

# Natural structures and disturbances in an old growth wet Norway spruce forest in the nature reserve Gruzdovas meži, Latvia

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## Abstract

To increase wood productivity, wet Norway spruce forests have been subject to drainage. In Latvia natural wet Norway spruce stands are rare, and research on these forest types is insufficient. We studied forest structures and disturbance in the nature reserve Gruzdovas meži, which appeared to include the largest (5.6 ha) old wet Norway spruce stand in Latvia. Four sampling plots were established in a *Myrtilloso-polytrichosa* stand. Data on tree species composition, age, diameter and height was collected. Periods of major disturbances were determined by growth release analysis. The stands had multi-age structure, characteristic of old, natural forest. The oldest Norway spruce was 273 years old. High numbers of Norway spruce seedlings indicated abundant natural regeneration. The maximal age of trees indicated the naturalness of the area. The age structure and growth release analysis indicated regeneration after the large-scale disturbances (wind, snow). The amount of dead wood was high ( $82 \text{ m}^3 \text{ ha}^{-1}$ ). The results showed that the investigated stand is oldest natural Norway spruce forest in Latvia.

**Key words:** dead wood, disturbance history, paludified forest, *Picea abies*, stand naturalness, stand regeneration..

**Abbreviations:** CWD, coarse wood debris; DBA, diameter at breast height.

## Introduction

Natural boreal forests have almost completely disappeared, leading to declining biodiversity. For example, in forests in Finland it has been estimated that approximately 1000 species have disappeared (Hanski 2000). Today, the total area of boreal forests is 10% of the land surface on earth (Bonan, Shugart 1989; Hytteborn et al. 2005), but they have been under human influence for many centuries (Rouvinen, Kouki 2008). Modern forest management is the major problem leading to the decline of natural forests (Kuuluvainen, Aakala 2011). As a result of the intensive forest management, the biggest and oldest trees that otherwise would have died naturally are removed (Linder, Östlund 1992). Areas of natural forest still exist at high northern latitudes (Hytteborn et al. 2005). Diversity of structures, present in natural forests, is needed for sustainability and quality of ecosystems (Clark, Richard 1996; Angelstam, Kuuluvainen 2004; Hytteborn et al. 2005). High amounts of dead wood in different decay classes present in natural forests (Chambers et al. 2000; Storaunet, Rolstad 2004; Aakala et al. 2008; Wallenius et al. 2010) are crucial for biodiversity (specialist species) (Siitonen 2001)

It takes many decades for a managed forest to attain part of the features of a natural forest and over 100 years to produce the full spectrum of structures (Fraver et al. 2008).

Natural Norway spruce forests, in contrast to managed forests, have higher age of trees; the stands are formed by trees of various age and dimensions, and contain high amounts (volume) of dead wood in different decay stages (Lilja et al. 2006; Fraver et al. 2008). Natural structures are created by disturbances, which vary depending on forest characteristics location and regional climate conditions (Motta 2003; Angelstam, Kuuluvainen 2004; Hytteborn et al. 2005). Natural disturbances can be divided into four groups based on the successional processes: (i) stand replacement dynamics, which is evident after large scale disturbance, when all trees have died at the same time (example, fire); (ii) cohort dynamics, which is related to partial shift of stand composition after medium scale disturbance, mortality of trees with specific characteristics; (iii) patch dynamics – tree mortality at intermediate scales ( $> 200 \text{ m}^2$ ) and (iv) gap dynamics driven by tree mortality at fine scales ( $< 200 \text{ m}^2$ ) (Kuuluvainen, Aakala 2011). Gap dynamics disturbance in natural Norway spruce (*Picea abies*) is the most common type (Kuuluvainen, Aakala 2011). Gap dynamics become the dominant regeneration type as trees age and suffer mortality, leaving place for new trees to establish. Formation of gaps when single trees or small groups of trees die is caused by wind, snow break, and by trees reaching their maximal ages (Aakala 2011). Such small scale disturbances (formation of gaps

in the canopy) create a heterogenic (mosaic structure) forest pattern (Fraver, White 2005; Shorohova et al. 2009). Gaps are an indication of natural disturbance processes, whereby trees suffer mortality naturally without human influence (Leemans 1991). Fire that promotes mineral turnover (DeBano, Neary 2005) and creates deadwood (Essen et al. 1997; Pennanen 2002) rarely occurs in Norway spruce stands (Clark, Richard 1996; Wallenius et al. 2004; Wallenius et al. 2005). In natural Norway spruce forests where regeneration and mortality are in balance, a J-shape age distribution is characteristic, with larger amounts trees in the youngest age classes (Groven et al. 2006; Lilja et al. 2006).

