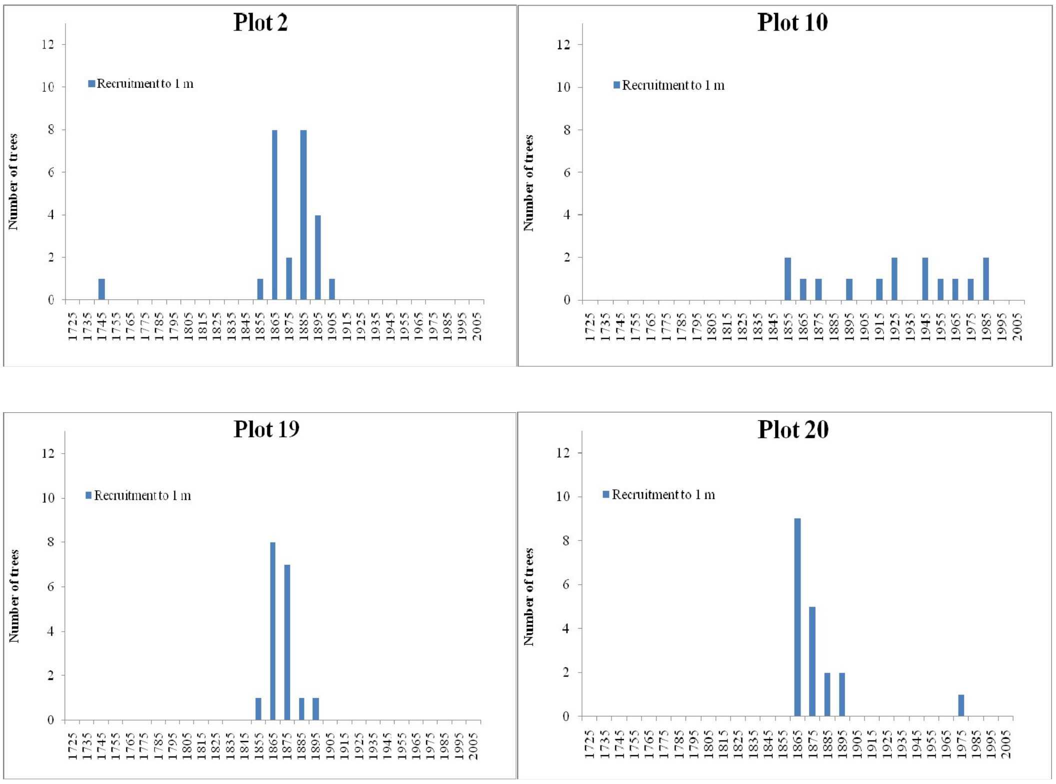

Figure 4-9. Frequencies of recruitment to the coring height expressed for all the discussed sub-plots in the group 2.

