Czech University of Life Sciences Prague

Faculty of Forestry and Wood Sciences

Department of Silviculture

# Disturbance History of the Spruce Mountain Forest in Romania

A Thesis
Presented for the
Master of Science Degree

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# CZECH UNIVERSITY OF LIFE SCIENCES PRAGUE

Department of Silviculture
Faculty of Forestry and Wood Sciences

# DIPLOMA THESIS ASSIGNMENT

Lehejček Jiří

Thesis title
**Disturbance history of the spruce mountain forest in Romania**

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### Objectives of thesis

The aim of the thesis is to reconstruct disturbance regime in the spruce mountain forest.

### Methodology

1. Selecting of the research plots.
2. Description of the tree layer.
3. Extracting the samples
4. Analyzing of the samples.
5. Data processing.
6. Finalizing the results and thesis preparation.

### Schedule for processing

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## The proposed extent of the thesis

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## Keywords

dynamika lesa, disturbance, dendrochronologie

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## Recommended information sources

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## Declaration

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

Praha 19.4.2012 signature

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# Abstract

Old-growth mountain Norway spruce forest in Giumalau Mountains, NE Romania provides unique opportunity to study forest dynamics of unmanaged stands in temperate zone. Cores of 300 trees from 12 plots were drilled and subsequently screened in laboratory in order to analyze radial growth patterns. Releases from suppression and gap recruitment are considered as events caused by disturbances. Two centuries long disturbance chronologies were constructed from obtained data. One stand replacing high-severity disturbance was observed in the very beginning of the series. Its legacy has shaped the forest and its dynamics which was further formed by occasional moderate-severity disturbances.

**Key words:** Boundary-line release event, dendrochronology, *Picea abies*, Forest dynamics, Romania, Giumalau Mountains

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# 1. Introduction

Old-growth forest used to be integral part of our landscape. They are defined as forests older than arbitrary age (e.g. 150 ys) with small human influence (Lund 2005). As such they have various ecological and social values (Frelich et Reich 2003), whereas among the most important we can list wildlife habitat, resource production, and protection against natural hazards such as avalanches, floods, and rock falls (Krumm et al. 2011). Nowadays, many of those extraordinary ecosystems are lost due to human pressures (Panayotov et al. 2011). Harvesting, pasture, and need of land for agriculture are among the most consequential causes. Nevertheless, turnover in thinking about old-growth forest can be noticed in recent decades. Increasing interest of public and its fear of irreversible lost has led into protection of those unique remnants of superb ecosystems which are considered essential for maintaining biodiversity (Mosseler et al. 2003).

Besides above mentioned values they provide great opportunity to study natural processes for scientists from various fields of interest. Some of them are methods studying forest dynamics. They can help to understand old-growth forest contexts to help to conserve or restore them (Esseen et al. 1997). Moreover, knowledge of processes unaffected by humans can be also implied to management of protection and production second-growth forests to increase overall profit in particular their non-productive functions (Schönenberger et Brang 2001).

Forest structure, growth, and composition are controlled by edaphic factors, the autoecological aspects of particular species, and long- and short-term climate patterns (Black et Abrams 2003). Nevertheless, to complete interpretation of forest stand development consideration of disturbance history is required (Black et Abrams 2003).

Natural disturbances used to be the main force in the dynamics of many forest landscapes shaping forest structure at the stand and landscape level (e.g. Attiwill 1994; Laska 2001; Svoboda et al. 2012) until human activities significantly changed its pattern (Frelich et Lorimer 1991, Kulakowski et Bebi

2004). The virgin or old-growth forests therefore provide unique mosaic of various successional and structural types of landscape as well as opportunity to describe natural disturbance regimes (Frelich et Lorimer 1991, Panayotov et al. 2011). It is important also for the reason that role of long-term natural disturbance cycles is not yet well understood (Panayotov et al. 2011).

General objective of this thesis is besides literature review also reconstruction of frequency and severity of natural disturbances over the past decades and centuries in old-growth forest in Giumalau Mountains, Romania by using the methods of dendrochronology. Specific objectives were focused on questions: (1) whether large-scale, high severity disturbances occurred in sampled history and how large they have been; (2) what were historical disturbance agents; (3) what have been the effects of past disturbances on forest structure?

# 2. Natural disturbances

Growth of trees and organic decay is relatively slow process in a cold environment close to the timber line which affects spatial, horizontal, and vertical forest stand structure (Svoboda 2005). Míchal et Petříček (1999) claim that regeneration and development of such mountain Norway spruce forest is driven by so called small cycle in which natural disturbance agents play an important role.

According to Pickett et White (1985) disturbance can be defined as: “any relatively discrete event in space and time that disrupts ecosystem, community, or population structure and changes resources, substrate, or the physical environment”.

Since disturbances differ in size, intensity, and frequency and since causal factors (or disturbance agents) often cooperate they are rather observed from complex point of view (Frelich 2002). Such view can be quantified and divides disturbances as follows (according to Frelich 2002):

1) low-severity, when only few individuals from the stand are affected or dying;
2) moderate-severity, when one storey or cohort is eliminated but other (e.g. seedlings) survives;
3) high-severity, which removes most from all stories.

Subsequent recovery (so called post-disturbance succession) is highly dependent on severity of previous disturbance. Korpeľ et al. (1989) believe that the smaller disturbance the faster regeneration because bigger amount of fertile trees which has been left behind can provide sufficient amount of reproductive material. On the other hand, much slower regeneration can be expected after stand replacing, high-severity (major) disturbance which does not leave enough fertile individuals.

Oliver et Larson (1996) generalized stand development into four stages as follows:

1) Stand initiation, when variety of pioneer species are reoccupying open and disturbed sites
2) Stem exclusion – elimination of less competitive individuals
3) Understory reinitiation – establishing of shade tolerant species in understory with subsequent possibility of reaching canopy in ideal conditions
4) Old-growth – (specified above)

It is important to note, that new disturbance can reinitiate this process in any developmental stage.

As indicated above, natural disturbances are highly responsible for maintaining biodiversity (Swanson et al. 2011) and drive forest ecosystem dynamics (Svoboda et al. 2012). Therefore, it is important to understand consequences which will be formulated bellow. Before we approach to description of windthrows and bark beetle – as the most important disturbance agents of this forest type (Schelhaas et al. 2003) – we focus on general methods for evaluation of disturbance history.

### *History of disturbances - assessment*

We know several techniques to quantify disturbance history. Such list can include identification of fire scars, stratigraphic analysis of sediment cores, historical written records, evidence documented in original land surveys, and in addition also dendroecological approaches (Frelich et Lorimer 1991, Black et Abrams 2003, Fraver et al. 2009). In our instance last mentioned possibility relying on core increments represents the most reliable option since series of historical land surveys is missing as well as written records. Observing of current forest structure can detect only recent disturbances because disturbed areas are usually closed in less than four decades (Lorimer et Frelich 1988). Stratigraphic analysis of sediment cores do not give accurate age even if dated absolutely. Neither fire scars nor charcoal horizons were detected during the field survey.

Recently, dendrochronological techniques start to be widely used for their advantages in detection of post-disturbance tree-ring reactions (Bergeron et al. 2002, Frelich 2002). Improved after-disturbance resource conditions (light, nutrients, water) are reflected by surviving individuals by abrupt increase in growth (Zielonka et al. 2010). Detection of release events has experienced decades of development. First studies were done by Lorimer (1980, 1983, 1985). His work led into paper focused on canopy turn-over rates which were traced by detection the canopy accession of trees (Lorimer et Frelich 1989). That is probably fundamental dendroecological concept for evaluating the disturbance history (Black et Abrams 2004). Nevertheless, not until publication Nowacki's et Abrams's (1997) work one statistical approach had been accepted. Their formula (1) gives us a strong tool for detection tree-ring series with enhanced growth which point to events of canopy disturbance. Black et Abrams (2003, 2004) strengthen this technique even more while assuming that slow growing or suppressed trees react to improved resource conditions by more marked reaction than fast growing individuals. They explain it by the fact that overstory trees generally receive adequate resources and grow near their optima. That is the reason for limited growth increases after canopy opening.

Their method boundary-line release criteria permits tracking of a disturbance independently on prior growth dynamics (Black et Abrams 2003, 2004). Calculation of releases is hence a powerful and unique tool for identifying both local and stand-wise disturbances at a high temporal resolution (Black et Abrams 2004). This concept can be used for relatively local purposes (Šamonil et al. 2009), as well as for stand-wise surveys (Zielonka et al. 2010).

For better integrity of the text and easier orientation in used methods wider explanation of above mentioned will be given stepwise in chapter 3.3. Dendrological analysis.

### *Windthrows*

Windthrows represent one of the most important natural disturbances in natural Norway spruce forests (Jonášová et al. 2010). They are responsible for creating gaps which are important part of forest dynamics and therefore are considered as one of the key ecological processes that mould *Picea abies* forests in Europe (Panayotov et al. 2011). Even though disturbances can vary in the size from small to large-scale (Ulanova 2000), in the mid latitudinal conditions of Europe large-scale wind disturbances are rarely observed (Jonášová et al. 2010). However, their frequency and intensity has recently increased (Schelhaas et al. 2003). Nevertheless, there is lack of information about natural mountain spruce forest behaviour in response on windthrows because most of natural forests have been altered by anthropogenic activities which marginalized the role of disturbances (Jonášová et al. 2010).

Svoboda et al. (2012) discuss interesting opinion regarding relation of forest structure and elevation. They believe that forest structural differences are rather driven by increasing severity of disturbances with elevation (mainly windthrows) than lower temperatures and shorter growing season.

### *Bark beetle*

Harsh windstorms are accompanied with generation of dead wood (Wichmann et Ravl 2001). That provides favourable environment for bark beetle of which outbreak can be further enhanced by high spring and summer temperatures (Faflák 2010). Although it is often seen by public as calamity, bark beetle is considered as keystone species and integral part of forest dynamic, and it should be rather seen as habitat engineer (Müller et al. 2008). Not only that its behaviour is beneficial for many other species but it also creates gaps which are important part of forest dynamics.

For the purposes of this thesis it should be kept in mind that partial or complete defoliation should be considered in regions that are prone to outbreaks (Black et Abrams 2003).

### *Other natural disturbances*

We recognize variety of other types of natural disturbances such as fire, high snow or frost pack, floods, avalanches, landslides etc. However, for purposes of this thesis it is useless to study them deeper because they do not occur at all in the place of interest (floods, avalanches) or have minor effect on forest dynamics (fire from lightening, landslides on sites with extremely favourable micro topography) and that is why can affect stand only on very local scale, usually not more than few individuals.

Snow or its other forms can be responsible for bigger losses occurring on stand or even landscape. High snow pack on branches makes them more susceptible to wind which in turn weakens the tree to withstand bark beetle attack.

# 3. Methods

## 3.1. Place of interest

*Location*

Field works took place in Giumalau Mountains, Southern Carpathians, Romania. Forest at the end of the nameless valley has been the subject of protection over the last 150 years when owner and foresters decided to keep this last piece of untouched forest unmanaged (Theodosiu, personal communication).

Study sites were located between 1312 and 1414 m a. s. l. in unmanaged natural *Picea abies* forest. Former human influence cannot be entirely ruled out, however human activities of small scale would have little impact on results (Svoboda et al. 2012).

Simplified map and location of study sites is represented by fig. 1.

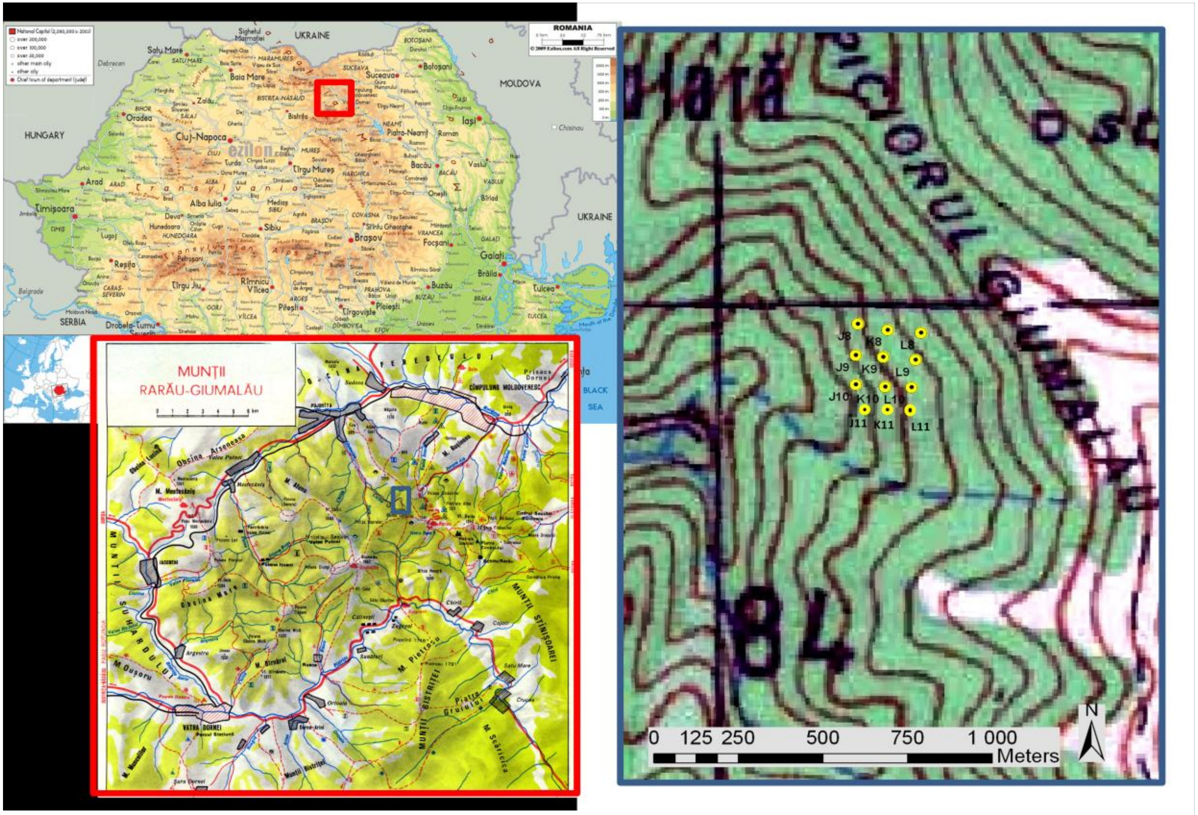


**Fig. 1.** Location of study site within Romania and Giumalau mountains. Red square in map of Romania refers to the position of Giumalau Mountains and blue rectangle in topographic map shows the location of valley where the old-growth forest is situated. Yellow points show location of permanent research plots in the end of valley.