In Latvia, boreal forests can be divided into boreal and boreo-nemoral forests (Hytteborn et al. 2005). Latvia is rich in forest lands (~55% of territory), but old forests are relatively rare (Tērauds et al. 2011). According to Latvian State Forest Service forest inventory data (2011), Norway spruce stands with age of 100, 150 and 200 years occupy 0.56%, 0.04% and 0.001% of the total forest area, respectively. The cutting age of Norway spruce was reduced from 150 years in 1871 (Zviedris 1960) to 81 years in 2009 in managed forests (Laiviņš 2005). It has been considered that Norway spruce stands with age > 200 years cannot be found in Latvia (Laiviņš 2005). In the present condition, when logging has reached a high intensity in Latvia, it is important for conservation of biological diversity to identify the most natural Norway spruce stands in Latvia. The aim of the study was describe naturalness of the oldest Norway spruce stand in the nature reserve Gruzdovas meži, which according to forest inventory data of the Latvian State Forest Service, contained some of the oldest stands in Latvia. This done by examining the stand structure and also disturbance history using growth release analysis.

## Materials and methods

### Study area

The studied stand was chosen from the Latvian State Forest register using criteria of age > 190 years and area > 4 ha. The stand, located in the nature reserve Gruzdovas meži, had an area of 5.6 ha. The nature reserve Gruzdovas meži is located in south-eastern Latvia (Fig. 1). The total area of the nature reserve is 274 ha. It was established in 1999, with the aim to protect biologically valuable wet paludified forest stands. Historically, forest management in the territory of the reserve has been minimal, due to lack of infrastructure, which has resulted in high biodiversity (Rove 2003). The study area is located in the Eastern Latvian lowland, which has level relief and altitude 123 m above sea level (Pūriņš 1975). The climate is fairly continental (hydrothermal coefficient 1.8 to 1.9 (Rove 2003). The average annual temperature is 4.8 °C. The coldest months are January and February, when mean temperature is -6.5 to -7.4 °C and minimum mean temperature is -27 °C. Mean temperature

in July is 16.5 to 17.3 °C. The average annual precipitation is 550 to 560 mm and snow depth is 25 to 35 cm (60 cm in some places). Snow cover remains 130 days yearly.

The studied forest is typical of the boreal forest zone (Hytteborn et al. 2005). The sampling plots were located in a flat depression with wet growing conditions. Microrelief in the sampling plots is formed by a dense pit and mound structure caused by wind throws. The site type according to the Latvian forest typology was *Myrtilloso-polytrichosa* (Bušs 1981). In the studied *Myrtilloso-polytrichosa* forest stand the overstorey tree species were Norway spruce, black alder (*Alnus glutinosa*), birch (*Betula* sp.) and Eurasian aspen (*Populus tremula*).

### Sampling

Four sampling plots (50 × 20 m) were established. Middle point coordinates (LKS92 TM) of sampling plots were X 717226 Y 350597; X 717231 Y 350617; X 717453 Y 350612; X 717517 Y 350420. In the plots height and diameter at breast height (DBH) were measured for all living trees with DBH ≥ 10 cm, and increment cores were taken with a Pressler increment borer as close as possible to stem base. We ensured that increment cores contained wood maximally close to the pith for more accurate estimation of age. Trees with DBH < 10 cm were counted and divided into five height classes: 0 to 1 m, 1.01 to 2 m, 2.01 to 5 m, 5.01 to 10 m. For estimation of coarse woody debris (CWD) amount, diameter at mid length and the length were measured for all logs originating in the sampling plot. Decay stage of CWD was determined according the 5-point scale of Spies et al. (1988).

### Laboratory procedures

Increment cores were dried and then glued into prefabricated wooden mounts. The cores were then gradually sanded with a vibration sander (Makita BO3700) using progressively finer sandpaper (120, 240, 400 and 600). Sawdust was removed by compressed air. Tree-ring width was measured on a LINTAB 5 table equipped with a MS5 microscope and the program TSAP (Time Series Analysis). For more precise age estimation from cores that lacked pith, age correction was made. For the last completely visible tree-ring the approximate radius (potential distance to the pith) was estimated. Number of missing tree-rings was calculated by dividing the estimated radius of last tree-ring with the mean width of the last 10 complete tree-rings.