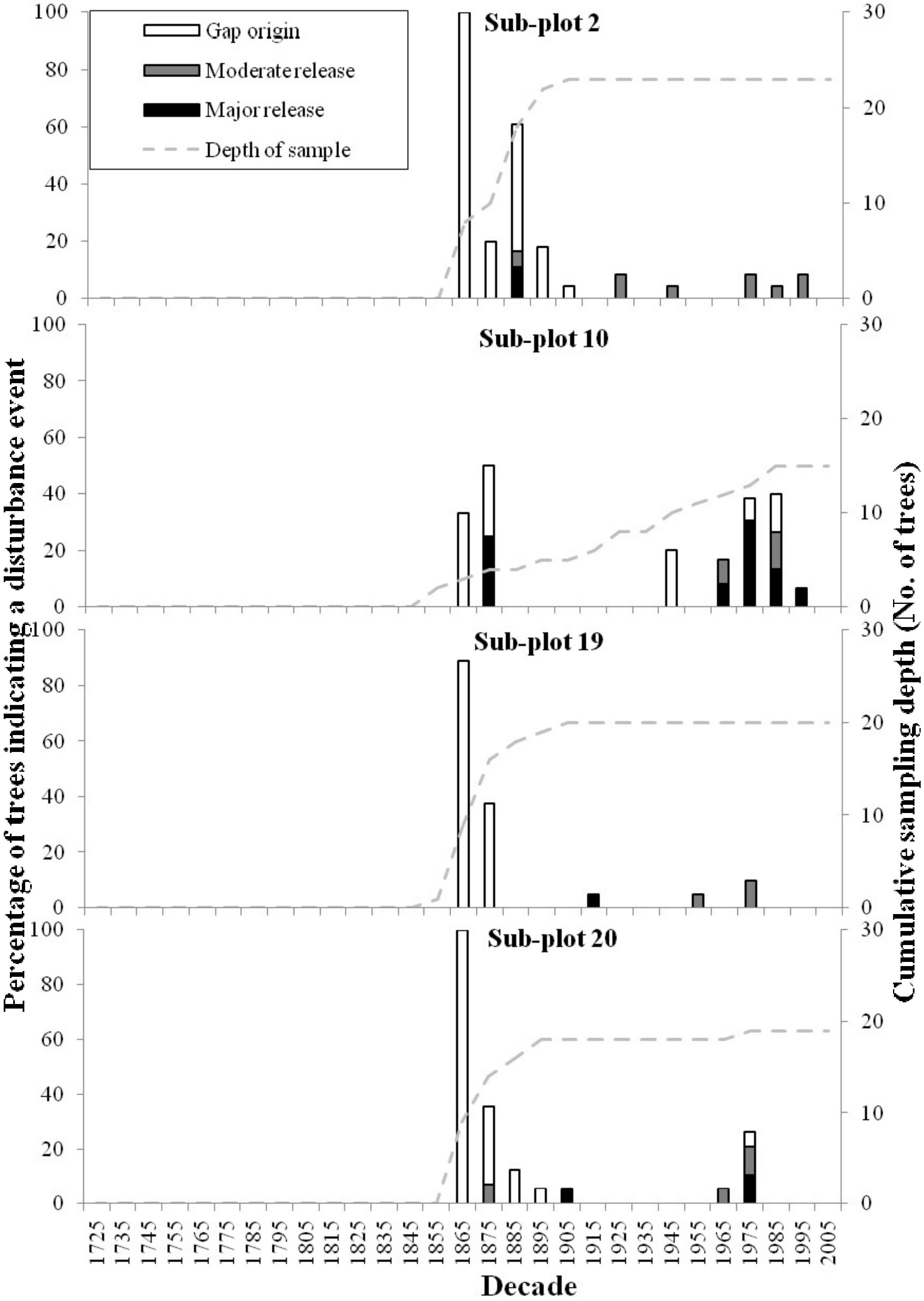

Figure 4-10. Disturbance chronologies of the sub-plots 2, 10, 19 and 20 displayed together.

### 4.2.3.3. Group 3

The group 3 follows the group 2 on the timelime with its higher intensity gap recruitment in the period starting with 1881 (Figure 4-12). This group links together the sub-plots 11, 12 and 22. Cores obtained from trees rooted in these 3 sub-plots revealed some minor occurrence of both moderate and major release events following the mentioned period of gap recruitment and at the end of the 20th century, respectively. However, none of the releases detected isn't more significant due to its low incidence in the sample. Figure 4-11. expresses the frequencies of recruitment to the coring height of 1 m and a high peak in the decade 1890-1899 is clearly visible in it.