### *Stand: composition and structure*

Composition of forest over-story at study site was Norway spruce (*Picea abies* Karst.) monoculture. Similarly to other forests in the Alps, Carpathians, or Balkan Mountains it is considered as the most important species (Panayotov et al. 2011).

Timber line and tree line are probably affected and lowered by pastures (and therefore not representative) but this has not influenced old-growth forest in lower altitudes where research took place.

### *Climate*

The mountains are in mid latitudes and relatively far from Atlantic air masses therefore climate is moderate-temperate-continental. It is influenced by western air masses, eastern climate and the arctic (borealis) climate of north. Higher altitudes of mountain range make the climate a bit cooler and more humid. Air circulation is highly dependent on season. During summer, the general air circulation usually comes from the Atlantic Ocean in the form of W and NW winds. In contrary, the masses of the polar and Siberian air reach these places during winter as N, NW, and NE winds (Câmpulung Moldovenesc 2007).

The annual global sun radiation never goes over 110 kcal/square cm. It is higher on the summits than in the valleys and has highest value during summer. The land cover variety (forest, alpine meadows etc.) generates important local differences in the matter of values of the radiant balance. The average annual temperature oscillates between 6,8 $^{0}$C in valley and 2 $^{0}$C on peaks. Generally, the highest temperatures are recorded in July while the lowest in January. The average number of frost days is 150 days annually. Thermal inversions are quite rare occurring only sporadically during particularly favourable conditions. There are 80-90 cloudless days annually and average amount of precipitation is

688,2 mm/year in Câmpulung Moldovenesc and 830 mm/year on Rarău Mountains. Precise records for Giumalau Mountains are not available but it is possible to estimate that amount of precipitation will be slightly higher than in Rarău Mountains because they somewhat form protective sheet on west and therefore receive precipitation first (the area has prevailing NW – SE wind direction. Precipitation is in the form of rain usually between the end of April till the beginning of October. Snow is responsible for 20-40 % of the annual precipitation and it has average depth of 20-30 cm and lasts over 100 days. (Câmpulung Moldovenesc 2007).

### *Pedology, geology, and geomorpholy*

Together with soil survey of site detailed inventory of site micro geomorphology was held. Number of pits and mounds as a relic of windthrows (Šamonil et al. 2009) was recorded to support analysis of disturbance history as well as prove the theory that higher proportion of mounds and depression has beneficial effects on tree regeneration (e.g. Kuuluvainen et al. 1998; Lilja et al. 2006). Pit-and-mound micro topography is believed (Ulanova 2000) to be an indicator of previously uprooted trees and therefore windthrows (Šamonil et al. 2009). Predominating soil types were Dystric Cambisols and Podzols.

Giumalau Mountains are formed mainly by metamorphic rocks (crystalline schist) with small limestone pockets (Král 1999).

Urdea et al. (2011) recognizes 10 Pleistocene cirque mountain glaciers with total extend of 0,07 km$^2$. He estimates equilibrium-line altitude around 1650 m a.s.l. depending on aspect which is more than 150 m below highest peak of the range – Vf. Giumalau (1809 m a.s.l.). Pleistocene glaciations therefore had some impact on topography of Giumalau Mountains. Nevertheless, glaciers were quite local and tectonics had incomparably higher impact on geomorphology. Eastern Carpathians have nappe structure (so called block nappes). Modern relief has been hence formed by combination of past glaciations, mass movements and action of rivers and streams (Král 1999).

## 3.2. Data collection

Forest structural and dendroecological data were collected during summer field works in July 2010.

For data collection was used regular quadrate net (100 x 100 m) which was established by I.C.A.S. institution (Institutul de Cercetari si Amenajari Silvice). Particular random points found using GPS were the centres of permanent research plot (PRP). PRP of circle shape had area of either 500 $m^2$ or 1000 $m^2$ and diameter 12,62 m or 17,84 m, respectively, depending on density of trees in PRP. Spatial distribution of PRP can be seen on fig. 1. Following characteristics were registered at each PRP: slope gradient, aspect, and terrain topography (shape of slope - “landform” - shows local topography of PRP [1 – top, 2 – convex shape, 3 – inflection point, 4 – concave shape, 5 – bottom]; and position on slope - “hillform” - [1 – top, 2 – middle, 3 – close to bottom of valley]).

Natural regeneration at each plot was recorded as well using following height categories: 0 – 1,3 m; 1,3 – 2,5 m; 2,5 m and more – all with the limit of 10 cm diameter at breast height (DBH). Particular individuals of regeneration were also divided into categories according to microsite where they occur: on mound, pit, dead wood, or not specified.

All trees with more than 10 cm at DBH were numbered. DBH, species, and state (alive/dead) were recorded. State of living individuals was also assessed in terms of growing in open or closed canopy conditions as released or suppressed (with 50% of shaded crown threshold). We also evaluated social status if particular tree is dominant or not. Same characteristics of microsite as formulated in regeneration paragraph above were used.

Twenty five released trees at each PRP were randomly selected for coring. The trees were drilled in 1 m height and perpendicularly to slope fall line to avoid later misinterpreting of compression wood. Even though we will not examine the exact age of tree by coring it in 1 m knowledge of time when seedling reached 1 m is even more valuable for better identification of disturbance since it shows timing of gap formation (Splechtna et al. 2005, Fraver et al. 2009).

Big attention was paid to drill the pith. If the pith was missed by more than 1 cm the tree was re-drilled. In case of rotten core of tree another with similar diameter was chosen from the list in order to follow the accidentalness. When list could not provide any more trees one of similar diameter another tree was chosen in the closest proximity of site. Similar method was used in case of lack of trees on the site. It was chosen random direction and closest non-drilled individual was drilled. That was repeated until samples of 25 trees were collected.

We also collected some samples of trees around 5 cm at DBH. Trees indicating gap originated development as well as those growing under closed canopy.

## 3.3. Dendrological analysis

### *Data laboratory analysis*

Increment cores were dried, attached on wooden holders, and shaved with razor blade. Tree ring widths were measured using the PAST 32 programme (SCIEM 2000) to an accuracy of 0,01 mm. The cores were cross-dated by using software PAST 32 following standard procedures. Principal chronology from dominant trees that were not affected by any disturbance was constructed and used as a reference for cross-dating procedure (Panayotov et al. 2011). Subsequently, traumatic resin ducts, wounds, frost rings, and light rings were recorded to serve as evidence of external mechanical influences as well as the marks for cross-dating (Schweingruber 1996).

In the cores where the pit was not reached exactly, number of missed ring was calculated according to visible initial growth using standardized translucent circled paper.

Subsequently, all 300 increment cores were screened for information of past disturbance. Specifically, sudden increases in radial growth known as “releases”, and rapid early growth rates indicating gap recruited trees (Lorimer et Frelich 1989). Detailed description of recognizing such characteristics follows bellow.

### *Growth release and boundary line*

According to (e.g. Lorimer et Frelich 1989, Panayotov et al. 2011) improved growth conditions are result of death of neighbouring trees. This theory is used to assume that identification of release events can significantly help in reconstruction of disturbance chronology (Zielonka et al. 2010). For such identification of abrupt radial growth events percentage change in growth rate (%GC) for each ring was calculated using the formula by Nowacki et Abrams (1997).

$$(1)\ \%GC = [(M2 - M1)/M1] \times 100 \quad ,$$

where M1 and M2 is represented by preceding and following 10 years mean growth, respectively. This smoothing substantially reduces the year to year variations possibly leading to mistakes. Conventionally, first and last decade of each tree ring series was excluded from further analysis because at least that many years are needed in the percent-growth-change formula (Black et Abrams 2003, Fraver et al. 2009, Zielonka et al. 2010). To date the disturbance, maximum % GC in each release pulse was used (Svoboda et al. 2012). But even if data were smoothened some growth response signals affected by short term climate shifts can be misinterpreted as releases (Abrams et Orwig 1995). Especially if disturbance signal occur during deteriorated climatic conditions such as drought (Black et Abrams 2003, 2004). It is worth to add that Nowacki et Abrams (1997) recommend to use this approach in temperate closed-canopy forests where competition for resources plays more important role than climate.

However, this approach is relatively flat because as release is examined every event when %GC of a tree's chronology exceeds a given minimum threshold, such as 50 %, for a certain duration (Black et Abrams, 2003). It ignores particular maximum of physiological potential defined by prior growth rate (e.g. slow growing/suppressed vs. fast growing/released, or shade-tolerant vs. shade intolerant individuals).

According to Black et Abrams (2003) radial growth rate is the most important factor of percent-growth change. Therefore, the boundary line release criteria were applied to identify release events because it uses %GC value as a fraction of its maximal potential while considering the level of prior growth (Black et Abrams 2003). Wide range of approaches have been used to construct boundary line including drawing a line by hand (Schmidt et al. 2000). Apparently, the most widely accepted procedure was developed by Black et Abrams (2003). They divided the data into 0,5-mm segments and averaged the top ten data points within each segment. The curve is then fit to the means of these points using regression.

For constructing own boundary-line is necessary humongous amount of samples (Splechtna et al. 2005, Black et Abrams 2003). Boundary-line was constructed from other measurements in Giumalau area which provide sufficiently large amount of samples (Fig. 2.).

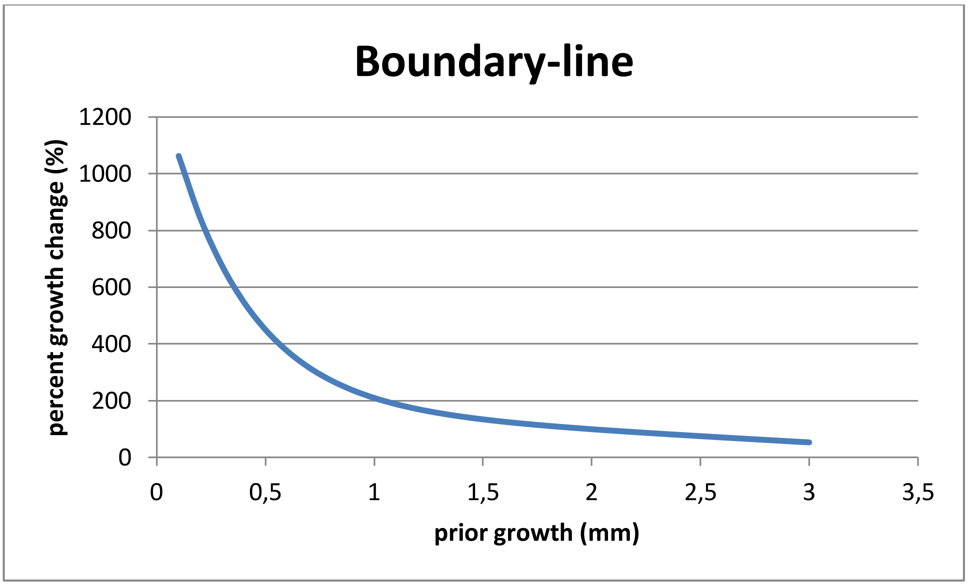


**Fig. 2.** Boundary-line constructed from obtained samples in Giumalau Mts.

Although Splechtna et al. (2005) mention that maximum release potential of very old or largest trees may be smaller than given by the boundary line this technique still remains the most powerful and offers high level of precision and flexibility.

Increases in radial growth of 20 % and 50 % were established to detect moderate and major releases, respectively. Moderate release can be characterized (sensu Svoboda et al. 2011) as partial removal of a canopy tree or loss of neighbouring trees, whereas overtopping canopy trees are entirely lost during a major release. This approach represents compromise between conservative and liberal attitude which should neither underestimate disturbance nor overestimate climatic variability. Unfortunately, some overlap of disturbance and climatic effects can occur. Therefore, threshold was set to favour relatively bigger disturbance events and ignore those of smaller scale in order to avoid inclusion of climatic effects into further analysis.

### *Gap recruited individuals*

In forest with low frequency of large disturbances, stand dynamics are often control by gap formation due to mortality of over-story trees (Kneeshaw et Bergeron 1998). These often large canopy trees tend to be the subject of greater wind stress (Coutts et Grace 1995) leading to fall sometimes even tree-to-tree impact resulting in gap formation (Rentch et al. 2010). Forest canopy gaps represent dynamic environment with frequent changes including their expansion, shrinking, and eventual disappearance (Ott et Juday 2002) by accelerated growth of young trees and lateral growth of the crowns of gap-border trees (Rentch et al. 2010). Establishment of saplings is consequential due to improved resource conditions formulated above.

Recognition of such gap originated trees is an essential step toward developing a disturbance chronology (Lorimer et Frelich 1988). Gap originated is considered every tree that experienced higher rate of growth during its transition from seedling to small tree than it is a given threshold (Splechtna et al. 2005, Fraver et al. 2009). This statement is supported by Lorimer and Frelich (1988) theory which assumes that average growth rates of suppressed individuals is substantially lower than growth rate of those originated in gaps. According to Lorimer et Frelich (1988) and Fraver et al. (2009) it does not necessarily mean germination in gap because seedlings of shade-tolerant species are able to germinate under a closed canopy and survive for decades waiting for their chance to recruit in the gap (Fig. 3.). In addition, Fraver et al. (2009) discuss the ability of shade-tolerant species to persist in understory for long time which leads to a mosaic of patches in various stages of structural development, but not in various stages of compositional succession.