### Data analysis

The stand visually appeared homogenous, but to ensure representative data for the stand, data for the four sampling plots (total area 0.4 ha) were pooled. Measurement quality was checked using the program COFECHA (Grissino-Mayer 2001) and graphically. The trees were difficult to cross-date, as is typical for slow-growing Norway spruce (Drobyshev, personal communication). To determine past

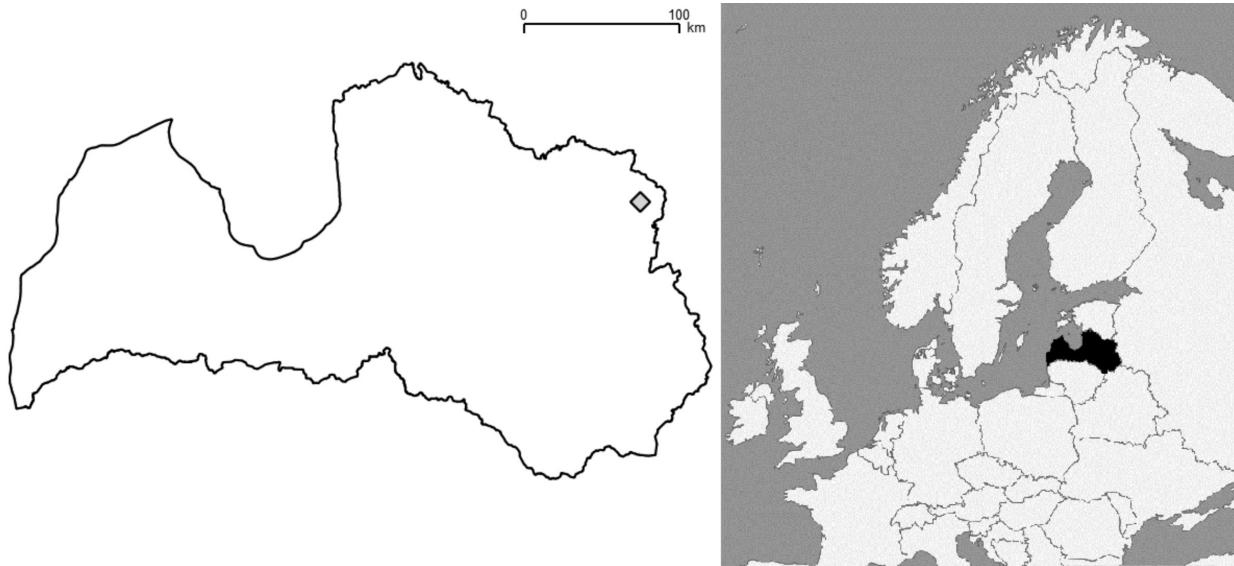


Fig. 1. Location of the study area.

disturbances, growth release analysis was conducted for Norway spruce. In the analysis, we only included trees that showed similar growth (interseries correlation > 0.15) with other trees during quality checking. From 232 originally measured time-series of tree-ring width, 180 were used for growth release analysis. For each tree ring, we calculated increase in growth in the subsequent 10-year period, compared to the previous 10-year period, as follows:

$$\Delta_i = \frac{M_2 - M_1}{M_1},$$

where  $M_1$  = mean tree-ring width in the previous 10-years and  $M_2$  = mean tree-ring width in next 10-years including the current year. For each year, the proportion of trees with  $\Delta_i > 0.5$  was determined. A large release period was considered to have occurred in years when the proportion of trees showing release was  $\geq 25\%$ .

Pearson correlation analysis (Sokal, Rohlf 1995) was performed to test the relationship between diameter and age of trees.

## Results

In total 1899 trees were measured, of which tree-ring width measured for 315 trees. Density of the stand was 802 trees  $\text{ha}^{-1}$ . Norway spruce trees were represented in all diameter classes (Fig. 2A), but with higher density in the < 10 cm diameter class. The maximum diameter of Norway spruce was 56 cm (mean 19.7 cm). Black alder mean diameter was 22.9 cm and birch 24.3 cm (Fig. 2A). The dominant species in the shrub/sapling layer with diameter < 10 cm were alder buckthorn (*Frangula alnus*), rowan (*Sorbus aucuparia*), willow (*Salix* sp.) and pedunculate oak (*Quercus robur*).

Most of the Norway spruce trees were in height classes 0 to 1 m and 1.01 to 2 m (Fig. 2B). Norway spruce mean height was 19.3 m, black alder 21.9 m and birch 23.6 m.

Birch and black alder were represented in all diameter classes.