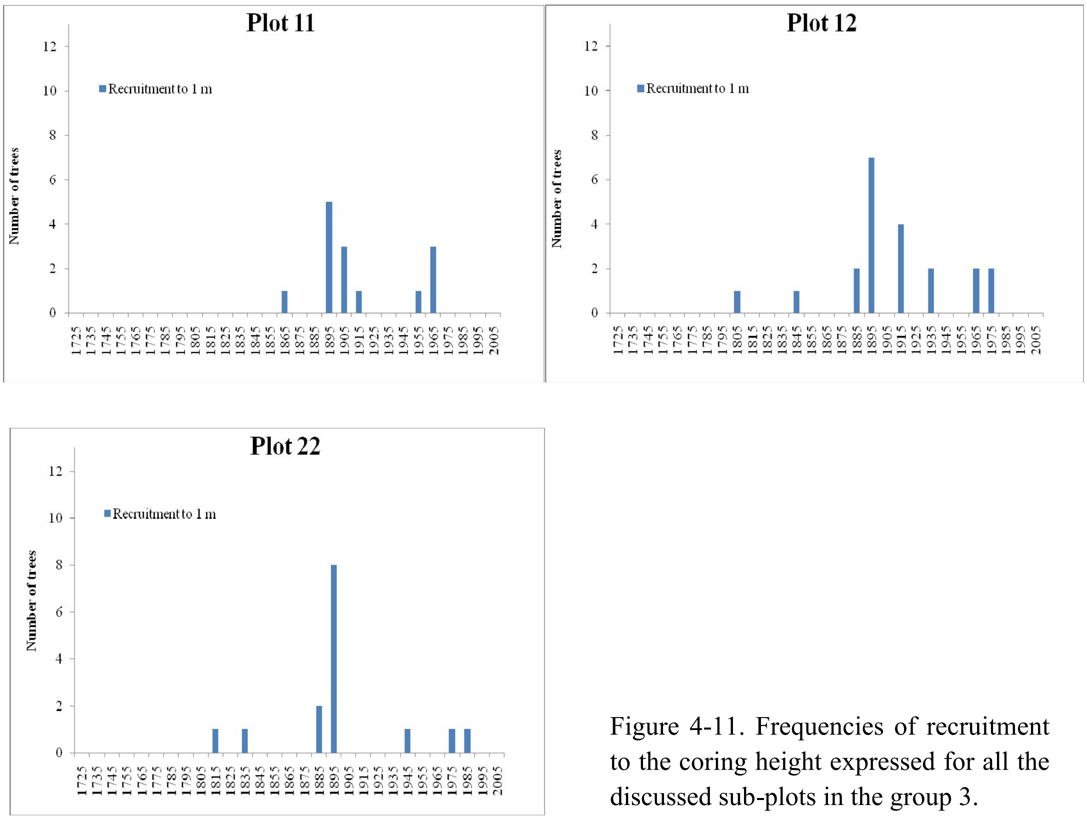

Figure 4-11. Frequencies of recruitment to the coring height expressed for all the discussed sub-plots in the group 3.