**Fig. 3.** Mountain old-growth forest on Vancouver Island, Canada – MASS site. Example of Norway spruce tree which can be over two hundred years old (B. Beese, personal communication). Author´s photography.

Threshold for recognizing gap recruited trees is usually set arbitrary (Svoboda et al. 2012). Nevertheless, in this case, it was calculated. Evidently suppressed and released saplings of similar DBH size were compared (respectively their 5-year growth rates) using logistic regression. For gap recruited trees were regarded those exceeding on average 1,06 mm year increment in the juvenile phase (according to Janda, personal communication).

### *Disturbance chronology*

Disturbance history can be expressed as proportion of trees showing release event or gap recruitment for each decade of the chronology (Black et Abrams 2004). For such release events were considered moderate and major releases (Svoboda et al. 2012).

The further back in disturbance chronologies is advanced the less reliable they are because increasing number of trees have been lost due to mortality (Fraver et al. 2009). This relationship is expressed as depth of sample (see Figs. 6, 7, and 8.). For that reason only the period from approximately beginning of 19th century was analysed because before this point the sample size per plot dropped bellow ten individuals. On the other hand, it is not without interest to see pure data which were not disconnected from those parts where depth of sample falls bellow ten individuals. Even this reduced depth of sample can give some indications when observed in the wider perspective of twelve plots. Therefore, results are presented in “non-cut” form.

It is worth to mention that canopy turnover time is very often considerably shorter than potential canopy tree lifespan (Lorimer et Frelich 1988).

# 4. Results

## 4.1. PRP and stand characteristics

Morphological characteristics for all twelve PRP´s are given in tab. 1.

**Tab. 1.** Morphological and site characteristics for every particular PRP.

| PRP | area ($m^2$) | hillform | landform | slope (°) | aspect (°) | elevation (m a. s. l.) | longitude E (°) | latitude N (°) |
|---|---|---|---|---|---|---|---|---|
| J08 | 500 | 3 | 3 | 22 | 230 | 1342 | 25,466830 | 47,446376 |
| J09 | 500 | 3 | 3 | 33 | 250 | 1319 | 25,466775 | 47,445495 |
| J10 | 500 | 3 | 4 | 13 | 360 | 1312 | 25,466813 | 47,444657 |
| J11 | 500 | 3 | 1 | 13 | 270 | 1326 | 25,466827 | 47,444202 |
| K08 | 1000 | 2 | 2 | 21 | 230 | 1358 | 25,468017 | 47,446230 |
| K09 | 1000 | 2 | 2 | 29 | 210 | 1357 | 25,467865 | 47,445454 |
| K10 | 1000 | 2 | 4 | 24 | 290 | 1350 | 25,467952 | 47,444605 |
| K11 | 1000 | 2 | 1/2 | 11 | 270 | 1350 | 25,468006 | 47,444115 |
| L08 | 1000 | 3 | 2 | 28 | 350 | 1414 | 25,469319 | 47,446161 |
| L09 | 1000 | 2 | 4 | 20 | 210 | 1387 | 25,469133 | 47,445387 |
| L10 | 1000 | 2 | 3 | 23 | 285 | 1383 | 25,468995 | 47,444608 |
| L11 | 500 | 2 | 2 | 27 | 270 | 1382 | 25,469199 | 47,444017 |
| **Modus/ Median** | **Mo = 1000** | **Mo = 2** | **Mo = 2** | **Me = 22,5** | **Mo/Me = 270** | **Me = 1354** | **-** | **-** |

Stand characteristics for all twelve plots are given in tab. 2. For completeness of this table it is important to add that all observed trees belonged to the *Picea abies* species.

**Tab. 2.** Stand characteristics for living and dead trees in every particular PRP.

| PRP | State | Number of trees per ha | Stand basal area ($m^2$ per ha) | Average DBH (cm) |
|---|---|---|---|---|
| **J8** | living | 460 | 32,7 | 30,1 |
| | dead | 20 | 3,1 | 44,5 |
| **J9** | living | 280 | 4,1 | 13,7 |
| | dead | 160 | 39,8 | 56,3 |
| **J10** | living | 260 | 58,0 | 53,3 |
| | dead | 60 | 5,1 | 33 |
| **J11** | living | 660 | 18,3 | 18,8 |
| | dead | 60 | 15,1 | 56,6 |
| **K8** | living | 360 | 59,1 | 45,7 |
| | dead | 110 | 12,9 | 38,6 |
| **K9** | living | 470 | 39,2 | 32,6 |
| | dead | 140 | 4,8 | 20,8 |
| **K10** | living | 330 | 24,7 | 30,9 |
| | dead | 30 | 2,0 | 29,2 |
| **K11** | living | 310 | 40,7 | 40,9 |
| | dead | 60 | 2,3 | 21,9 |
| **L8** | living | 400 | 24,1 | 27,7 |
| | dead | 40 | 3,3 | 32,6 |
| **L9** | living | 310 | 37,0 | 39 |
| | dead | 50 | 4,3 | 33,1 |
| **L10** | living | 320 | 25,3 | 31,7 |
| | dead | 90 | 8,9 | 35,5 |
| **L11** | living | 280 | 37,5 | 41,3 |
| | dead | 40 | 7,7 | 49,5 |

Fig. 4. shows distribution of classes according to diameter at the breast height.

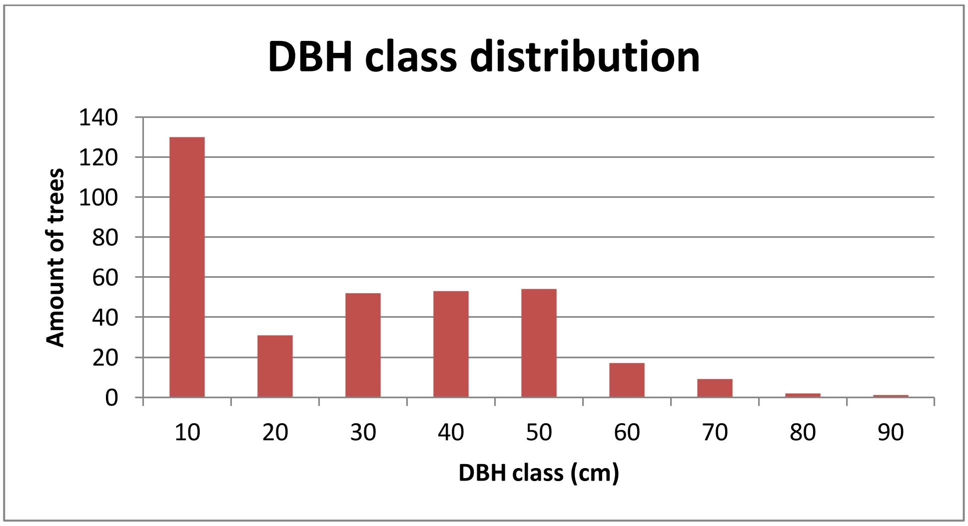


**Fig. 4.** DBH class distribution for all alive individuals in all twelve PRP´s.

## 4.2. Natural regeneration

Natural regeneration of spruce for all microsite categories is shown in tab. 3. Spruce was by far the most dominant species. Extremely rarely some seedlings of *Sorbus aucuparia* were detected as well but they never exceeded 5 % in total share.

**Tab. 3.** Natural regeneration according to microsite for all twelve PRP´s.

| PRP | Microsite | Height (DBH) class | | | |
|---|---|---|---|---|---|
| | | 0,5-1,3 m | 1,3-2,5 m | >2,5 m | >2,5 m (5- |
| **J8** | pit | - | - | - | - |
| | mound | - | - | - | - |
| | dead wood | 31 | 2 | - | - |
| | other | 5 | 8 | 3 | 6 |
| **J9** | pit | - | - | - | - |
| | mound | 2 | - | - | - |
| | dead wood | 5 | - | - | - |
| | other | 13 | 9 | 6 | 18 |
| **J10** | pit | - | - | - | - |
| | mound | - | - | - | - |
| | dead wood | 2 | - | - | - |
| | other | - | - | - | - |
| **J11** | pit | - | - | - | - |
| | mound | - | - | - | - |
| | dead wood | 30 | 10 | 15 | 15 |
| | other | - | - | 10 | 5 |
| **K8** | pit | - | - | - | - |
| | mound | - | - | - | - |
| | dead wood | 20 | 1 | - | - |
| | other | 14 | 5 | - | - |
| **K9** | pit | - | - | - | - |
| | mound | - | - | - | - |
| | dead wood | 11 | 4 | 3 | 2 |
| | other | 5 | 7 | 3 | 3 |
| **K10** | pit | - | 1 | - | - |
| | mound | 18 | 9 | 1 | 5 |
| | dead wood | 43 | 20 | 10 | 4 |
| | other | 17 | 32 | 8 | 22 |
| **K11** | pit | - | - | - | - |
| | mound | - | 6 | - | - |
| | dead wood | 2 | - | - | - |
| | other | 3 | 4 | - | - |
| **L8** | pit | - | - | - | - |
| | mound | - | - | - | - |
| | dead wood | - | - | - | - |
| | other | - | - | - | - |
| **L9** | pit | - | - | - | - |
| | mound | 1 | 3 | - | - |
| | dead wood | 6 | 8 | 2 | - |
| | other | 5 | 3 | 4 | - |
| **L10** | pit | - | - | - | - |
| | mound | - | - | - | - |
| | dead wood | 10 | 10 | 5 | 5 |
| | other | 15 | 10 | 5 | 7 |
| **L11** | pit | - | - | - | - |
| | mound | - | - | - | - |
| | dead wood | 21 | 18 | 2 | 2 |
| | other | 5 | 5 | 1 | 3 |

Natural regeneration on dead wood was dominant while natural regeneration on pit and mound was only occasional. Last category (“other”) was occupied by more than two fifths of all individuals (see summarizing tab. 4.).

**Tab. 4.** Natural regeneration according to microsite for all twelve PRP´s together.

| | **Microsite** | **Total** |
|---|---|---|
| **All PRP** | pit | 1 |
| | mound | 45 |
| | dead wood | 319 |
| | other | 269 |

## 4.3. Dendrological analysis

The pith was reached in 210 out of 300 samples which represents 70 % of the samples. For remaining cores the number of missed rings was estimated based on average growth and arcing (sensu Duncan 1989).

Age class distribution for all sites together, respectively the time which has passed since the tree reached 1 m is represented on fig. 5. Two distinct peaks in age are possible to observe. The first peak represents trees between 30-39 years and the second one is for those between 180-189 years since they reached 1 m height.

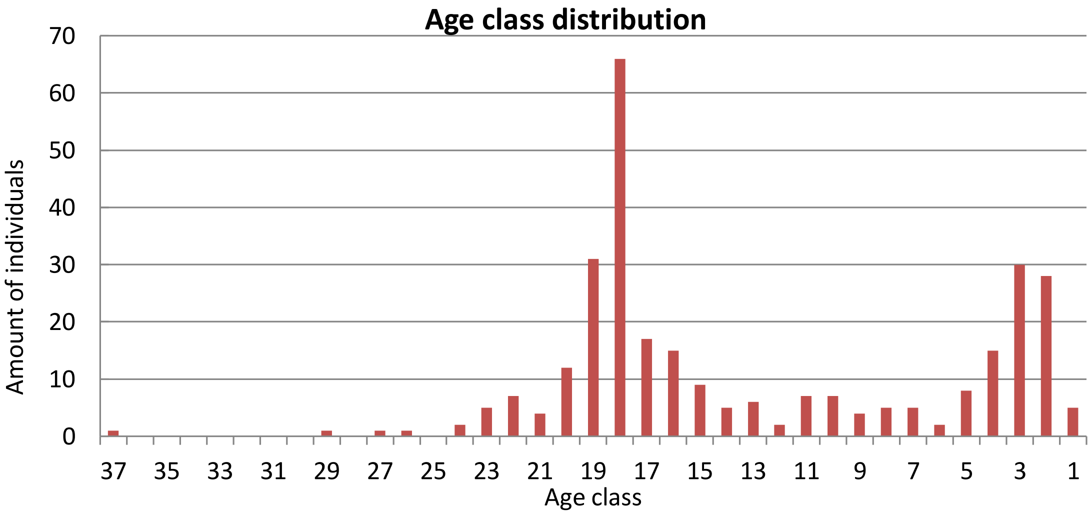
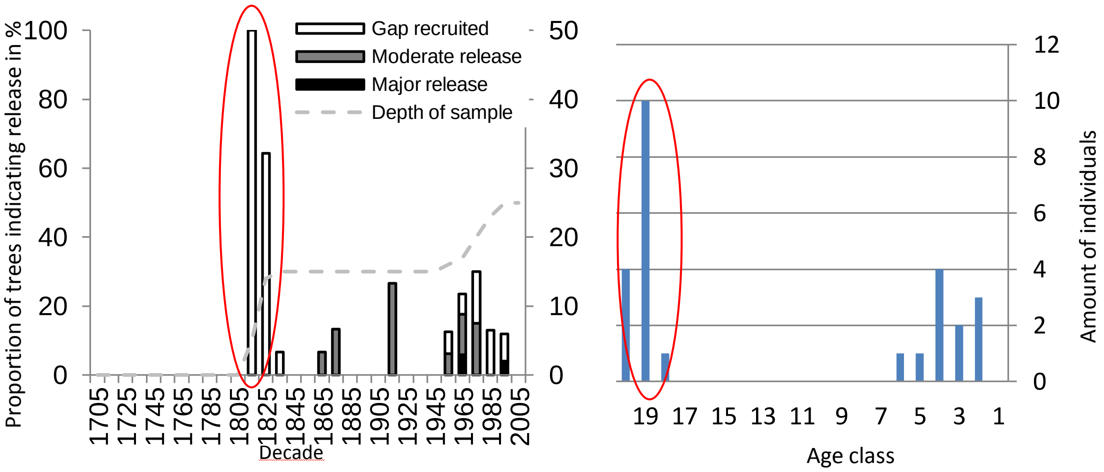


**Fig. 5.** Distribution of age classes (ten years interval: 1=0-10, 2=11-20, 3=21-30, etc.) and their absolute amount for all twelve plots together.