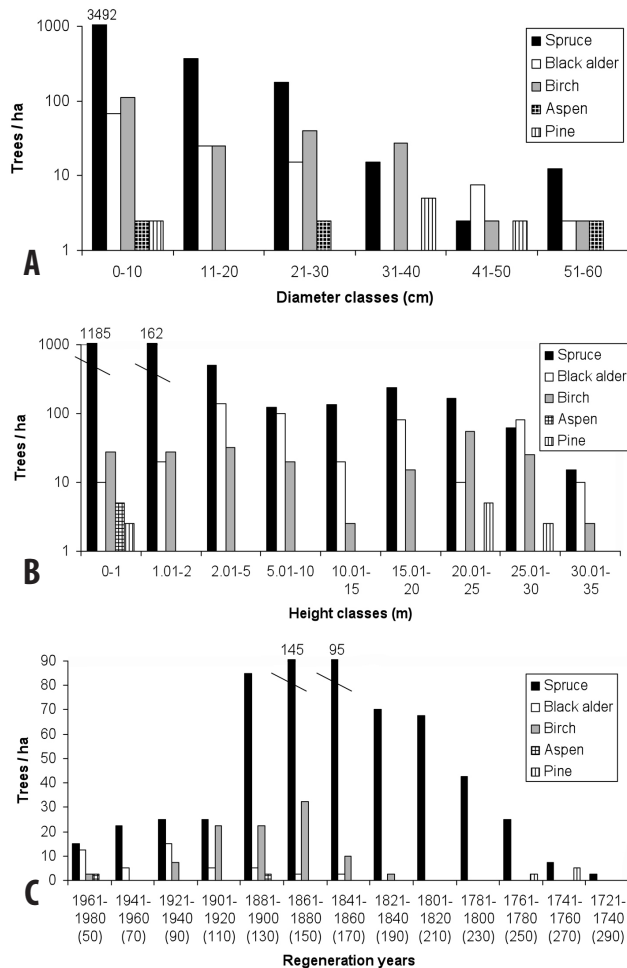
The oldest Norway spruce was 273 years. Most of the Norway spruce trees were in the 131 to 150 age class, which had established in the period from 1861 to 1880 (Fig. 2C). Density of Norway spruce was low in the youngest age classes (50 to 130 years), as age was determined only for trees with DBH  $\geq 10$  cm (Fig. 2C). Norway spruce density was lower in the oldest age classes. In the 1861 to 1920 period, abundant birch had established (Fig. 2C). The oldest birch age was 178, which was in the age class 1821 to 1840. Black alder regeneration was higher in 1921 to 1940 (Fig. 2C). The oldest black alder tree was 166 years. All Scots pine (*Pinus sylvestris*) trees in the sampling plot had regenerated in 1741 to 1780 and the oldest Scots pine was 264 years (Fig. 2c).

The correlation of Norway spruce age with diameter was low ( $r = 0.23$ ) and explained only 5% of the variation (Fig. 3). However, the age-diameter relationship for black alder was strong ( $r = 0.85$ ), explaining 72% of the variability. Mean log diameter was 19 cm and deadwood volume was 82  $\text{m}^3 \text{ha}^{-1}$ .

Growth release analysis showed four pronounced peaks of abrupt large tree-ring width increase of many trees in the stand during the period from 1800 to 2011 (Fig. 4). These peaks occurred in 1853, 1875, 1943 and 1970. The strongest increase (release) of growth occurred in 1970. In the analysed period there were also several weaker releases, however they were visible in about 30% of trees.

## Discussion

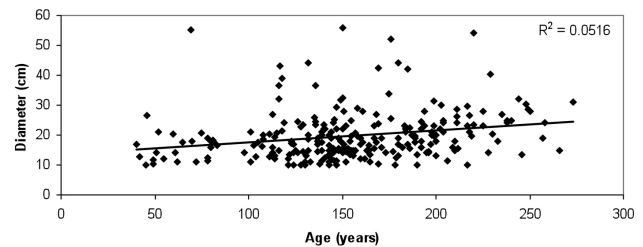
According to the Latvian State Forest Service data base, age of the studied stand was 192 years. The difference in age compared to the oldest tree (273 years) in the stand was



**Fig. 2.** Diameter (A), height (B) and age structure (C) of dominant tree species in the studied *Myrtilloso-polytrichosa* forest stand (trees ha<sup>-1</sup>): Norway spruce, black alder, birch, Eurasian aspen, and Scots pine. Number of trees is shown on broken columns. In 2C, maximal ages of age classes are given.

81 years. According to expert view (M. Laiviņš, personal communication), according to the observed ages of Norway spruce in reserve Gruzdovas meži, the stand is the oldest known Norway spruce stand in Latvia. In Finland, Norway spruce rarely survives to 300 years (Sirén 1955; Wallenius 2002; Angelstam, Kuuluvainen 2004; Lilja et al. 2006), which implies high biological value of studied stand also on a Northern European scale. In the stand the maximum age of birch was 178 years. This surpasses the average lifespan of 150, but birch can live up to even 300 years (Hytteborn et al. 2005). According to the literature, maximal age of black alder is 300 years (Mauriņš, Zvirgzds 2006). In the studied stand black alder was represented in all diameter classes up to 170 years (oldest black alder age was 166 years).

