Drivers of annual variation in tree growth and forest sensitivity to storm damage in Finland

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Abstract

In this thesis, my aim is to study the drivers of tree growth variation and forest predisposition to storm disturbance in Finland. More specifically, the thesis aims to answer the following research questions: (1) What is the role of tree provenance in the climatic control of radial growth variation in Norway spruce (Picea abies (L.) Karst.)? (2) How do weather conditions outside of growing season affect radial growth variation in Norway spruce and Scots pine (Pinus sylvestris L.)? (3) How are forest properties, forest management and abiotic environmental factors connected to the storm damage probability of forest stands and individual trees? (4) Do the same factors affect stand-level damage probability in different storm types: autumn extra-tropical cyclones and summer thunder storms? (5) Is fine-scale topographic information connected to tree-level storm damage probability?

The thesis addresses these questions by analyzing extensive empirical data sets. The different climatic drivers of Norway spruce provenances were studied using a tree-ring data from seven Norway spruce provenance experiments in Finland, established already in the 1930s and located in different climatic conditions and containing a large variety of provenances. The effects of non-growing season climatic conditions on tree-growth were studied by comparing tree-ring data from unmanaged forests with variables describing winter conditions and modelled tree frost hardiness levels. Storm damage probability on stand and tree levels was examined with storm damage data sets collected at Finnish National Forest Inventory plots after major storms. A statistical modeling approach was used throughout the thesis, utilizing methods such as generalized mixed effects models and statistical distributions of extreme values.

The results revealed provenance differences in radial growth variation in Norway spruce. Provenances differed most in their growth response to winter temperature, as adaptation to low winter temperatures was weaker in Central European than in Northern European provenances. While cold winter temperatures were associated with frost damage and declined radial growth in Central European spruce provenances transferred north, simple temperature variables were not sufficient in studying the responses of trees to conditions outside of the growing season in natural forests. Instead, the results showed signs of reduced growth after events of insufficient frost hardiness levels and winters with high frost sum of snowless days. This indicates that accounting for a complexity of factors, such as frost hardiness of trees, snow cover and soil frost, is needed to understand the implications of weather conditions outside of growing season to tree growth.

Stand-level damage probability was affected by stand characteristics and previous management operations. On tree-level, damage probability was connected to type of the tree species (conifer or broad-leaved) and tree height as well as recent changes in wind exposure and wood decay in the stand. Storm damage probability in autumn storms and summer thunder storms was affected by similar factors, and the similarities were clearest in the effects of forest management history and topography. However, due to the limitations of the data, the results may have missed subtler differences between the storm types. Topography was associated with storm damage probability on both stand and individual tree level. The results also show that high-resolution topographical information, describing the local topography near the tree, can improve models of tree-level storm damage probability.

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In Kerava, 24th February, 2018

Susanne Suvanto

Contents

List of original publications

This thesis is based on the following publications:

I Suvanto, S., Nöjd, P., Henttonen, H.M., Beuker, E. & Mäkinen, H. (2016). Geographical patterns in the radial growth response of Norway spruce provenances to climatic variation. *Agricultural and Forest Meteorology* 222, 10–20.

II Suvanto, S., Henttonen, H.M., Nöjd, P., Helama, S., Repo, T., Timonen, M. & Mäkinen H. (2017). Connecting potential frost damage events identified from meteorological records to radial growth variation in Norway spruce and Scots pine. *Trees – Structure and Function* 31, 2023–2034.

III Suvanto, S., Henttonen, H.M., Nöjd, P. & Mäkinen, H. (2016). Forest susceptibility to storm damage is affected by similar factors regardless of storm type: Comparison of thunder storms and autumn extra-tropical cyclones in Finland. *Forest Ecology and Management* 381, 17–28.

IV Suvanto, S., Henttonen H.M., Nöjd, P. & Mäkinen, H. (Manuscript). High-resolution topographical information improves tree-level storm damage models.

The publications are referred to in the text by their roman numerals.

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Author contributions

I SS, PN, HH and HM planned the study. SS was responsible for conducting the analysis and writing the manuscript. EB, HM and PN provided the data. All authors contributed to writing the manuscript.