Disturbance history of selected PRP which are distinctly indicating some releases is represented by figs. 6, 7, 8. For easier orientation and better understanding the data of age class distribution for every particular PRP are given as well if helpful. Disturbance histories as well as age class distributions for all PRP’s are published in Appendix.

a) J8



b) K8

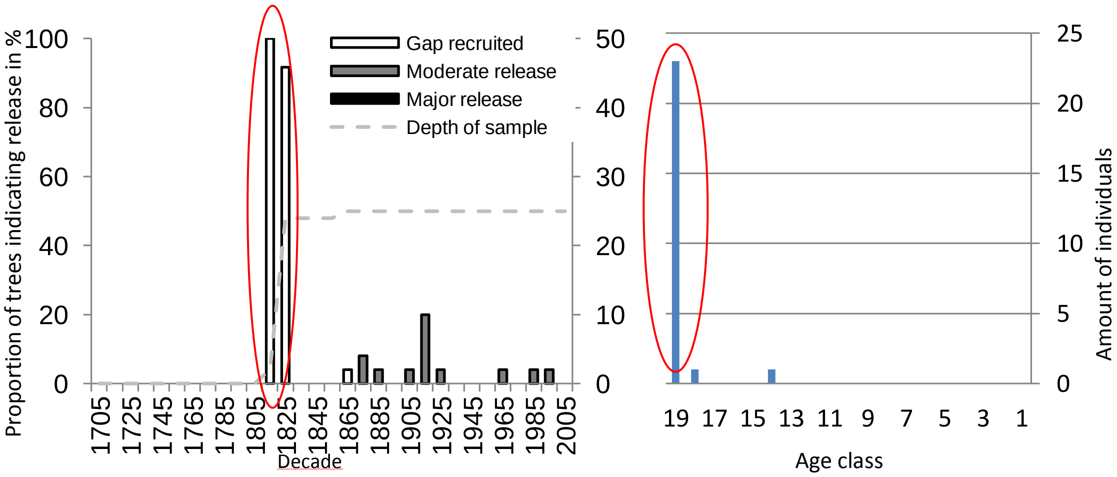
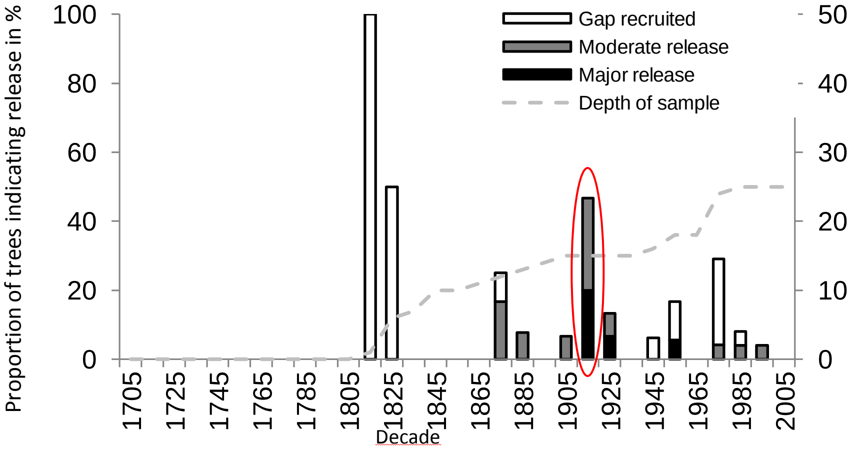


**Fig. 6.** General disturbance history and age class distribution for PRP L8 (a) and PRP J8 (b).

PRP L8 and especially K8 strongly indicate big disturbance event in the first decades of 19th century. Depth of sample is representative, exceeding ten individuals in both cases. This theory is also indirectly proved by age class distributions which show that big amount of trees reached 1 m at the beginning of 19th century. In case of PRP K8 we can trace the effect of large disturbance on later forest dynamic. There is no major release occurring and only limited amounts of moderate releases. Closer look to other PRP general disturbance histories (see in appendix) gives even more confidence about relatively large scale disturbance in the first decades of 19th century.

a) K9



b) L8

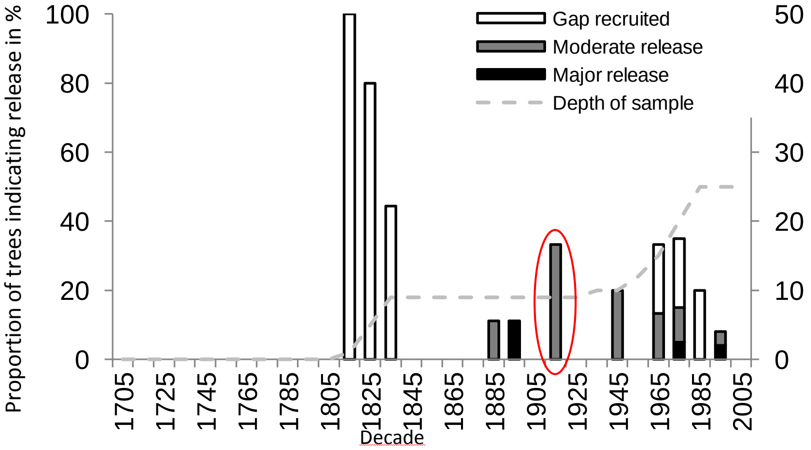
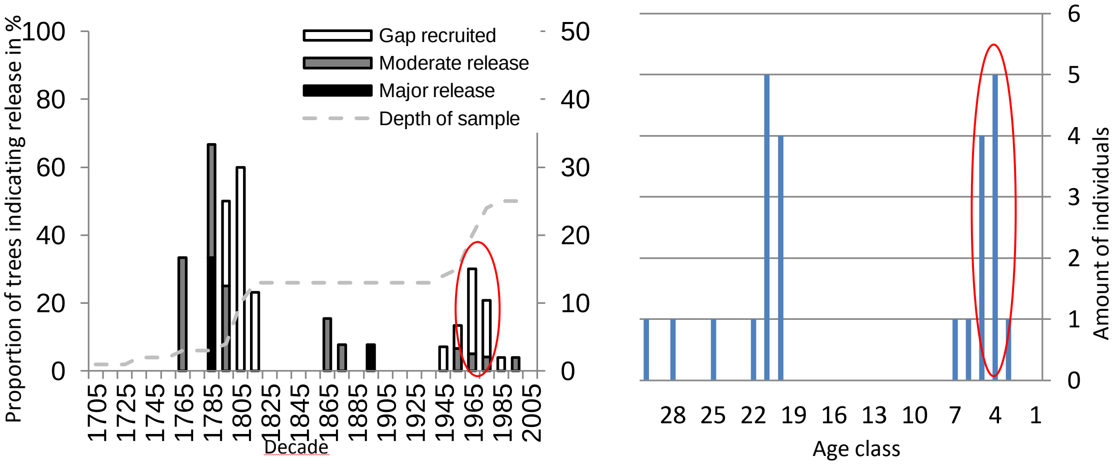


**Fig. 7.** General disturbance history for PRP K9 (a) and PRP L8 (b).

PRP K9 and L9 are the best representatives of release event in decade around the year 1915. In spite of the relative smallness of peaks they are quite distinct. If other datasets are compared we get the same results even though the peaks are sometimes even smaller.

Comparison of diagrams with age class distribution of particular PRP does not make any sense because release events in 1915-decade were not gap originated. Therefore, advanced growth experienced only already mature individuals.

a) K10



b) L8

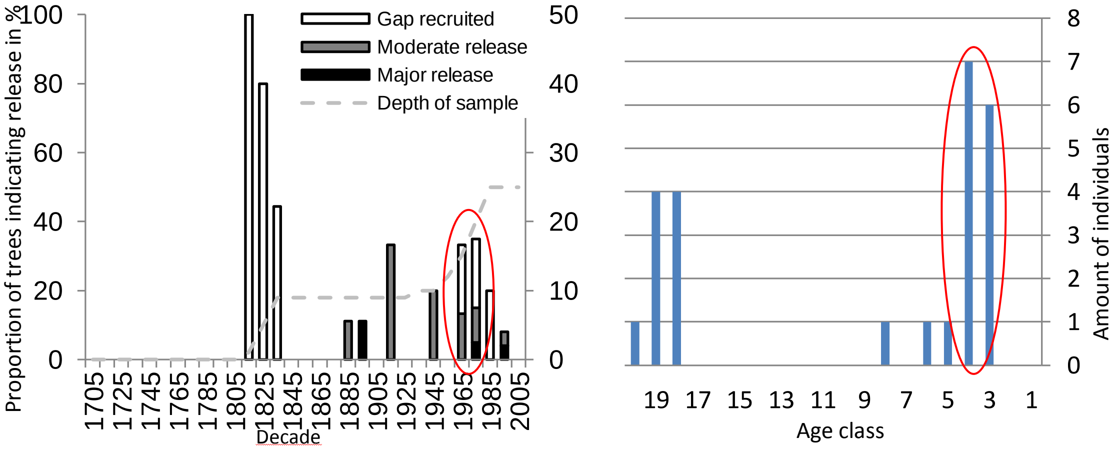


**Fig. 8.** General disturbance history and age class distribution for PRP K10 (a) and PRP L8 (b).

PRP K10 and L8 show composite release event in two subsequent decades around 1965 and 1975. The peaks are distinct in most of the PRP (see in Appendix) with ranging maxima in 1965 and 1975, respectively. This is supported by both age class distribution and fig. 9. showing amount of localities with release event per decade.

To simplify all twelve PRP’s general disturbance histories, fig. 9. was developed. It was constructed by summing peak decadal release events for all sites. If more than one peak was observed all of them were adopted for purposes of this chart. The most repeated timing of release events were: beginning of 19th century, 1915-decade, and two decades around 1965 and 1975.

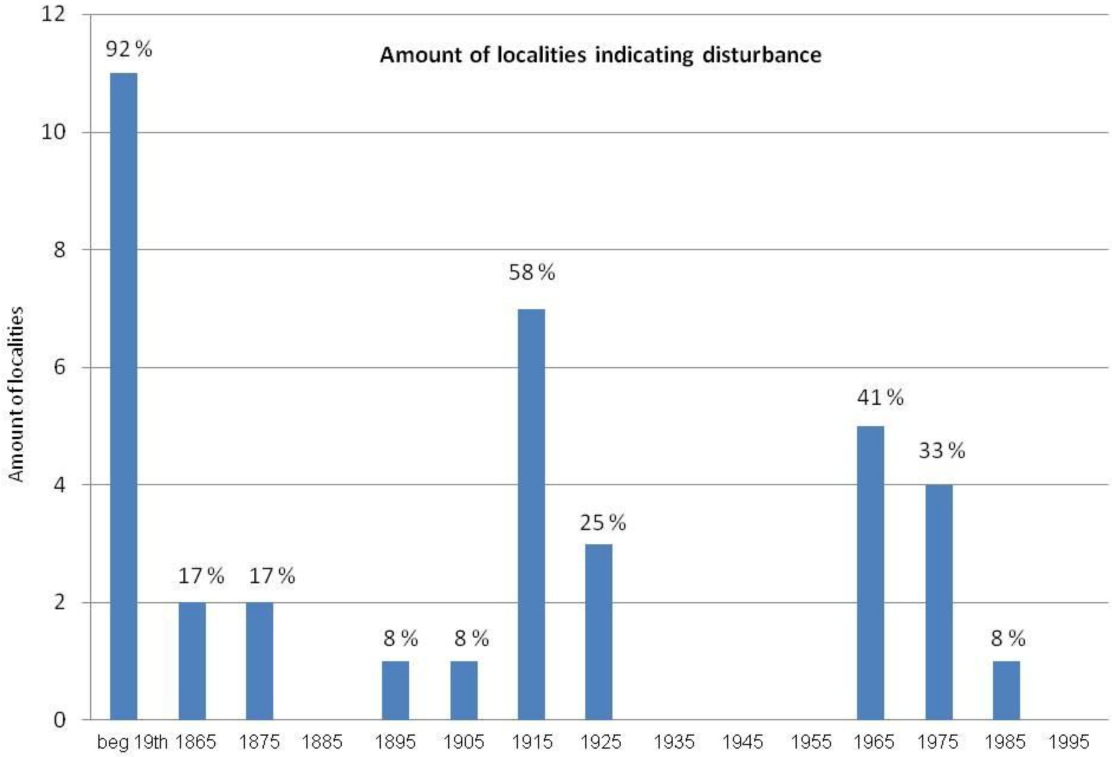


**Fig. 9.** Absolute amount of PRP (out of twelve) indicating natural disturbance from the beginning of 19th century. Numbers on tops of bars represent relative share of disturbed PRP’s on total amount of all PRP’s.

# 5. Discussion

### *Suitability of dendroecological approach*

Release response of every individual tree is different since some trees react immediately to increased space and light with a radial growth release, and others first use the energy for stabilization of root system (Urban et al. 1994). This statement is in agreement with Nowacki et Abrams (1997) who believe that radial growth response to disturbance is affected by variables as follows: (1) crown size and position, (2) gap proximity, size, and duration, (3) prior growth rate, (4) age and diameter, (5) species, and (6) climate. Therefore, it is not easy to precisely determine exact timing of disturbance especially if sample size is relatively small (Zielonka et al. 2010). Another constraint of this method is discussed in Panayotov et al. (2011): authors discuss possible suppressed growth of post-disturbance surviving individuals due to experienced damage which had greater influence on photosynthetic capacity than decline in competition. This method, nevertheless, remains one of the most accurate ones and as such is used by wide range of authors. It is also supported by fact that identification of releases is more obvious when detecting shade-tolerant species (e.g. *Picea abies*) which show release with more vigour (e.g. Lorimer et Frelich 1989, Nowacki et Abrams 1997, Black et Abrams 2003).

### *Reconstruction of natural disturbance chronology*

General disturbance history that emerges from this work is one of time by time occurring moderate-severity disturbances (small-scale disturbances are not possible to detect by used method) caused probably by host-specific agents or windstorms. The whole presented disturbance history provides only one insight into dynamics of post-disturbance development after large-scale stand replacing disturbance.