Natural Norway spruce forests have multi-age structure, as opposed to planted Norway spruce monoculture (Zviedris 1960; Angelstam, Kuuluvainen 2004; Lilja et al. 2006). Norway spruce diameter structure showed a



**Fig. 3.** Relation between age and diameter for Norway spruce in the studied *Myrtilloso polytrichosa* forest stand (coefficient of determination is given).

continuous structure, with trees in all diameter classes (Fig. 2A), which is typical in natural Norway spruce forests (Angelstam, Kuuluvainen 2004; Fraver et al 2008; Shorohova et al. 2009). Most of the Norway spruce trees were in the smallest diameter class (0 to 10 cm), which is common for shade-tolerant species, like Norway spruce (Lilja et al. 2006). Height structure (Fig. 2B), similarly as diameter structure (Fig. 2A) showed variable vertical structure, as is typical of natural forests (Angelstam, Kuuluvainen 2004; Lilja et al. 2006; Shorohova et al. 2009). Mean diameter of black alder (22.9 cm) and birch (24.3 cm) was higher than Norway spruce diameter (20 cm), but with lower ages, indicating higher greater radial growth of these species (Hytönen, Jylhä 2005; Mauriņš, Zvirgzds 2006). In other words, the Norway spruce trees were slow growing, but attained older age. Considering that Norway spruce with diameter < 10 cm were not cored, there were few trees in youngest age classes in Fig. 2C. Apparently age data from smaller trees would partially supplement youngest age classes. Thus age structure likely represents a J-form of continuous regeneration, which is typical of natural forest (Groven et al. 2006; Lilja et al. 2006). However, we need to consider that also small dimension Norway spruce (understorey) in the swamp forests can reach considerable age (up to 120 years) (Lilja et al. 2006; Niklasson 2002), This implies that presumptions should be made critically from diameter of trees to reflect age.

Growth release analysis (Fig. 4) in the studied stand indicated four large-scale disturbances during the period 1850 to 1970, which also coincided partly with regeneration of the pioneer tree species Eurasian aspen and birch (Fig. 2C). This suggests that the disturbances created large canopy gaps, which allowed better growth of Norway spruce and establishment of pioneer species (Angelstam, Kuuluvainen 2004). It is not known if these disturbance events were of natural origin (wind, snow) or caused by logging. A growth release period for Norway spruce occurred in 1853 (Fig. 4), indicating a major disturbance at that time. It is known that extremely deep snow up to 2 m occurred in 1850 in eastern Latvia (Eberhards 2012), which was likely associated with snow break, as occurred recently in the winter of 2010 – 2011. Trees need some years to respond to a disturbance (Speer 2010), which