II SS had the main responsibility in planning the study, conducting the analysis and writing the manuscript. HH, HM, PN, TR and SH participated in planning the study. HM, PN, MT and SH provided the data. HH, HM, PN, SH and TR contributed to writing the manuscript.

III SS, HH, PN and HM planned the study. SS was responsible for conducting the analysis and writing the manuscript. All authors contributed to writing the manuscript.

IV SS had the main responsibility in planning the study, conducting the analysis and writing the manuscript. HH, HM and PN contributed to planning the study and writing the manuscript.

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Abbreviations

AIC	Akaike information criterion
AUC	Area under curve
BA	Basal area
DBH	Diameter at breast height
DEM	Digital elevation model
GEV	Generalized extreme value distribution
GIS	Geographic information systems
GLMM	Generalized linear mixed model
GP	Generalized Pareto distribution
MS-NFI	Multi-source NFI
NFI	National Forest Inventory
ROC	Receiver operating characteristic
RWI	Ring width index

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1. Introduction

1.1 Radial growth variation of trees

1.1.1 Main drivers of radial growth variation

In dendrochronology, the factors affecting variation in annual radial growth are typically described with a conceptual model, where tree-ring width is presented as a function of tree age, climate factors, endogenous disturbances within the forest stand and exogenous disturbances from outside the forest stand (Cook 1990, Speer 2010). The main climatic factors related to growth variation are temperature and moisture. In the high latitude and altitude areas, temperature and growing season length are typically strongly related with tree growth whereas moisture limitations are more common at lower latitudes and altitudes (Fig. 1) (Mikola 1950, Mäkinen *et al.* 2003, Andreassen *et al.* 2006, Wettstein *et al.* 2011, King *et al.* 2013, Lyu *et al.* 2017).

In Finland, the radial growth variation of the most common tree species Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.) is positively connected to growing season temperature and the length of the growing season (Miina 2000, Henttonen *et al.* 2009, 2014). This temperature-growth response is stronger in the northern parts of the country (Mäkinen *et al.* 2000, Helama *et al.* 2005, Helama *et al.* 2013). Even though severe droughts are rare in Finland, growth variation in both species has also been found to respond positively to precipitation, especially at dry sites in southern Finland (Mielikäinen *et al.* 1996, Mäkinen *et al.* 2001, Henttonen *et al.* 2014).

In addition to climatic variation, other factors such as tree age, status of the tree within the forest and forest management operations influence the radial growth variation of a tree greatly. Furthermore, radial growth variation is also affected by resource allocation within a tree. For example, in years of intensive flowering and seed production significant amounts of resources are directed to reproduction, leading to reduced radial growth (Pukkala 1987, Koenig and Knops 1998, Selås *et al.* 2002, Hacket-Pain *et al.* 2015). If only radial growth is considered, the perceived growth variation is also influenced by resource allocation between different parts of the tree (e.g., radial and height growth, foliage and roots).

1.1.2 Climatic conditions outside of growing season

While growing season conditions are the main climatic factors affecting tree growth, temperature conditions outside of growing season may also have a role in interannual tree growth variation. Radial growth variation in Norway spruce has been shown to be negatively correlated with winter time temperatures in the northern parts of its range (Jonsson 1969, Miina 2000, Mäkinen *et al.* 2000, Lyu *et al.* 2017), indicating that cold winters are associated with increased growth and mild winters with a growth decline.

The reasons for this pattern are unclear. Frost hardiness of boreal trees is highest during the cold winter months and therefore trees are unlikely to suffer frost related damage. Instead, trees are more vulnerable to damage in spring as they start to decrease their frost hardiness levels in order to start growth (Bannister and Neuner 2001). As temperature is a major driver of spring phenology (Hänninen and Tanino 2011), trees may start dehardening too early in warm winters, leading to higher risk of frost damage if temperature suddenly drops (Hannerz 1994, Raitio 2000). Early activation may be harmful to trees even if no frost damage occurs. If respiration rates increase too early in the spring when less light is available, respiration may consume more resources than photosynthesis produces (Skre and Nes 1996, Linkosalo *et al.* 2014).