Based on presented results composite natural disturbance chronology was interpreted as follows:

a) Large scale, stand replacing disturbance in the beginning of 19th century

It is documented in almost all disturbance chronologies in spite of often low depth of sample. There are extremely rarely any trees which reached 1 m before this severe event. Many trees established exactly after this disturbance (in PRP K8 it is absolutely dominant cohort) which also supports this theory. It is very likely that this disturbance has been shaping forest dynamics including later disturbances and it has still significant impact on present forest structure (see discussion bellow).

b) Disturbance in 1915-decade

Despite 1915-decade disturbance appears in chronologies relatively indistinct it should not be underestimated. It should be kept in mind that this event occurred only less than century after the stand replacing one mentioned above. Individuals of Norway spruce in this ages are still in a good shape and therefore quite resistant. It can be therefore the reason why effect of disturbance seems quite low. Accordingly, it is very uncertain whether this event was not bigger than it appears.

c) Disturbance in 1965/1975-decade

Interpretation of this event is very complicated. There is no doubt that it was landscape level incident. But disperse (or double peak) within two decades cannot be explained by one event. Possible interpretation provides so-called synchronizing of agents (Fraver et al. 2009). The most common linking for spruce monocultures are windthrows followed by bark beetle infestation (Wichmann et Ravn 2001).

### *Occurrence of large-scale natural disturbances*

Kuuluvainen et al. (1998) believe that stand structural and spatial heterogeneity is created via small scale disturbances which dominate the landscape matrix. Similarly, Dahir et Lorimer (1996) discuss considerably high frequency of small gaps as the most common form of disturbance in temperate old-growth forests which are believed to shape the long-term structure of old-growth coniferous forest (Panayotov et al. 2011).

In contrary, Svoboda et al. (2011) believe that management practises make forest more vulnerable and therefore disturbance events affect large areas. Several works (e.g. Svoboda et Pouska 2008; Zielonka et al. 2010) demonstrated big disturbance events within coniferous forests which had experienced decades of management which did not followed natural guideline.

Above mentioned provides two quite different concepts for old-growth and managed spruce monocultures.

Presented study provides indirect confirmation of both when deducing that middle sized scale disturbances are among the most important and most common structural components of unmanaged mountain *Picea abies* forest. On the other hand, even though stand replacing disturbances occur only sporadically they can have harsh effect on forest. Simply, if disturbance is severe enough it does not make differences between old-growth and managed forest. Resulting forest structure is respecting its legacy and it is further shaped by disturbances of smaller extend.

### *Historical disturbance agents*

Many authors (e.g. Lorimer et Frelich 1989, Panayotov et al. 2011) believe that releases usually indicate either windthrow or bark beetle event. Therefore it is possible to conclude that those agents were in the most cases responsible for past disturbances. Unfortunately, using dendroecological methods do not give the possibility to distinguish those two agents from each other as proposed in Svoboda et al. (2012). Even in his work which dealt with substantially larger amount of data he could not recognize those agents in disturbance chronology. Other methods - presented in introduction – are hence important for recognizing different disturbance agents.

Ulanova (2000) proposes a way how to estimate agent of last disturbance: presence of pit-and-mound topography should be recorded because it can be used as an indicator of uprooted trees as a result of windthrow. In case of this study pits and mounds are rather occasional than ultimately ruling site topography. By far the most used type of site for natural regeneration is dead wood. The presence of dead wood and relative absence of mounds and pits especially (only 1 pit on all 12 plots!) do not indicate windthrow. Bark beetle is therefore probably responsible for last natural disturbance which occurred. According to (Zielonka et Niklasson 2001) it takes about 100 years or even longer in conditions of temperate mountain spruce forest to decompose dead wood. It is consequently possible that bark beetle was the agent of last observed disturbance during 1965-, 1975-decade. Indirect confirmation of this theory can give comparison of figures of general disturbance history and tab. 3. with natural regeneration data. PRP´s with only a little natural regeneration (K8, K11) show no or minor disturbances in recent decades. On the other hand, those with intense natural regeneration (J11, K10) simultaneously experienced significant disturbance events over the past decades. Further research and different approach is nevertheless needed to confirm this theory.

Some authors (e.g. Fraver et al. 2009) were able to find some synchronization between disturbance pulses driven by different agents (e.g. bark beetle outbreak following windthrow). In case of this study, it is unfortunately impossible to do this statement since only dendroecological approach was used. Some indicators (double or disperse peak) suggesting synchronization of disturbances can be seen during 1965-, 1975-decade. This concept has to be, nevertheless, proved by using other approaches.

The role of fire was ruled out. Although it is possible that fire could contribute to the development of some stands many centuries ago (Panayotov et al. 2011) we can exclude its influence on present stand since no evidence was observed at all.

### *Effects of past disturbances on forest structure*

It should be mentioned that one big disturbance event makes subsequent events relatively smaller because affected forest is younger, trees are smaller (Zielonka et al. 2010), and therefore ecosystem has overall higher resilience. That can be in some cases reason for declining severity of disturbances after the big event. That is in agreement with (e.g. Kulakowski et Veblen 2002, Panayotov et al. 2011) who present the idea that structure of forest which had been left by past disturbances has strong influence on responses to later disturbances as well as on recovery from them. Presented results support this theory. Large - possibly stand replacing - event from the beginning of 19th century is for almost one hundred years the only significant disturbance event. It is highly unlikely that for nearly a century no windstorm, bark beetle, or other disturbance-causing-factor occurred. More possible explanation is high resilience of young and healthy ecosystem which can easily withstand such impacts. Perfect example of such site development is PRP K8 (disturbance chronology chart see in Appendix). What is more, by observing the further record of this PRP it is obvious that reaction of trees on later disturbances is very low. It can be explained by fact that individual in even-aged forest with all trees reaching canopy reacts only very indistinctly on improved site conditions which is in agreement with e.g. Splechtna et al. (2005).

Presented forest chronologies with displayed disturbance events ranging in the size and frequency provide strong argument that those were integral part of forest dynamics for long time and one is influencing the other via its imprint into resulting forest structure.

### *Effects of other factors on forest response – field for further investigations*

It is not without interest that screening results charts of disturbance chronology some sites show relatively intensive natural disturbance impacts (J11, K9, L8) while others seems relatively stable over their lifespan (K8, K11). Natural disturbances are not the only agent affecting stand mortality. As such it is also influenced by site conditions as slope, quality and depth of soil, aspect, local geomorphology, and hydrological properties. It can be therefore expected that variety of reactions on the same disturbance will be wide even in even aged forest. This different sensitivity on same disturbance should be taken into account when interpreting results because it possibly represents reason why some sites shows bigger portion of disturbed individuals in contrary with the other sites often closely located. Considering this problem from opposite site, it is important to remember that same scale release events in different types of disturbance chronologies (rough vs. smooth) can represent different magnitude of disturbance. Ignoring this fact can possibly lead to misinterpretation. It is hence crucial in further studies to put more emphasis on distinguishing those two types of disturbance chronologies and quantify their effects on results to improve quality of interpretation for both stand and landscape level.

# 6. Conclusion

Disturbance history of old-growth mountain spruce forest in Giumalau Mountains is complex phenomenon. Specifically, large event in the beginning of 19th century has changed the forest landscape significantly. Resulting even-aged forest was able to withstand natural impacts for almost a century due to its low age and accompanied high resilience. Since 1915-decade disturbance it is possible to observe subsequent replacement of trees always after smaller events. One more event in 1965-, 1975-decade changed the forest structure more significantly; in the most sites resulting in enhanced natural regeneration. Relatively long duration (or double peaking) of this event can be explained by synchronization of agents. This concept, nevertheless, has to be verified using capable methods.

It has been proven that middle sized disturbance events are important and integral part of forest dynamics of temperate old-growth mountain spruce forests. High severity – stand replacing – disturbances occur only sporadically but they have strong influence on age and spatial forest structure for subsequent decades.

This study provides insight into the natural disturbance regime of mountain *Picea abies* old-growth forest in Carpathians. Knowledge of past forest dynamics of old-growth is essential from the point of view of applied forest management using nature as a guide to maintain maximal structural and habitat diversity. But it is also important in context of climatic changes. Disturbance chronology can help to distinguish trends and patterns of changing climate.

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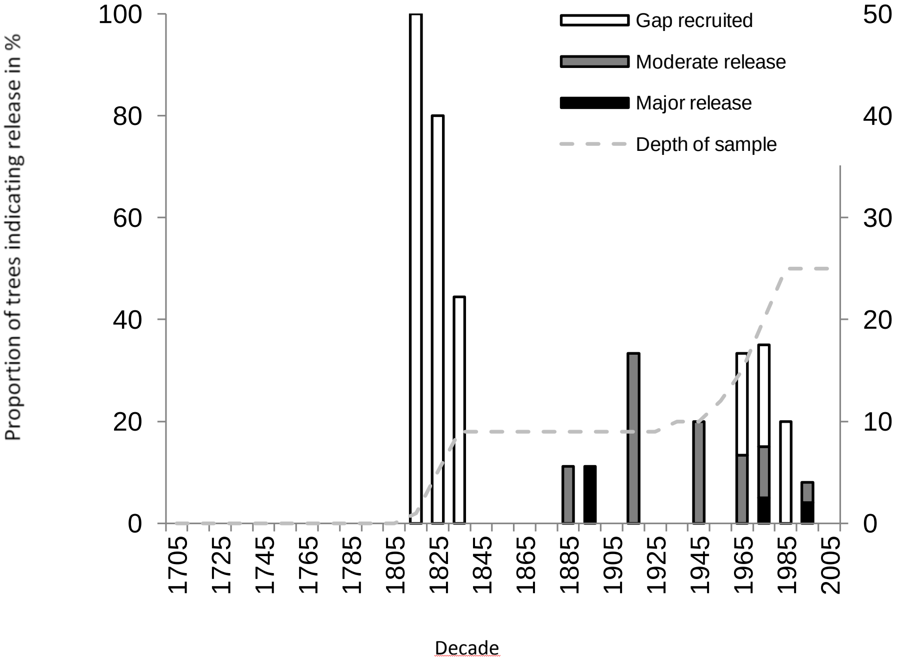
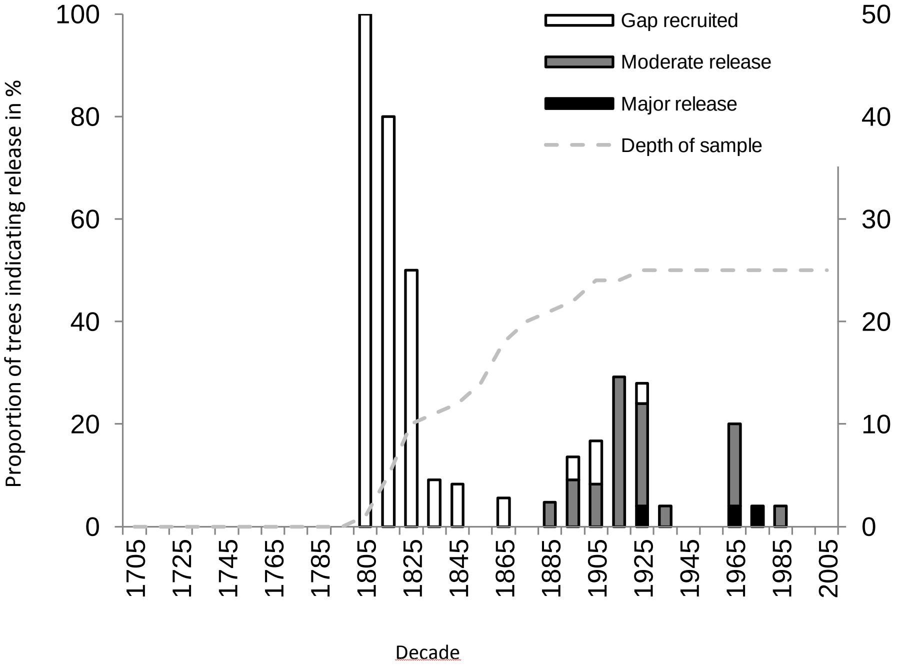
# Appendix