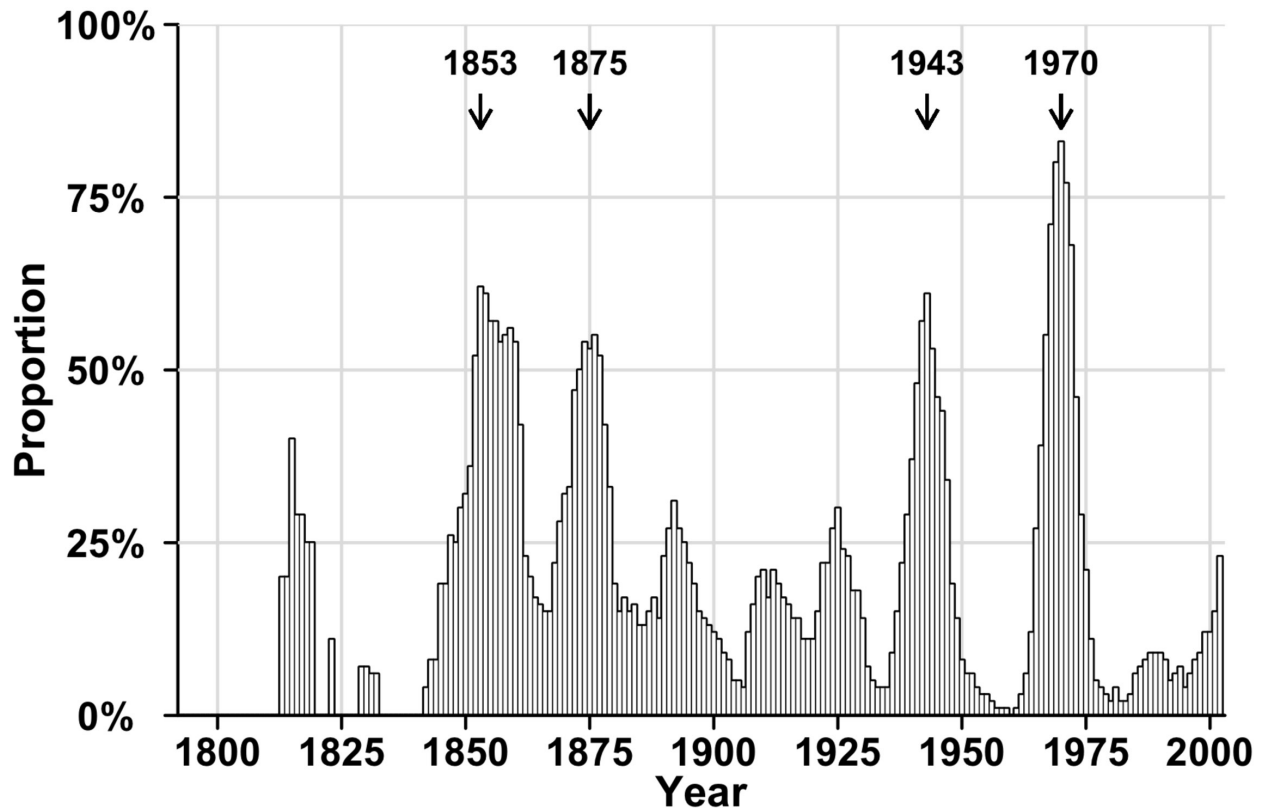


Fig. 4. Growth release analysis for Norway spruce in the studied *Myrtilloso-polytrichosa* forest stand (date shows estimated year when a disturbance occurred).

might explain the gap in the maximum release between 1850 and 1853. Another major disturbance occurred in 1875, but the cause is not known. Also, the abundant birch in age classes corresponding to establishment in 1861 to 1920 suggest well it conditions (Fig. 2C). The release period in 1943 might be due to the extreme winter in 1940 when January and February minimal temperature was  $-40$  oC. In wet soils, Norway spruce root systems are shallow and vulnerable to frost, which can cause mortality (Puhe 2003; Gaul et al. 2008) in particular under a thin snow layer (Hardy et al. 2001). The 1970 release year is without doubt associated with storms in 1967 and 1969 (data from the Latvian Environment, Geology and Meteorology Centre), which caused major windbreak in Latvia (Fig. 4). This release year was also associated with regeneration of birch and Eurasian aspen, indicated by large numbers of stems of these species in the 1961 to 1980 age classes (Fig. 2C). Scots pine occurred in age classes from 231 to 270 years (regenerated in 1741 to 1780). As this species is light-demanding and requires disturbed soil to establish (Kuuluvainen et al. 2002; Brümelis et al. 2005), perhaps secondary succession began after fire on abandoned slash and burn cultivated land.

Patch dynamics is defined as originating from disturbance that affects an area  $> 200$  m<sup>2</sup> and less than 1 ha (Kuuluvainen, Aakala 2011). This corresponds to the

disturbances in the major release periods, as the plot area was 4000 m<sup>2</sup> and the release periods affected up to 80% of Norway spruce trees. Gap dynamics disturbances affect an area  $< 200$  m<sup>2</sup>, which reflects disturbance in years with release of low numbers of trees. We found poor correlation between Norway spruce age and diameter, as is typical in stands with continuous regeneration of a shade-tolerant species, such as Norway spruce (Lilja et al. 2006). Age of Norway spruce trees with diameter  $\sim 10$  cm ranged from 45 to 220 years, indicating heterogenic growth conditions. On the other hand, diameter of black alder was correlated with age, as this is a light-demanding species (Mauriņš, Zvirgzds 2006) and growth was possible only in well lit gaps after disturbance. Birch diameter was not correlated with age, which might be explained by the lack of separation of this genus into species (Silver birch *Betula pendula* or downy birch *Betula pubescens*) in our study.

The average diameter of dead trees was 19 cm. It is known that species diversity on dead wood is higher when diameter exceeds 20 to 25 cm (Gmizo 1999). In Finland and Sweden in natural forests dead wood volume has been estimated to be 59.4 to 105.2 m<sup>3</sup> ha<sup>-1</sup> (Lilja et al. 2006; Aakala 2011; Timonen et al. 2011). In the studied stand, dead wood volume was 82 m<sup>3</sup> ha<sup>-1</sup>, which is therefore comparable to that in natural forest. Also, a large part of the dead wood was in decay classes 4 and 5, indicating

continuity of supply. Dead wood has a significant role in maintaining biodiversity. For example, in Finland one-quarter species which live in forests depend on the dead wood (Wallenius et al. 2010; Siitonen 2001). Considering maximal age of trees, the investigated stand in the nature reserve Gruzdovas meži is the oldest known Norway spruce forest in Latvia. Patch and gap dynamics were the main forest regeneration types. This disturbance regime, which is characteristic for old Norway spruce forests, resulted in diversity of age and diameter structures, characteristic of natural forests. Abundance of deadwood in different decay classes indicates lack of wood removal. Thus we argue that natural wet Norway spruce stands can be found in Latvia, however their area is very low.