In addition to temperature, winter damage in trees is affected by a complex set of variables, such as snow cover and soil freezing (Sakai and Larcher 1987). Snow cover and its properties have a particularly important role, as snowpack forms an insulating layer between soil and air (Groffman *et al.* 2001, Hardy *et al.* 2001, Repo *et al.* 2005, Repo *et al.* 2011). Snow depth and duration of snow cover have been found to be connected to tree growth variation (Vaganov *et al.* 1999, Helama *et al.* 2013) and years with discontinuous snow cover and deep soil frost have been associated with tree damage and decreased growth in both Norway spruce and Scots pine (Tikkanen and Raitio 1990, Kullman 1991, Raitio 2000, Solantie 2003, Tuovinen *et al.* 2005).

1.1.3 Within-species differences in climate-growth relationship

If the distribution area of a species is large, geographically distant populations adapt to different local climatic conditions, which leads to adaptive genetic diversity within a species (Alberto *et al.* 2013, Schueler *et al.* 2013). Within-species differences between populations have traditionally been studied with provenance experiments, where trees originating from different parts of the species range are grown in one place. The results from these experiments may provide information for climate change adaptation since provenances suitable for the future climatic conditions can be identified (Kapeller *et al.* 2012, Eilmann *et al.* 2013, Williams and Dumroese 2013). On the other hand, the experiments provide long-term experimental data of how trees are affected by changes in climatic conditions (Matyas 1994, Carter 1996, Leites *et al.* 2012). Accounting for population differences instead of treating a species as a homogeneous group improves the estimates of climate change effects to species range and growth (O'Neill *et al.* 2008, O'Neill and Night 2011, Huang *et al.* 2013, Oney *et al.* 2013, Ikeda *et al.* 2017).

In the case of Norway spruce, populations originating from the northern parts of the species range have developed strategies to avoid frost damage and utilize the short growing season (Heikinheimo 1949, Beuker *et al.* 1998, Westin *et al.* 2000, Hannerz and Westin 2005) whereas populations less sensitive to drought have been identified from warmer and drier locations (Kapeller *et al.* 2012, Schueler *et al.* 2013). The differences between populations can arise from genetic adaptation but also from epigenetic effects. Several studies on Norway spruce have shown that temperature conditions during seed production affect the frost hardiness and phenology of the progenies (Johnsen *et al.* 1996, Johnsen et al. 2005, Gömöry *et al.* 2015).

While previous studies on Norway spruce provenance experiments have documented within-species differences in tree phenology and frost hardiness, the understanding of how these differences are reflected to the annual growth variation is incomplete. Previous studies on the topic have shown inconsistent results. While Zubizarreta-Gerendiain *et al.* (2012b) found the effect of July temperature on radial growth to vary between Finnish Norway spruce clones, Burczyk and Giertych (1991) did not find different growth responses to drought in Polish provenances and King *et al.* (2013) concluded that environmental factors rather than genetics cause the different responses to temperature on an altitudinal gradient in Swiss Alps. However, these studies cover very limited range of provenances and site conditions, thus providing only a restricted understanding of the