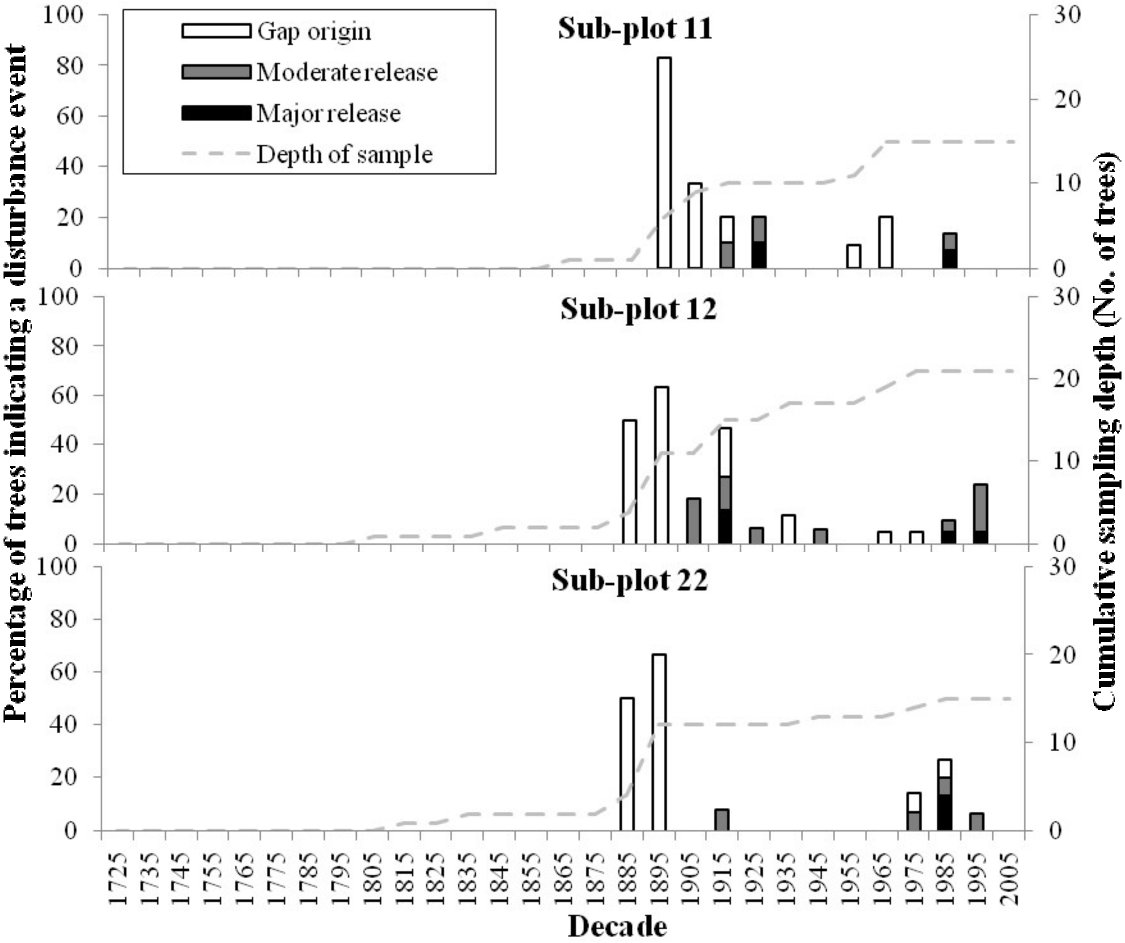

Figure 4-12. Disturbance chronologies of the sub-plots 11, 12 and 22 displayed together.

#### 4.2.3.4. Group 4

Disturbance histories of the sub-plots 4 and 5 were linked together to create the last group (Figure 4-14.). High percentage of trees sampled within these 2 sub-plots indicate gap recruitment in the period starting with the year 1910 and this also applies to the number of trees recruited to 1m in Figure 4-13. After 1 decade the number of recruited trees falls down and then it disappears. The disturbance chronology constructed for the sub-plot 4 is specific with another significant pattern and that is the decade starting with the year 1900 where the percentage of trees indicating a disturbance event reaches 100.

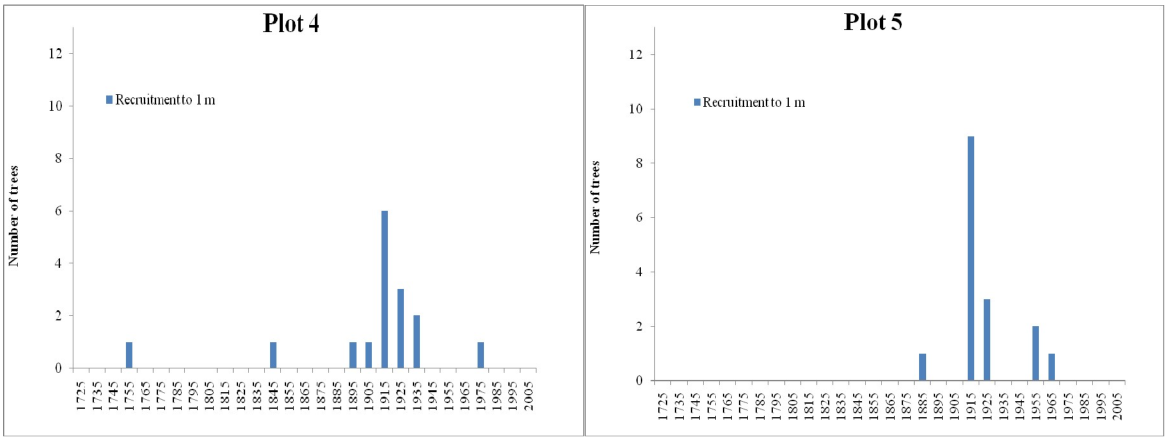

Figure 4-13. Frequencies of recruitment to the coring height expressed for all the discussed sub-plots in the group 2.