## 1) Disturbance chronologies of permanent research plots

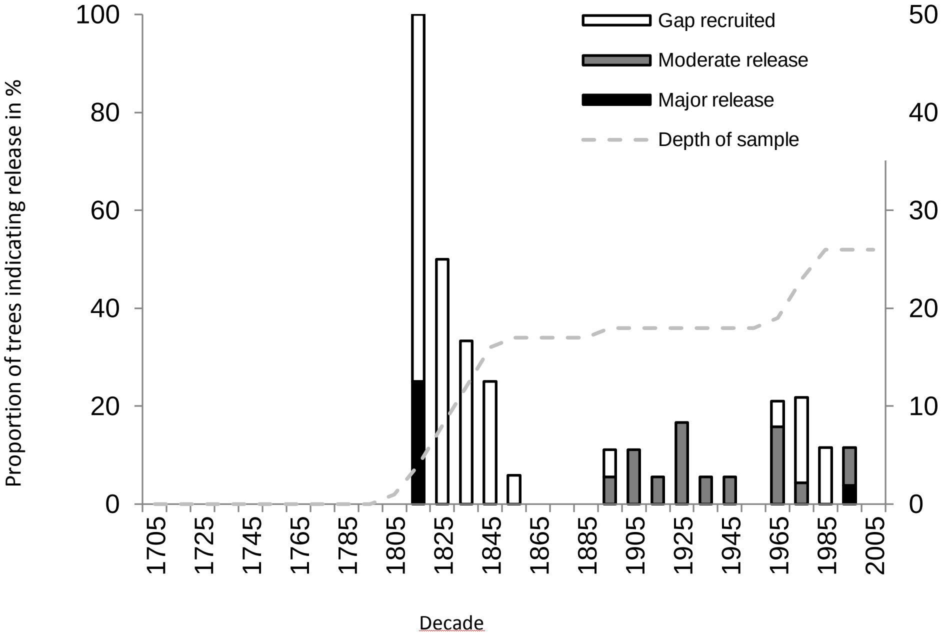
a) L8



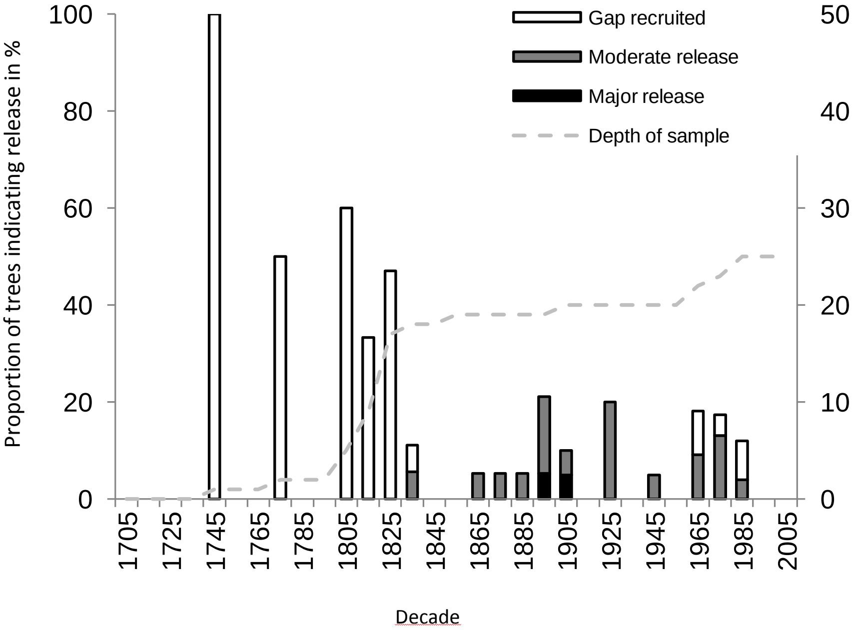
b) L9



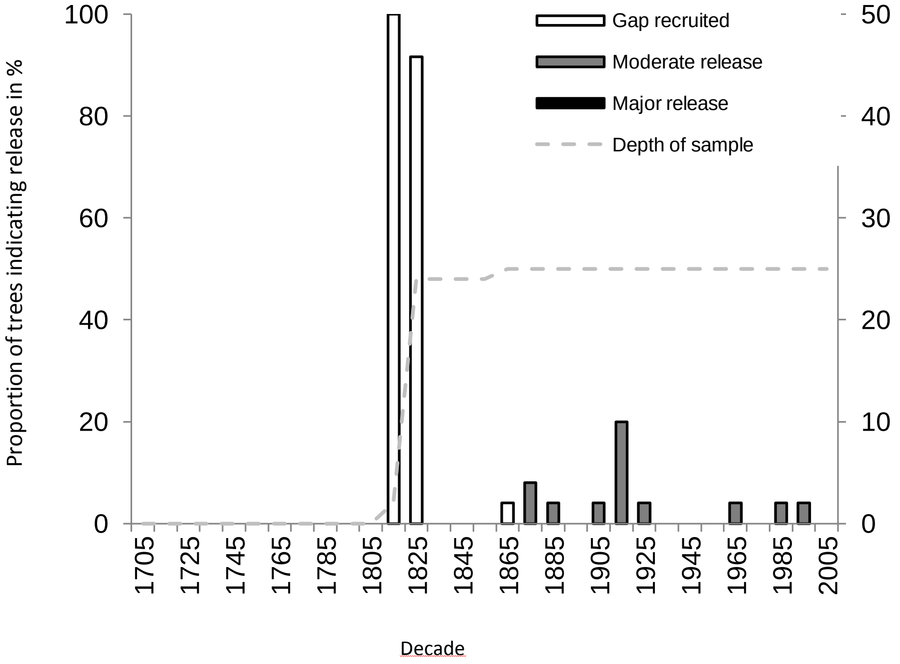
c) L10


Proportion of trees indicating release in %
0
20
40
60
80
100
0
10
20
30
40
50
Gap recruited
Moderate release
Major release
Depth of sample
1705
1725
1745
1765
1785
1805
1825
1845
1865
1885
1905
1925
1945
1965
1985
2005
Decade

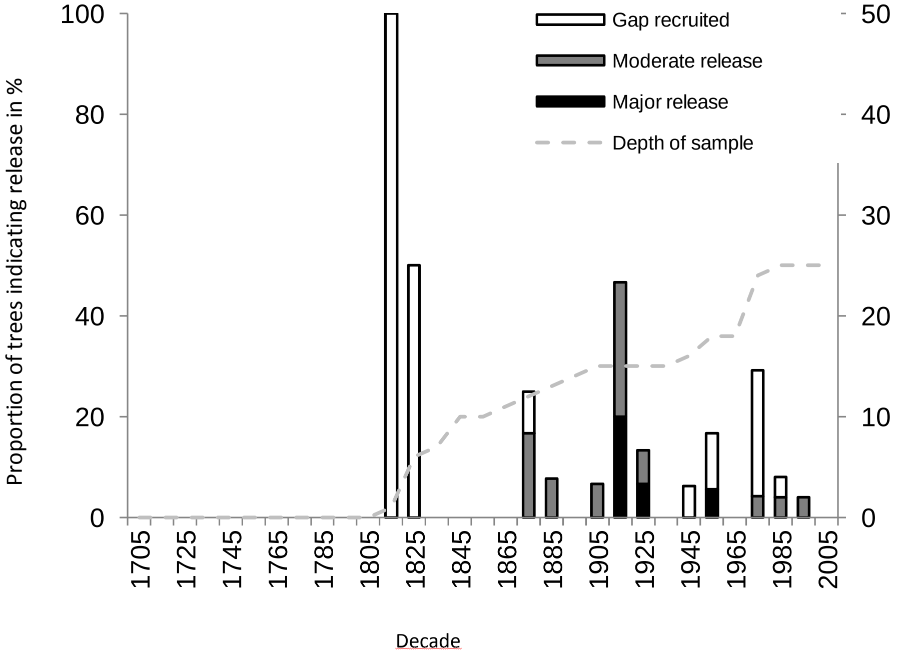
d) L11


Proportion of trees indicating release in %
0
20
40
60
80
100
0
10
20
30
40
50
Gap recruited
Moderate release
Major release
Depth of sample
1705
1725
1745
1765
1785
1805
1825
1845
1865
1885
1905
1925
1945
1965
1985
2005
Decade

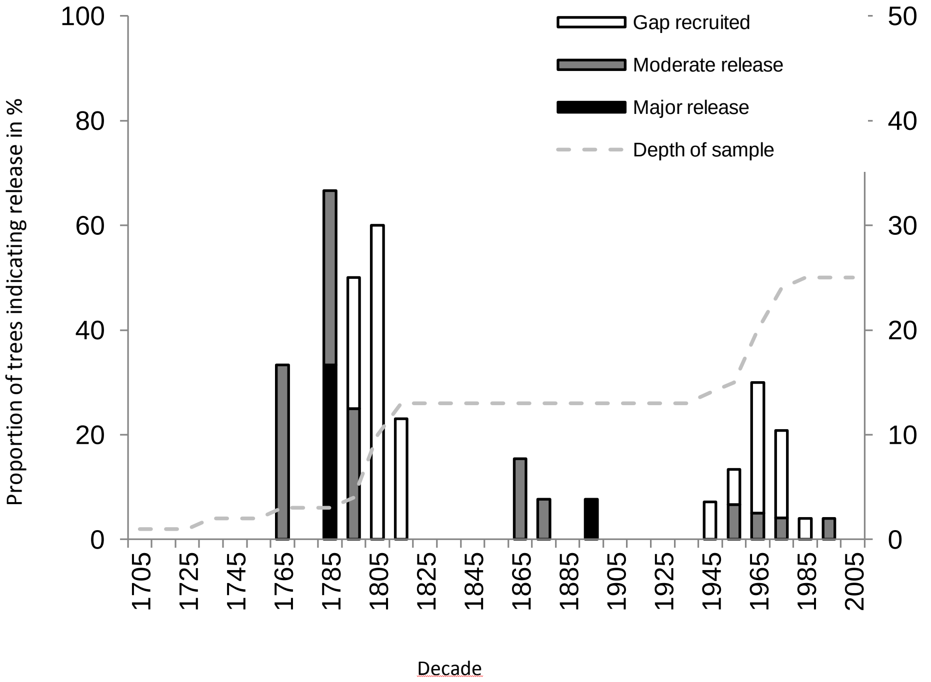
e) K8


Proportion of trees indicating release in %
100
80
60
40
20
0
50
40
30
20
10
0
Gap recruited
Moderate release
Major release
Depth of sample
1705
1725
1745
1765
1785
1805
1825
1845
1865
1885
1905
1925
1945
1965
1985
2005
Decade

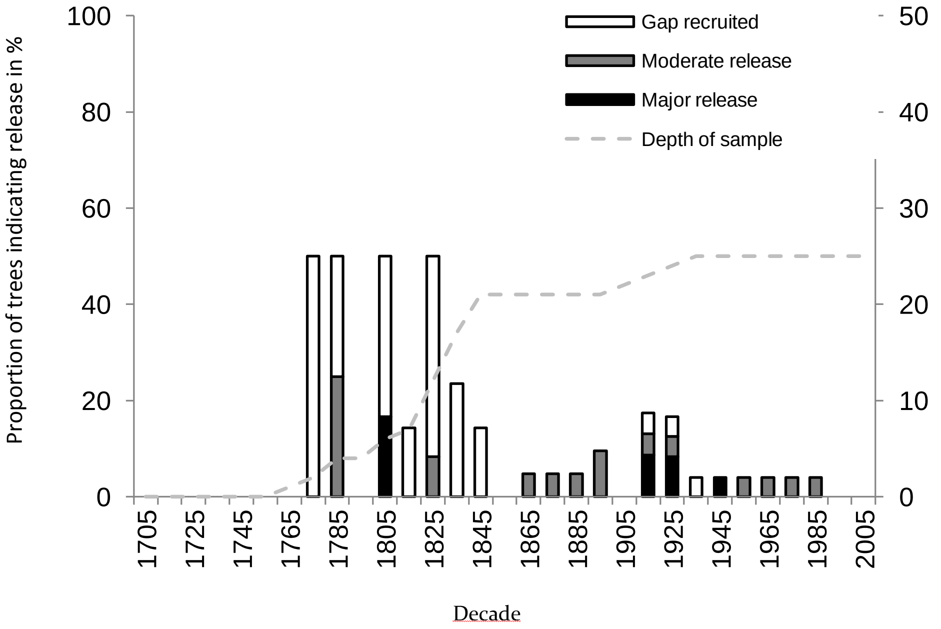
f) K9


Proportion of trees indicating release in %
100
80
60
40
20
0
50
40
30
20
10
0
Gap recruited
Moderate release
Major release
Depth of sample
1705
1725
1745
1765
1785
1805
1825
1845
1865
1885
1905
1925
1945
1965
1985
2005
Decade

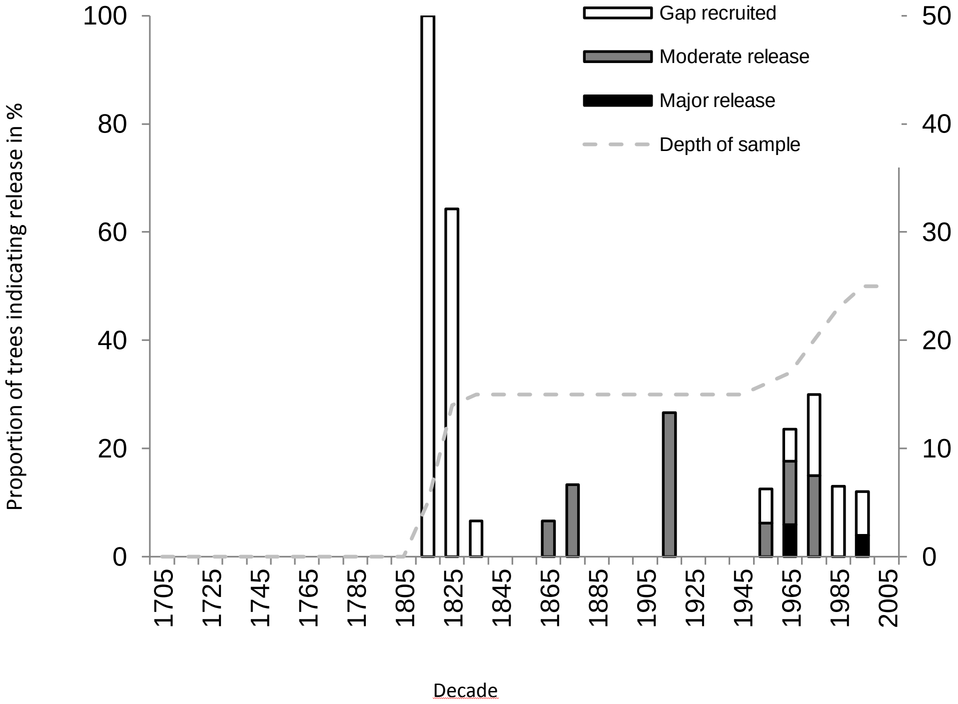
g) K10


Proportion of trees indicating release in %
100
80
60
40
20
0
50
40
30
20
10
0
Gap recruited
Moderate release
Major release
Depth of sample
1705
1725
1745
1765
1785
1805
1825
1845
1865
1885
1905
1925
1945
1965
1985
2005
Decade