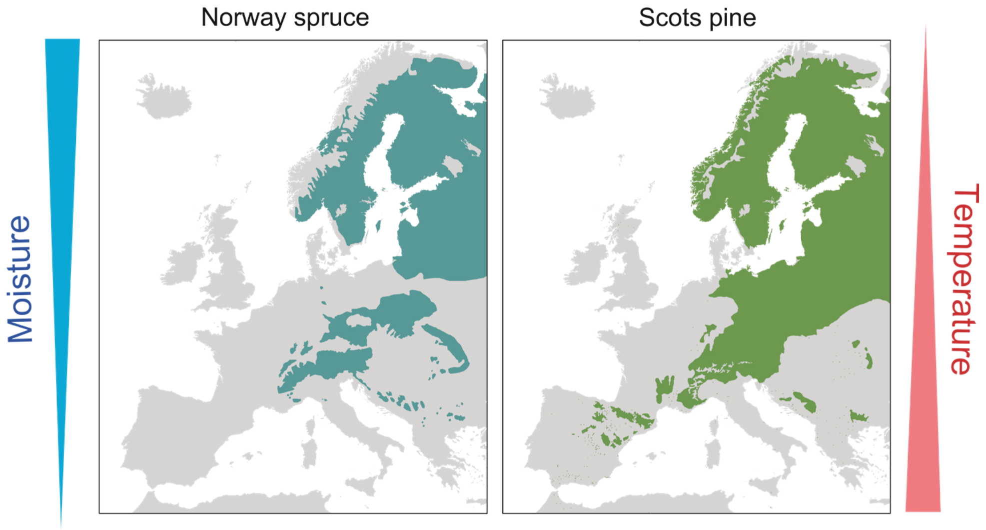

Figure 1. Distribution areas of the study species Norway spruce and Scots pine in Europe and major trends in moisture and temperature in the region.

variation within Norway spruce populations. Therefore, more research is needed to understand how Norway spruce provenances differ in their growth responses to climatic conditions.

1.2 Storm damage in forests

1.2.1 Storms and their impacts

Storm damage and other natural disturbances in forests have substantial effects on forest productivity and carbon storage (Lindroth *et al.* 2009, Seidl *et al.* 2014, Reyer *et al.* 2017). Storms are a major cause of natural forest disturbance in Europe and the amount of forest storm damage is increasing (Schelhaas *et al.* 2003, Gregow *et al.* 2017, Seidl *et al.* 2017). Although the amounts of storm-induced forest damage in Finland have been lower compared to many other countries, storms do regularly cause significant damage also here (Ihalainen and Ahola 2003, Viiri *et al.* 2011).

The economic consequences of storms are substantial and arise from several factors, including damaged wood left in the forests, lowered quality of harvested wood, costs of salvage logging and lower wood prices due to increased supply of wood (Gardiner *et al.* 2010). Wind thrown trees also harm infrastructure, for example, by blocking roads and causing power shortages.

In Europe, most storm damage in forests is related to severe winter storms (Gardiner *et al.* 2010). In Finland, most damage occurs during autumn storms, because the frozen soils during mid-winter provide strong anchorage for trees and, thus, reduce their sensitivity to windthrow (Laitakari 1952, Gregow *et al.* 2008, Gregow *et al.* 2011b). Most research on forest storm damage in Europe has concentrated on these winter and autumn storms (e.g., Gardiner *et al.* 2010, Schmidt *et al.* 2010, Zubizarreta-Gerendiain *et al.* 2012a, Jung *et al.* 2016, Kamimura *et al.* 2016). Less research is available on other types of storms, such as thunder storms, even though they may also cause significant forest damage (Viiri *et al.* 2011) and different meteorological characteristics may affect the dynamics of the caused forest damage. For example, Uotila (2015) suggested that because of the high wind speeds in thunder storm downbursts, damage cannot be prevented with forest management practices.

The Finnish Meteorological Institute (FMI) defines storm as a strong wind with 10 minute average wind speed above 21 ms^{-1} (FMI 2017). In Finland, average wind speeds on forested land areas rarely exceed this limit (Gregow *et al.* 2008, Venäläinen *et al.* 2017). In this thesis I will use the term 'storm' to refer more broadly to exceptional weather events that cause substantial damage to forests. Similar approach, focusing on damage instead of wind speed, was used by Gardiner *et al.* (2010) in defining storm severity. While most of the damage in the studied storms is caused by wind, also snow damage occurred in one of the storms. Therefore, 'storm damage' in this thesis contains also snow related damage.

1.2.2 Factors affecting storm damage probability

The probability of damage to a tree in a storm is a function of tree susceptibility to damage and the intensity of the storm conditions (wind speed, gustiness, snow etc.). It is affected by several factors relating to the tree, its biotic and abiotic environment, and anthropogenic influence. These factors are typically closely linked to each other (Fig. 2, Seidl *et al.* 2011b, Mitchell 2013).