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### References

- Aakala T. 2011. Temporal variability of deadwood volume and quality in boreal old-growth forests. *Silva Fenn.* 45: 969–981.
- Aakala T., Kuuluvainen T., Gauthier S., De Grandpre L. 2008. Standing dead trees and their decay-class dynamics in the northern eastern boreal old-growth forests of Quebec. *Forest Ecol. Manage.* 255: 410–420.
- Angelstam P., Kuuluvainen T. 2004. Boreal forests disturbance regimes, successional dynamics and landscape structures – a European perspective. *Ecol. Bull.* 51: 117–136.
- Bonan G.B., Shugart H.H. 1989. Environmental factors and ecological processes in boreal forests. *Annu. Rev. Ecol. Syst.* 20: 1–28.
- Brūmelis G., Elferts D., Liepiņa L., Luce I., Tabors G., Tjarve D. 2005. Age and spatial structure of natural *Pinus sylvestris* stands in Latvia. *Scand. J. Forest Res.* 20: 471–480.
- Bušs K. 1981. *Forest Ecology and Typology*. Zinātne, Rīga. 68 p. (in Latvian)
- Chambers J., Higuchi N., Schimel J., Ferreira L., Melack J. 2000. Decomposition and carbon cycling of dead trees in tropical forests of the central Amazon. *Oecologia* 122: 380–388.
- DeBano L.F., Neary D. G. 2005. Part A – The soil resource: Its importance, characteristics, and general responses to fire. *USDA Rocky* 42: 21–28.
- Eberhards G. 2012. Unusual weather conditions in Latvia (900–1860). In: Kļaviņš M., Briede A. (eds) *Climate Change in Latvia and Adaptation to It*. University of Latvia Press, Rīga, pp. 44–61.
- Essen P.A., Ehnstrom B., Ericson L., Sjöberg K. 1997. Boreal forests. *Ecol. Bull.* 46: 16–47.
- Fraver S., Jonsson G.B., Jönsson M., Essen A.P. 2008. Demographics and disturbance history of a boreal old-growth *Picea abies* forest. *J. Veget. Sci.* 19: 789–798.
- Fraver S., White A. 2005. Disturbance Dynamics of old-growth *Picea rubens* forests of northern Maine. *J. Veget. Sci.* 16: 597–610.
- Gaul D., Hertel D., Leuschner C. 2008. Effects of experimental soil frost on the fine-root system of mature Norway spruce. *J. Plant. Nutr. Soil. Sci.* 171: 690–698.
- Gmizo I. 1999. Affect of dead wood amount on snail abundance and species richness. Bachelor thesis. University of Latvia, Rīga. 36 p. (in Latvian)
- Clark J.S., Richard P.J.H. 1996. The role of paleofire in Boreal and Other cool-coniferous forests. In: Goldammer J.G., Furyaev V.V. (eds) *Fire in Ecosystems of Boreal Eurasia: Ecological Impacts and Links to Global System*. Kluwer Academic Publisher, London, pp. 65–89.
- Grissino-Mayer H.D. 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. *Tree Ring Res.* 57: 205–221.
- Groven R., Rolstad J., Storaunet K.O. 2006. Stand structures and dynamics of old growth *Picea abies* forest in southeastern Norway. In: Storaunet K.O. (ed) *Dead Wood Dynamics, Stand History, and Biodiversity in Boreal Picea abies Forests of Norway*. Norwegian University of Life Sciences, Norway, pp. IV: 1–20.
- Hanski I. 2000. Extinction debt and species credit in boreal forests: modelling the consequences of different approaches to biodiversity conservation. *Ann. Zool. Fenn.* 37: 271–280.
- Hardy J.P., Groffman P.M., Fitzhughen R.D., Henry K.S., Welman A.T., Demers J.D., Fahey T.J., Driscoll C.T., Tierney G.L., Nolan S. 2001. Snow depth manipulation and its influence on soil frost and water dynamics in a northern hardwood forest. *Biogeochemistry* 56: 116–128.
- Hytönen J., Jylhä P. 2005. Effects of competing vegetation and post-planting weed control on the mortality, growth and vole damages to *Betula pendula* planted on former agricultural land. *Silva Fenn.* 39: 365–380.
- Hytteborn H., Maslov A.A., Nazimova D.I., Rysin L.P. 2005. Boreal Forests of Eurasia. In: Andderrsson F. (ed) *Coniferous Forests, Ecosystems of the World*, 6<sup>th</sup> edition. Elsevier, Amsterdam, pp. 23–99.
- Kuuluvainen T., Aakala T. 2011. Natural forests dynamics in Boreal Fennoscandia: a review and classification. *Silva Fenn.* 45: 823–841.
- Kuuluvainen T., Maki J., Karjalainen L., Lehtonen H. 2002. Tree age distribution in old growth forest sites in Vienansalo wilderness, eastern Fennoscandia. *Silva Fenn.* 36: 169–184.
- Laiviņš M. 2005. Geography of Norway spruce (*Picea abies*) stands in Latvia. *Proc. Latvian Univ. Agric.* 14: 5–14.
- Leemans R. 1991. Canopy gaps and establishment patterns of spruce (*Picea abies* (L.) Karst.) in two old-growth coniferous forests in central Sweden. *Plant Ecol.* 93: 157–165.
- Lilja S., Wallenius T., Kuuluvainen T. 2006. Structure and development of old *Picea abies* forests in northern boreal Fennoscandia. *Ecoscience* 13: 181–192.
- Linder P., Östlund L. 1992. Changes in the boreal forests of Sweden 1870–1991. *Svensk Bot. Tidskr.* 68: 199–215.
- Mauriņš A., Zvirgzds A. 2006. *Dendrology*. Latvijas Universitāte, Rīga. 447 p. (in Latvian)
- Motta R. 2003. Ungulate impact on rowan (*Sorbus aucuparia* L.) and Norway spruce (*Picea abies* (L.) Karst.) height structure in mountain forests in the eastern Italian Alps. *Forest Ecol. Manage.* 181: 139–150.
- Niklasson M. 2002. A comparison of three age determination methods for suppressed Norway spruce: implications for age structure analysis. *Forest Ecol. Manage.* 161: 279–288.
- Pennanen J. 2002. Forest age distribution under mixed-severity fire regimes – a simulation based analysis for middle boreal