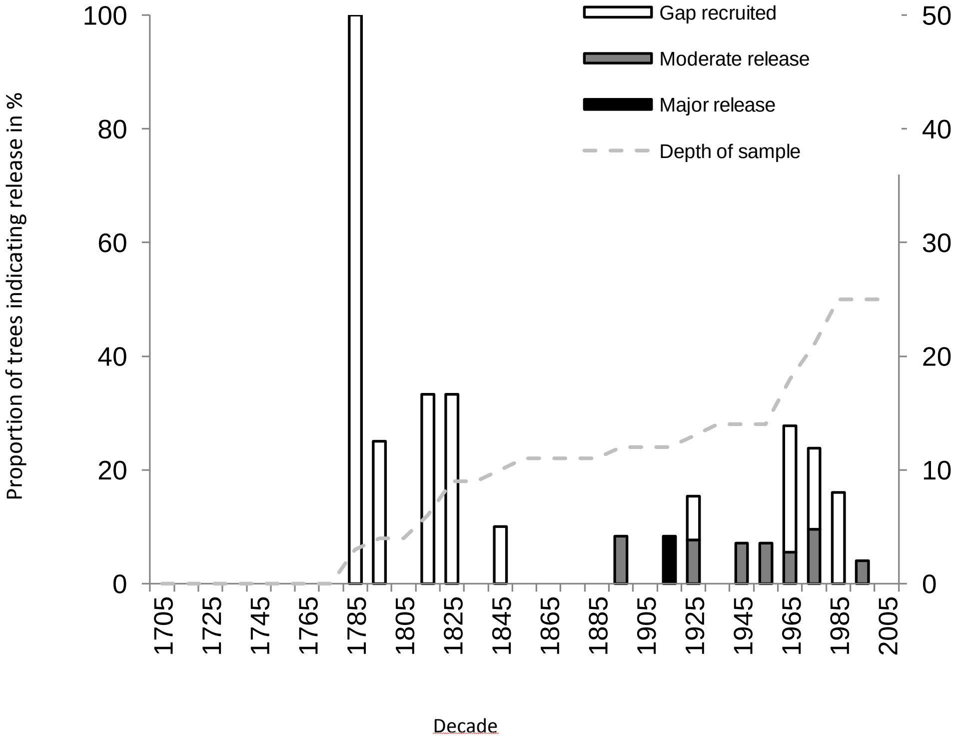
h) K11


Proportion of trees indicating release in %
100
80
60
40
20
0
50
40
30
20
10
0
Gap recruited
Moderate release
Major release
Depth of sample
1705
1725
1745
1765
1785
1805
1825
1845
1865
1885
1905
1925
1945
1965
1985
2005
Decade

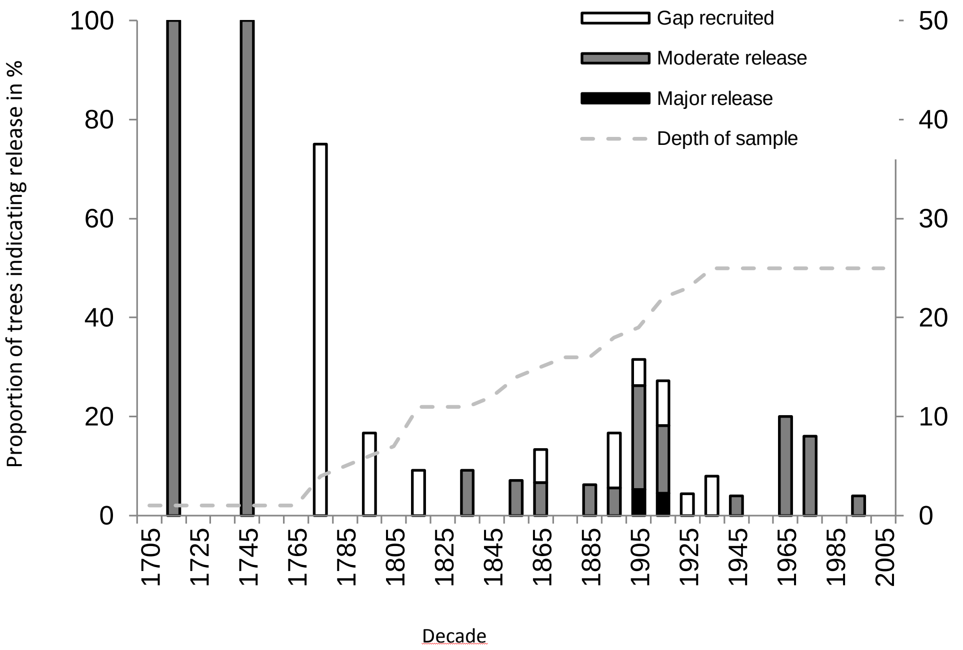
i) J8


Proportion of trees indicating release in %
100
80
60
40
20
0
50
40
30
20
10
0
Gap recruited
Moderate release
Major release
Depth of sample
1705
1725
1745
1765
1785
1805
1825
1845
1865
1885
1905
1925
1945
1965
1985
2005
Decade

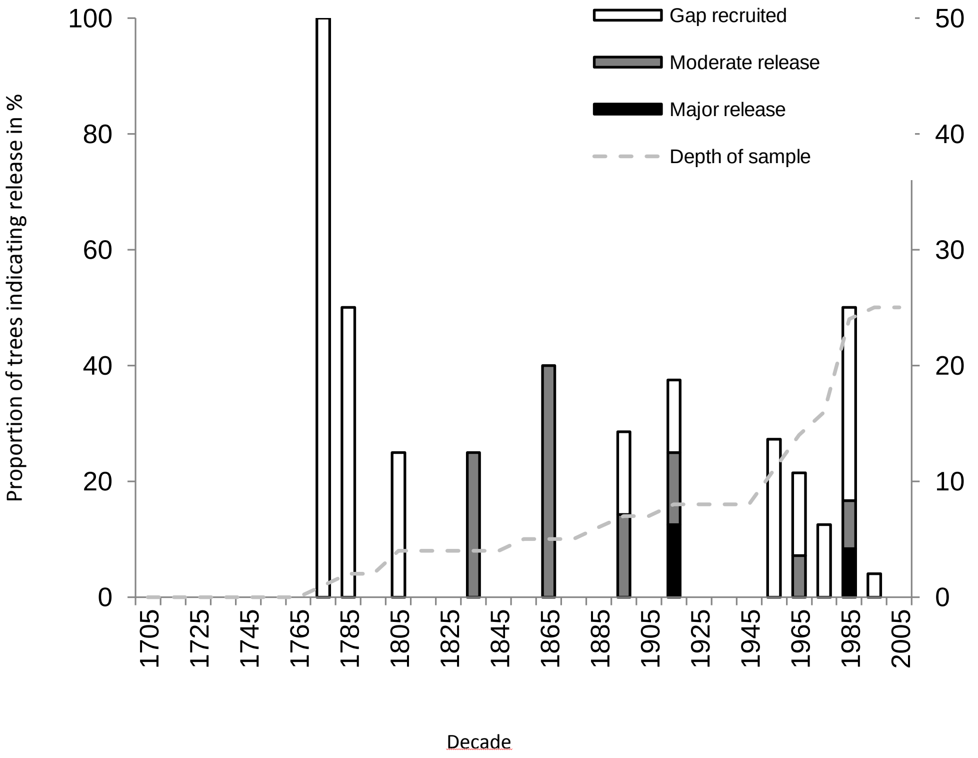
j) J9


Proportion of trees indicating release in %
100
80
60
40
20
0
50
40
30
20
10
0
Gap recruited
Moderate release
Major release
Depth of sample
1705
1725
1745
1765
1785
1805
1825
1845
1865
1885
1905
1925
1945
1965
1985
2005
Decade

k) J10


Gap recruited
Moderate release
Major release
Depth of sample
Proportion of trees indicating release in %
Decade
100
80
60
40
20
0
50
40
30
20
10
0
1705
1725
1745
1765
1785
1805
1825
1845
1865
1885
1905
1925
1945
1965
1985
2005

l) J11

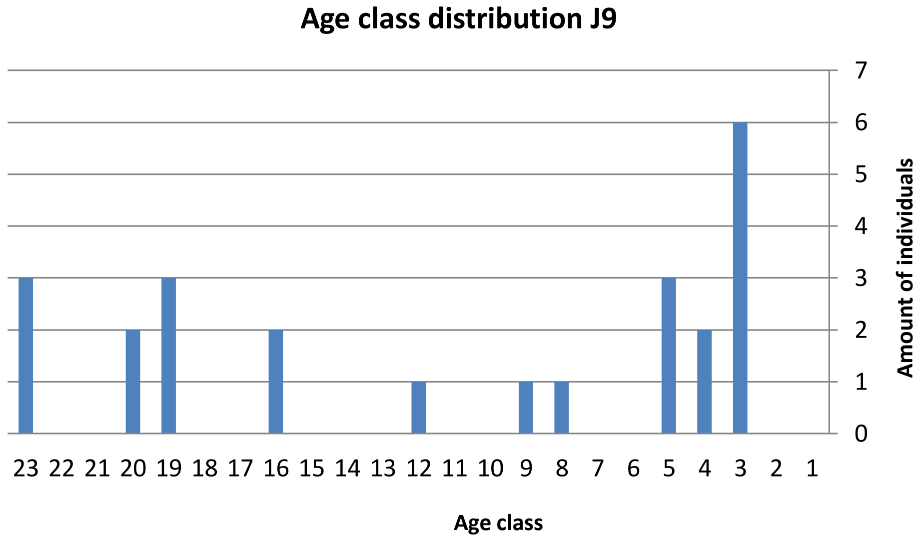

Gap recruited
Moderate release
Major release
Depth of sample
Proportion of trees indicating release in %
Decade
100
80
60
40
20
0
50
40
30
20
10
0
1705
1725
1745
1765
1785
1805
1825
1845
1865
1885
1905
1925
1945
1965
1985
2005

## 2) Age class distributions for permanent research plots

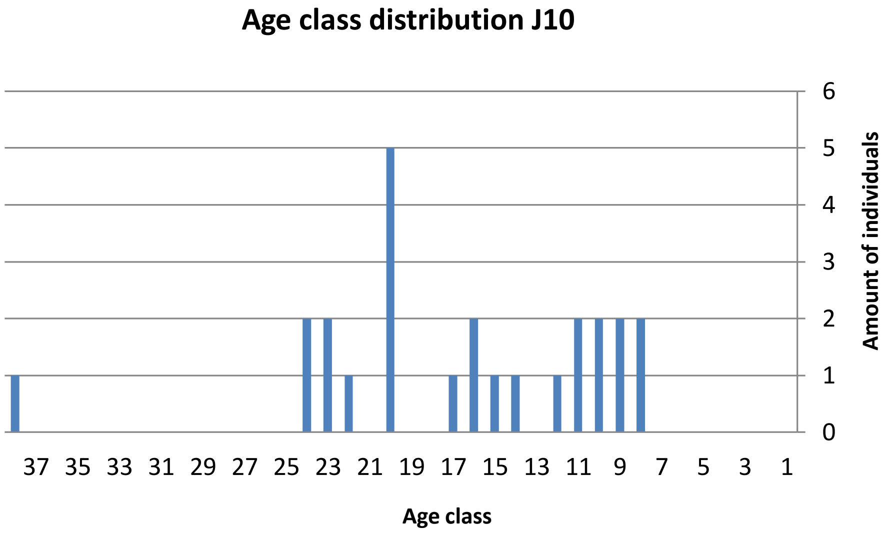
(after 1 m recruitment)

a) J8

b) J9

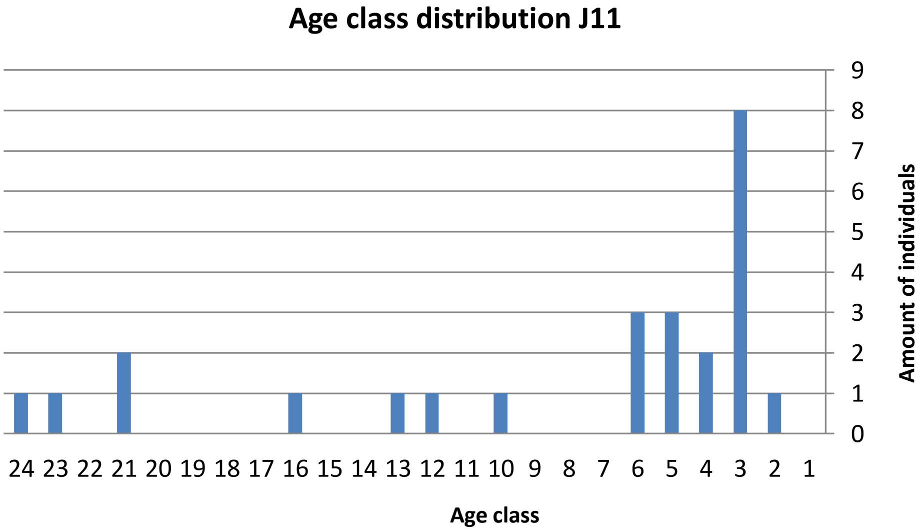


c) J10



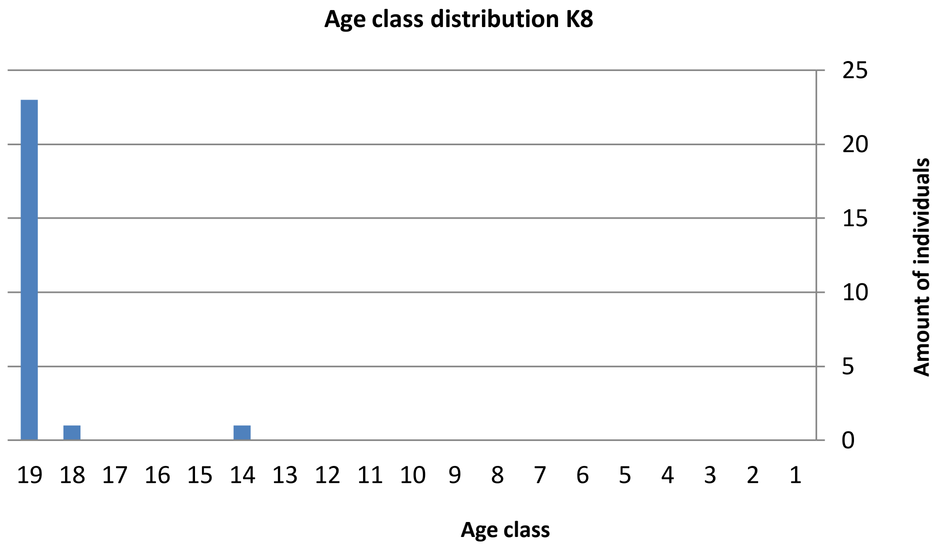
Age class distribution J10
6
5
4
3
2
1
0
Amount of individuals
37 35 33 31 29 27 25 23 21 19 17 15 13 11 9 7 5 3 1
Age class