Tree susceptibility to damage is affected by properties such as tree species, size and shape. Damage probability is found to increase with increasing tree height (Lohmander and Helles 1987, Schmidt *et al.* 2010, Albrecht *et al.* 2012) and slender trees are more vulnerable to damage (Peltola *et al.* 1999). Norway spruce is considered more vulnerable to wind damage than Scots pine (Peltola *et al.* 1999, Dobbertin 2002, Valinger and Fridman 2011), as its relatively shallow root system provides a weaker anchorage to the ground (Kalela 1949, Peltola *et al.* 2000). On the other hand, Scots pine may be more vulnerable to snow damage than Norway spruce, due to differences in the crown shape between the species (Nykänen *et al.* 1997). Deciduous species have a lower risk of wind damage, as they do not have leaves during autumn and winter when most storms

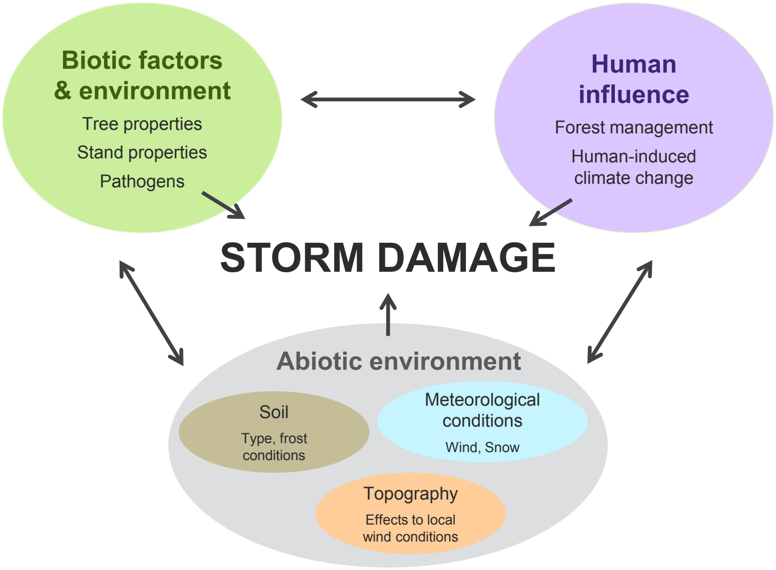

Figure 2. Conceptual figure describing different factors related to storm damage in forests. Storm damage probability is affected by several biotic, abiotic and anthropogenic factors, which are also linked to each other.

and strongest winds in Finland occur, and have therefore lower wind load compared to evergreen species (Peltola *et al.* 1999). Pathogens that cause wood decay and weaken trees also make them more vulnerable to uprooting and stem breakage (Gordon 1973, Whitney *et al.* 2001, Papaik *et al.* 2005, Honkaniemi *et al.* 2017).

Forest management is strongly linked to damage risks. Increased storm damage in Europe has been largely attributed to increasing standing stock resulting from intensified forest management and increased use of conifer species (Schelhaas *et al.* 2003, Nilsson *et al.* 2004, Seidl *et al.* 2011a). In finer scale, damage probability is typically increased when trees are exposed to new wind conditions. For example, thinnings increase the wind load of the remaining trees and clear cutting of a neighboring stand exposes the trees in the stand border to wind (Laitakari 1952, Peltola *et al.* 1999, Jalkanen and Mattila 2000, Uotila *et al.* 2015). Because trees acclimate effectively to the surrounding wind conditions (Jaffe 1973, Nicoll *et al.* 2008, Bonnesoeur *et al.* 2016, Gardiner *et al.* 2016) damage probability only increases after a change in wind exposure whereas trees grown in windy conditions are less susceptible to damage.

Abiotic factors such as soil type and soil conditions during the storm also play an important role. In Finland, soil frost during winter anchors trees to the ground making them resistant to uprooting. Therefore, most storm and wind damage occurs during unfrozen soils (Laitakari 1952, Gregow *et al.* 2008). Soil conditions also affect the root system of a tree and, therefore, the anchorage to ground (Mitchell 2013). Areas of shallow or poorly drained soil have been found to be prone to wind damage (Dobbertin 2002). In Finland, lower levels of wind damage have been observed in peatlands compared to mineral soils (Laiho 1987, Jalkanen and Mattila 2000).