- Fennoscandia. *Silva Fenn.* 36: 213–231.
- Puhe J. 2003. Growth and development of the root system of Norway spruce (*Picea abies*) in forest stands – a review. *Forest Ecol. Manage.* 175: 253–273.
- Pūriņš V. (ed) 1975. *Geography of Latvian SSR*. Zinātne, Rīga. 671 p. (in Latvian)
- Rouvinen S., Kouki J. 2008. The natural northern European boreal forests: Unifying the concepts, terminologies, and their application. *Silva Fenn.* 42: 135–146.
- Rove I. (ed) 2003. Nature protection plan of the Nature reserve “Gruzdovas meži”. Latvijas Dabas fonds, Rīga. 48 p. (in Latvian)
- Shorohova E., Kuuluvainen T., Kangur A., Jõgiste K. 2009. Natural stand structures, disturbances regimes and successional dynamics in the Eurasian boreal forests: a review with special reference to Russian studies. *Ann. For. Sci.* 66: 201.
- Sii-tonen J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecol. Bull.* 49: 11–41.
- Sirén G. 1955. The development of spruce forest on raw humus sites in northern Finland and its ecology. *Acta For. Fenn.* 62: 1–408.
- Sokal R.R., Rohlf F.J. 1995. *Biometry: The Principles and Practice of Statistics in Biological Research*. 3<sup>rd</sup> edition. W.H. Freeman and Company, New York. 837 p.
- Speer J.H. 2010. *Fundamentals of Tree-ring Research*. The University of Arizona Press, Tuscon. 334 p.
- Spies T.A., Franklin J.F., Thomas T.B. 1988. Coarse woody debris in douglas fir forests of Western Oregon and Washington. *Ecology* 69: 1689–1702.
- Storaunet K.O., Rolstad J. 2004. How long do Norway spruce snags stand? Evaluating four estimation methods. *Can. J. For. Res.* 34: 376–383.
- Tērauds A., Brūmelis G., Nikodemus O. 2011. Seventy-year changes in tree species composition and tree ages in state-owned forests in Latvia. *Scand. J. For. Res.* 1: 1–11.
- Timonen J., Gustafsson L., Kotiaho J.S., Mönkkönen M. 2011. Hotspots in cold climate: Conservation value of woodland key habitats in boreal forests. *Biol. Conserv.* 144: 2061–2067.
- Wallenius T. 2002. Forest age distribution and traces of past fires in a natural boreal landscapes dominated by *Picea abies*. *Silva Fenn.* 36: 201–211.
- Wallenius T.H., Kuuluvainen T., Vanha-Majamaa I. 2004. Fire history in relation to site type and vegetation in Vienansalo wilderness in eastern Fennoscandia, Russia. *Can. J. For. Res.* 34: 1400–1409.
- Wallenius T.H., Pitkanen A., Kuuluvainen T., Pennanen J., Karttunen H. 2005. Fire history and forest age distribution of an unmanaged *Picea abies* dominated landscape. *Can. J. For. Res.* 35: 1540–1552.
- Wallenius T., Niskanen L., Virtanen T., Hottola J., Brūmelis G., Angervuori A., Julkunen J., Pihlström M. 2010. Loss of habitats, naturalness and species diversity in Eurasian forest landscapes. *Ecol. Indic.* 10: 1093–1101.
- Zviedris A. 1960. *Norway Spruce and Spruce Forests in Latvian SSR*. Latvijas PSR Zinātņu akadēmijas izdevniecība, Rīga. 240 p. (in Latvian)