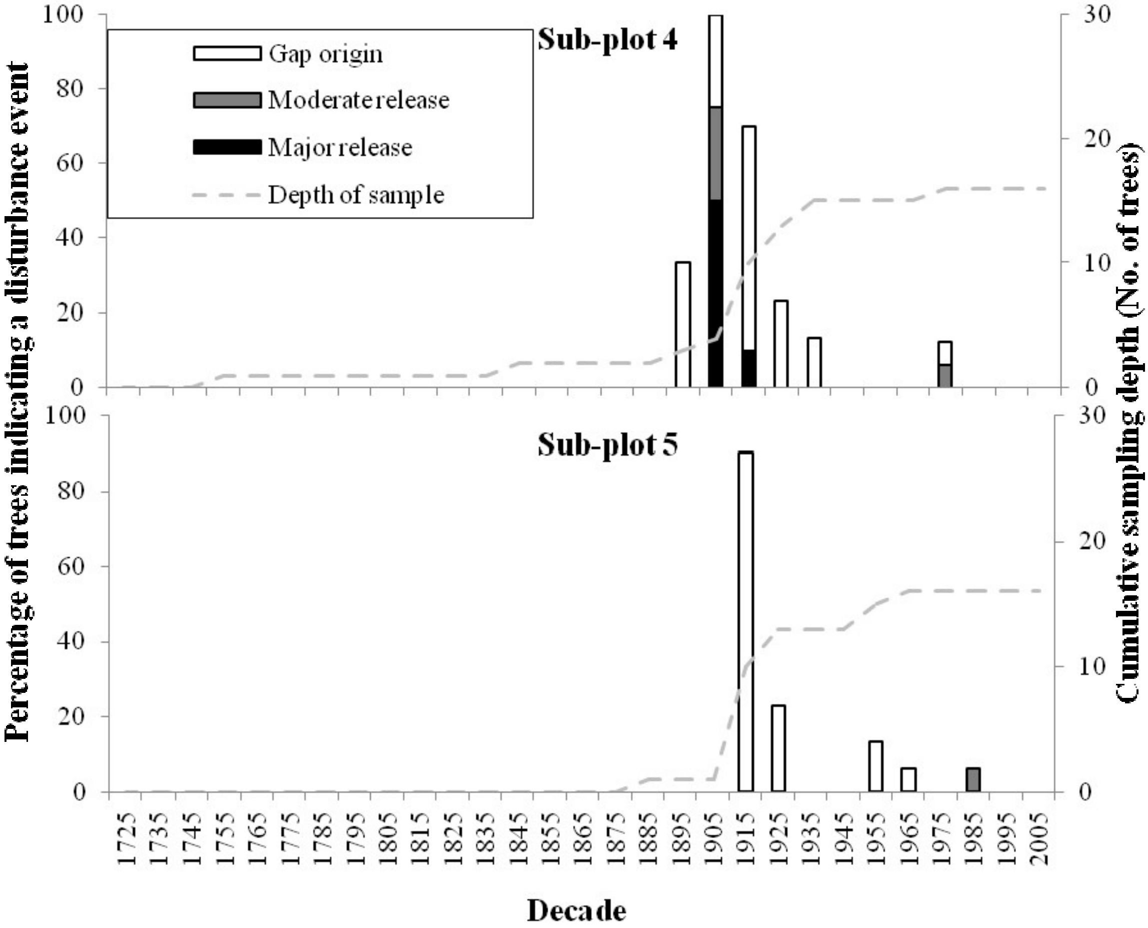

Figure 4-14. Disturbance chronologies of the sub-plots 4 and 5 displayed together.

#### 4.2.3.5. Other patterns

Finally I have to comment on the patterns that haven't been commented yet or have been mentioned only marginally.

There is visible occurrence of both moderate and major release events in two other time periods than in the one mentioned for the group 1. Both of these periods were already mentioned in the summary of the 12 sub-plots and none of them is of higher importance since the percentage of trees in the sample showing some releases doesn't exceed 30 in vast majority of cases. The only exception is the sub-plot 4 where 75% percent of trees in the sample revealed a release from suppression in the decade starting with the year 1900. However we have to consider the sampling depth and that is only 4 at that time. The first minor period of release events is evident since the very beginning of the 20th century and can be observed particularly in the disturbance chronologies of the sub-plots 3, 4, 12 and (one decade later) 11. The second slight increase of detected releases occurs from 1970 to 1999.

There's also random occurrence of gap recruited trees visible in most of the chronologies; in some cases (*e.g.*: sub-plots 4, 10 and 12) it directly follows the above mentioned releases.