Meteorological conditions during storms control the damage probability. Because local wind conditions are mediated by variation in topography (Dupont *et al.* 2008, Venäläinen *et al.* 2017) topography is often included in storm damage models, either as variables describing topographical properties, such as elevation, slope, aspect, topographic exposure indices (e.g., Quine and White 1998, Schmidt *et al.* 2010, Schindler *et al.* 2012) or by taking topography into account in calculation of wind variables (Jung and Schindler 2016, Schindler *et al.* 2016). While the availability of high-resolution topographical information has improved with the increased amounts of laser scanning data, few studies have used it in storm damage studies (although see Saarinen *et al.* 2016).

1.3 Climate change impacts on forests

The observed and predicted rates of warming are more pronounced in Northern Europe compared to other parts of the continent (IPCC 2014). The rate of warming is strongest during winter and spring months, whereas the change in summer temperatures is expected to be less evident (Mikkonen *et al.* 2015, Ruosteenoja *et al.* 2016).

Climate change is expected to increase forest productivity in Finland (Briceño-Elizondo *et al.* 2006, Lindner *et al.* 2010, Peltola *et al.* 2010). Indeed, 37% of the total volume increment increase in Finnish forests from the 1970s to the 2010s was attributable to environmental factors (Henttonen *et al.* 2017). While forest productivity in general is expected to increase, drought events are projected to become frequent, and therefore the conditions may become less favorable for Norway spruce, especially in Southern Finland (Kellomäki *et al.* 2008, Peltola *et al.* 2010, Ge *et al.* 2013). The drought sensitivity of Norway spruce has also raised concerns in Central Europe (Hanewinkel *et al.* 2013, Lévesque *et al.* 2013).

Warming climate changes the forest

disturbance regime. Storminess in Northern Europe may increase (Gregow *et al.* 2011a) and warming of winter months decreases the length of soil frost period, weakening the anchorage of trees during winter storms (Venäläinen *et al.* 2001, Peltola *et al.* 2010, Gregow *et al.* 2011b). Snow damage risk in forests is expected to decrease in most parts of Finland, while increases in snow loads are possible in eastern and northern parts of the country (Kilpeläinen *et al.* 2010, Lehtonen *et al.* 2016). The interaction between different disturbance agents, such as wind, snow, drought, insects and pathogens, may amplify the effects of climate change (Seidl *et al.* 2017, Seidl and Rammer 2017).

1.4 Aims and research questions

The aim of this thesis is to improve the current understanding of factors affecting growth variation and storm disturbance in Finland.

Specifically, the thesis aims to answers the following research questions:

- What is the role of tree provenance in the climatic control of radial growth variation in Norway spruce?
- How do weather conditions outside of growing season affect radial growth variation in Norway spruce and Scots pine?
- How are forest properties, forest management and abiotic environmental factors connected to the storm damage probability of forest stands and individual trees?
- Do the same factors affect stand-level damage probability in different storm types: autumn extra-tropical cyclones and summer thunder storms?
- Is fine-scale topographic information connected to tree-level storm damage probability?

2. Materials and methods

2.1 Tree-ring data

2.1.1 Tree-ring data sets

Tree-ring data sets were used in papers I and II as time-series of radial growth variation. The used tree-ring data consists of two separate data sets: one from Norway spruce provenance experiments and another that combines data from several Norway spruce and Scots pine sites in unmanaged forests (Fig. 3b and c, Table 1).

The Norway spruce provenance experiments were established in 1931 and 1932 when seedlings originating from 30 different provenances ranging from Central Europe to Northern Finland were planted at seven experimental sites in Finland (Fig. 3c). Before planting, the seedlings were grown for six years in a nursery. For a detailed description of the experiments see paper I and Beuker (1994, 1996). The provenance experiments were sampled in two separate occasions. In 1992 all sites were sampled and in 2013 only two sites, Punkaharju and Rovaniemi, were sampled.