d) J11

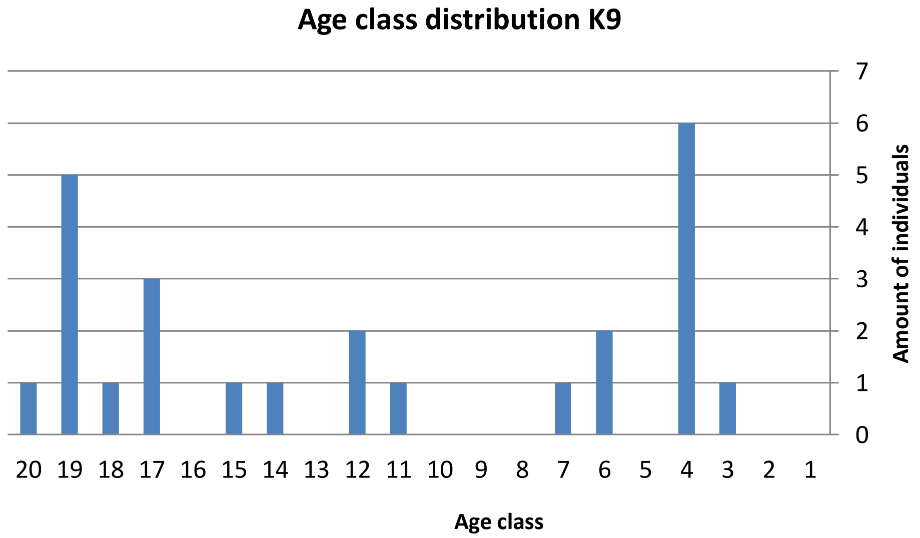


Age class distribution J11
9
8
7
6
5
4
3
2
1
0
Amount of individuals
24 23 22 21 20 19 18 17 16 15 14 13 12 11 10 9 8 7 6 5 4 3 2 1
Age class

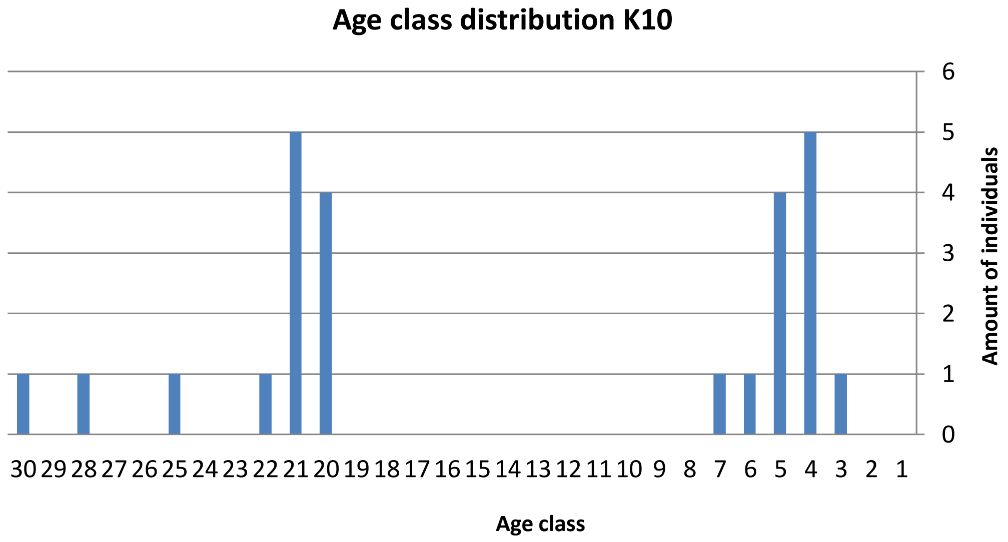
e) K8


Age class distribution K8
25
20
15
10
5
0
Amount of individuals
19 18 17 16 15 14 13 12 11 10 9 8 7 6 5 4 3 2 1
Age class

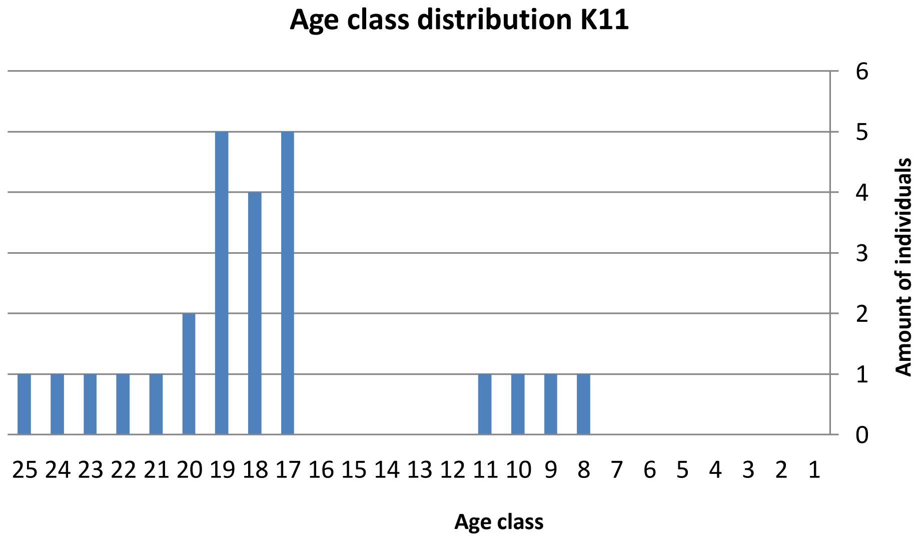
f) K9


Age class distribution K9
7
6
5
4
3
2
1
0
Amount of individuals
20 19 18 17 16 15 14 13 12 11 10 9 8 7 6 5 4 3 2 1
Age class

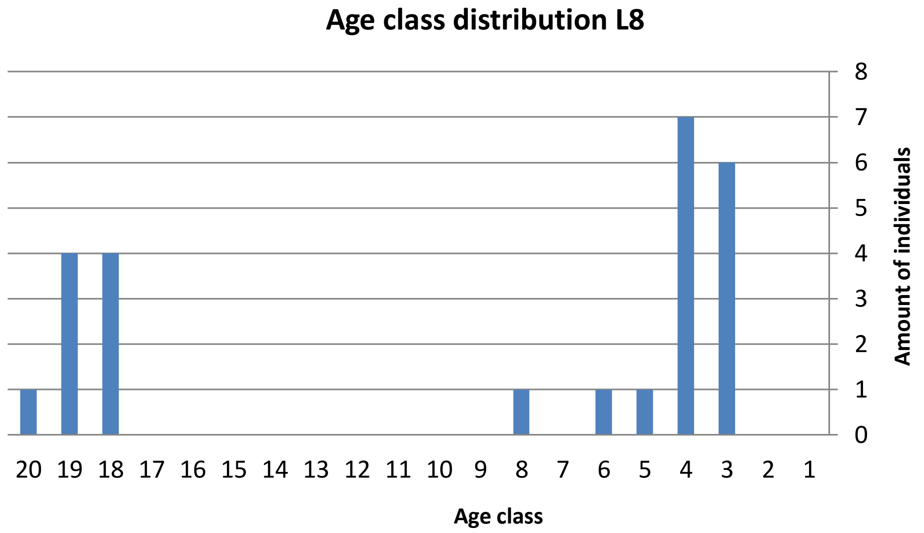
g) K10


Age class distribution K10
6
5
4
3
2
1
0
Amount of individuals
30 29 28 27 26 25 24 23 22 21 20 19 18 17 16 15 14 13 12 11 10 9 8 7 6 5 4 3 2 1
Age class

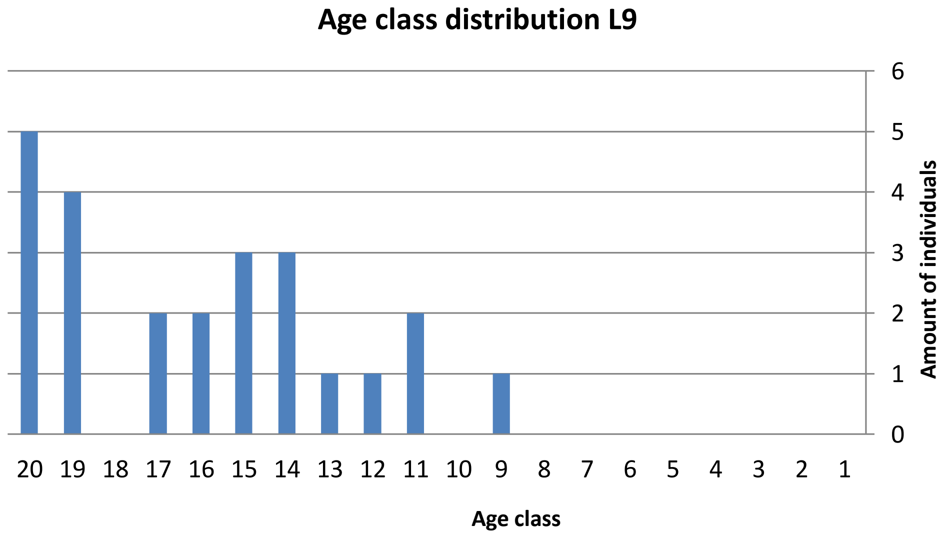
h) K11


Age class distribution K11
6
5
4
3
2
1
0
Amount of individuals
25 24 23 22 21 20 19 18 17 16 15 14 13 12 11 10 9 8 7 6 5 4 3 2 1
Age class

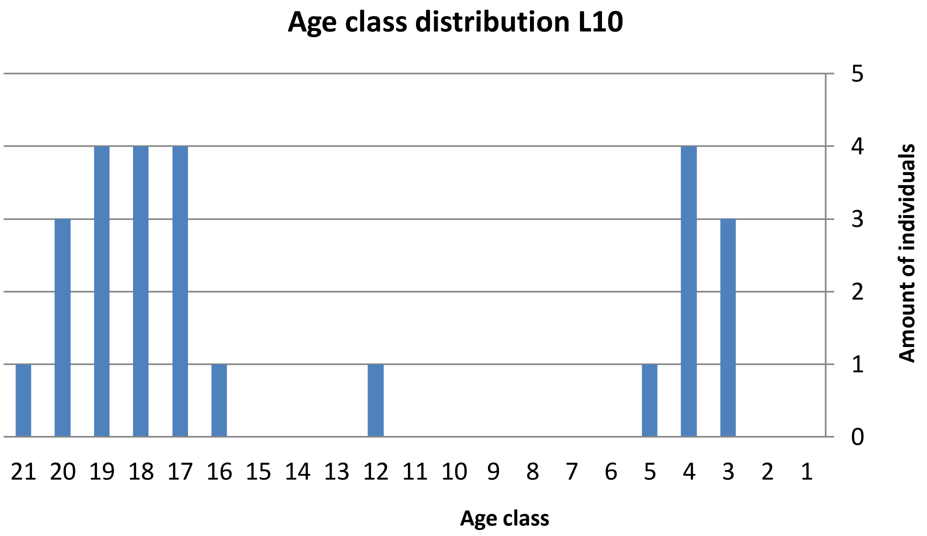
i) L8


Age class distribution L8
Amount of individuals
0
1
2
3
4
5
6
7
8
20 19 18 17 16 15 14 13 12 11 10 9 8 7 6 5 4 3 2 1
Age class

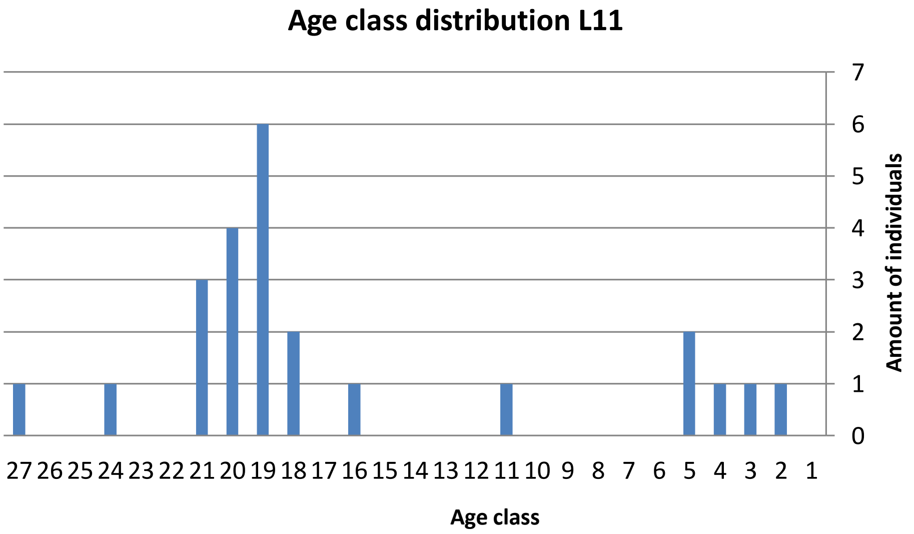
j) L9


Age class distribution L9
Amount of individuals
0
1
2
3
4
5
6
20 19 18 17 16 15 14 13 12 11 10 9 8 7 6 5 4 3 2 1
Age class

k) L10


Age class distribution L10
0
1
2
3
4
5
Amount of individuals
21 20 19 18 17 16 15 14 13 12 11 10 9 8 7 6 5 4 3 2 1
Age class

l) L11


Age class distribution L11
0
1
2
3
4
5
6
7
Amount of individuals
27 26 25 24 23 22 21 20 19 18 17 16 15 14 13 12 11 10 9 8 7 6 5 4 3 2 1
Age class