## 5. Discussion

### 5.1. Age structure

The results obtained from the trees rooted in the sub-plots indicate that the age structure (*i.e.* recruitment to the coring height of 1 m above ground) varies considerably among the study area. As stated by (KORPEĽ, 1989), the age structure of an old-growth forest in general is greatly diversified and irregular, which is based on differentiated regeneration and death of trees caused by various agents or senescence. Even-aged stands on larger areas are an exception conditional on extensive stand-replacing disturbances. However, KORPEĽ (1989) describes the chance that all the age classes would be present in an old-growth forest at once as very low. The graphs based on the age structure data support the disturbance chronologies with their peaks in most cases but as LORIMER and FRELICH (1989) present, disturbance chronologies are more informative than age structures in the case of forests dominated by shade-tolerant species. The data from tree ring series were surprising in comparison with the subjective stand structure assessment in some cases. As mentioned in the methods, the number of trees cored on each sub-plot was lower if the stand seemed homogenous; namely the sub-plots 4, 5, 9, 10, 11, 21 and 22 seemed relatively homogenous but their age structure revealed recruitment to the coring height during a fairly long period of time, in most cases extending over one century. That could be caused by very scarce presence of evidently older and thicker trees we were aware of (in the sub-plots 4, 9 and 21) or by presence of trees suppressed for a longer period of time that are difficult to distinguish from the younger trees because of their similar diameter.

### 5.2. Disturbance history

The interpretation of disturbance chronologies that extend further back in time is difficult because more trees would have been lost through mortality (FRAVER *et al.* 2009) and therefore the chronologies were truncated if the sampling depth was low. In the consequence past dynamics of the studied forest was reconstructed for only less than two centuries.

No stand-replacing disturbance was indicated during the inspected period. Both disturbance chronologies constructed for all the sub-plots and all the reference samples indicate that the studied stand was affected by a higher-severity canopy disturbance about the year 1845 and inspection of the individual sub-plots' chronologies opens up more details. The event was obvious mainly in the plots 3, 9 and 21 but if we take into account distinct recruitment peaks, immediately following this event on the timeline, it likely influenced the plots 2, 10, 19 and 20. While the sub-plots are considered to be representative samples of the whole 1 ha plots, the disturbance that occurred in 1840s influenced probably the area of couple of hectares. Since the tree-ring chronologies were cross-dated (Yamaguchi, 1990, Schweingruber *et al.*, 1990), the occurrence of disturbance-induced changes in radial growth should be precisely dated. On the other hand, different growth responses to new conditions created by a disturbance could cause some variety in recorded dates (Nowacki and Abrams, 1997). Disturbance interactions are a well known phenomenon (Pickett and White, 1985; Oliver and Larson, 1996) and we could expect especially interaction between disturbances caused by wind (potentially snow) and bark beetle in the mountain spruce forest (Holuša, 2004; Lieutier *et al.*, 2004; Vicena *et al.*, 2004; Økland and Bjørnstad, 2006; Oliver and Larson, 1996). Therefore release events detected in the decade before and after could be interpreted as precondition and consequence of the disturbance in 1840s. For instance one of the explanations could be a windstorm of lower intensity that occurred in 1830s, disturbed smaller part of the stand but made it more susceptible to a more harsh windstorm which came a couple of years later (in 1840s) and was followed by some bark beetle outbreak. After some time, as a result of the outbreak, better conditions for growth of seedlings in the understory let them reach the coring height (plots 11, 12 and 22).

Unfortunately, comparison of this pattern with historical records or scientific papers regarding similar topic is not included in this thesis since there are no historical documents about the study area or its surrounding available and the papers regarding the Calimani Mountains that are available do not consider longer history. Therefore, the question what type of disturbance affected the study area remains. It could even have been an anthropogenic disturbance but this is very unlike mainly due to the inaccessibility of the site.

Further inspection of the disturbance chronologies reveals some random low-intensity canopy-disturbances occurring on the timeline at irregular intervals. This may suggest that more frequent and irregular small-scale canopy disturbances in combination with less frequent higher-severity disturbances drive the dynamics of mountain spruce forests. Similar view shows, for instance, the study conducted by Splechtna et al. (2005) in European Alpine forest dominated by *Picea abies*.

# 6. Conclusion

This thesis described the possible development of mountain spruce forest in the Calimani Mountains, Romania. Based on the inspection of the constructed disturbance chronologies, it presented the combination of more frequent small-scale canopy disturbances and less frequent higher-severity disturbances as a probable driving force of the stand's dynamics.

Such result can be considered a small contribution to knowledge about natural dynamics of European mountain spruce forests and should serve as a challenge for further research with the aim to gather more data regarding this little explored field. However, there are so striking differences between forest stands, just a few meters distant, that understanding of their natural functioning is a very complex matter.

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