The other tree-ring data set was compiled from previously published data sets from Norway spruce (Mäkinen *et al.* 2000, Mäkinen *et al.* 2001) and Scots pine (Helama *et al.* 2013) sites at national parks and other unmanaged forests in Finland. In total, the data set consists of 47 Norway spruce sites and 20 Scots pine sites ranging from Southern Finland to the northern distribution limits of the species (Fig. 3b).

In all tree-ring sites, increment cores were taken from trees at breast height (1.3 m). Ring-widths were measured from the cores to the nearest 0.01 mm with a computer aided light microscope measuring system. As the tree-ring data consists of several previously collected and measured data sets, the details of the measurement systems vary.

2.1.2 Processing of the tree-ring data

Cross-dating of the tree-ring data sets was carried out to ensure that each annual ring was associated with the correct calendar year. Ring-width variation and especially the locations of anomalous ring-widths were compared between the trees to check that each tree-ring is dated correctly (see Speer 2010 for more detailed description of the approach). Cross-dating of the samples was conducted visually when the ring-widths were measured and checked computationally with the R package dplR (Bunn *et al.* 2015) following the procedure described by Bunn (2010).

In tree-ring studies, standardization of the tree-ring width data is often done to remove variation related to factors not of interest in the study (Speer 2010). In this thesis, standardization was done to remove long-term trends related to tree age and stand dynamics, while preserving the shorter term variation related to annual variation in temperature and precipitation. Ring-widths were transformed into standardized ring-width indices (RWI) by first fitting a spline function to the ring-width series of individual trees, and then dividing the ring-widths by the modelled spline curve values (Cook and Peters 1981). In paper I, where all trees were the same age, a spline with a 50% frequency cut-off in 30 year was used. In paper II a 50% frequency cut-off in 67% of the length of the tree-ring series was used. After standardization, temporal autocorrelation between consecutive years was removed with a first-order autoregressive model (Speer 2010). The RWIs from individual trees were then combined into mean RWI chronologies within each plot of the provenance experiment data set and within each site in the unmanaged forests data set. The RWI chronologies were formed by calculating annual averages from all the trees within a plot or a site using Tuckey's biweight robust mean (Cook and Kairiukstis 1990). The chronologies were then cropped to contain only the common years of all chronologies in a data set. In the provenance experiment data, the covered years were 1950-1991 and 1950-2013. The final chronologies from the tree-ring data from unmanaged forests covered years 1922-1997.

2.2 Storm damage data and the Finnish National Forest Inventory (NFI)

The storm damage data consisted of two data sets collected from NFI plots after major storm events: two autumn storms in November 2001 and a series of severe thunder storms in summer 2010 (papers III and IV, Table 1). In November 2001, two storms hit Southern and Western Finland, causing an estimated damage of 7.3 million cubic meters of stemwood. First storm, Pyry (1.11.2001), was associated with wet snowfall that damaged trees. In the second storm, Janika (15.11.), the damage was caused by exceptionally strong and gusty winds, with average wind speed (10 minutes) ranging between 16 to 18 ms^{-1} and strongest measured gusts in land areas reaching 27.8 ms-1. Soils were unfrozen and broad-leaved trees without leaves during both of the storms. After the storms field work documenting the storm damage was conducted at 1 722 permanent NFI plots in the storm affected areas. For each plot, damage occurring in the forest stand was documented, as well as damage in trees within the plot (Fig. 3d, Ihalainen and Ahola 2003). The severity of the damage was estimated on a five step scale (no damage, slight, moderate, severe or complete damage), but in the analysis of the data this information was reclassified into two classes: "no damage" and "damage". Therefore, the "damage" class contains damage cases from slight to complete damage.

In July and August 2010 four severe thunder storms hit Eastern and Central Finland causing damage of 8.1 million cubic meters of stemwood. After the storms NFI field teams visited permanent and temporal NFI plots, selected using a stratified sampling design based on aerial images of the damaged area. In the thunder storm data set only

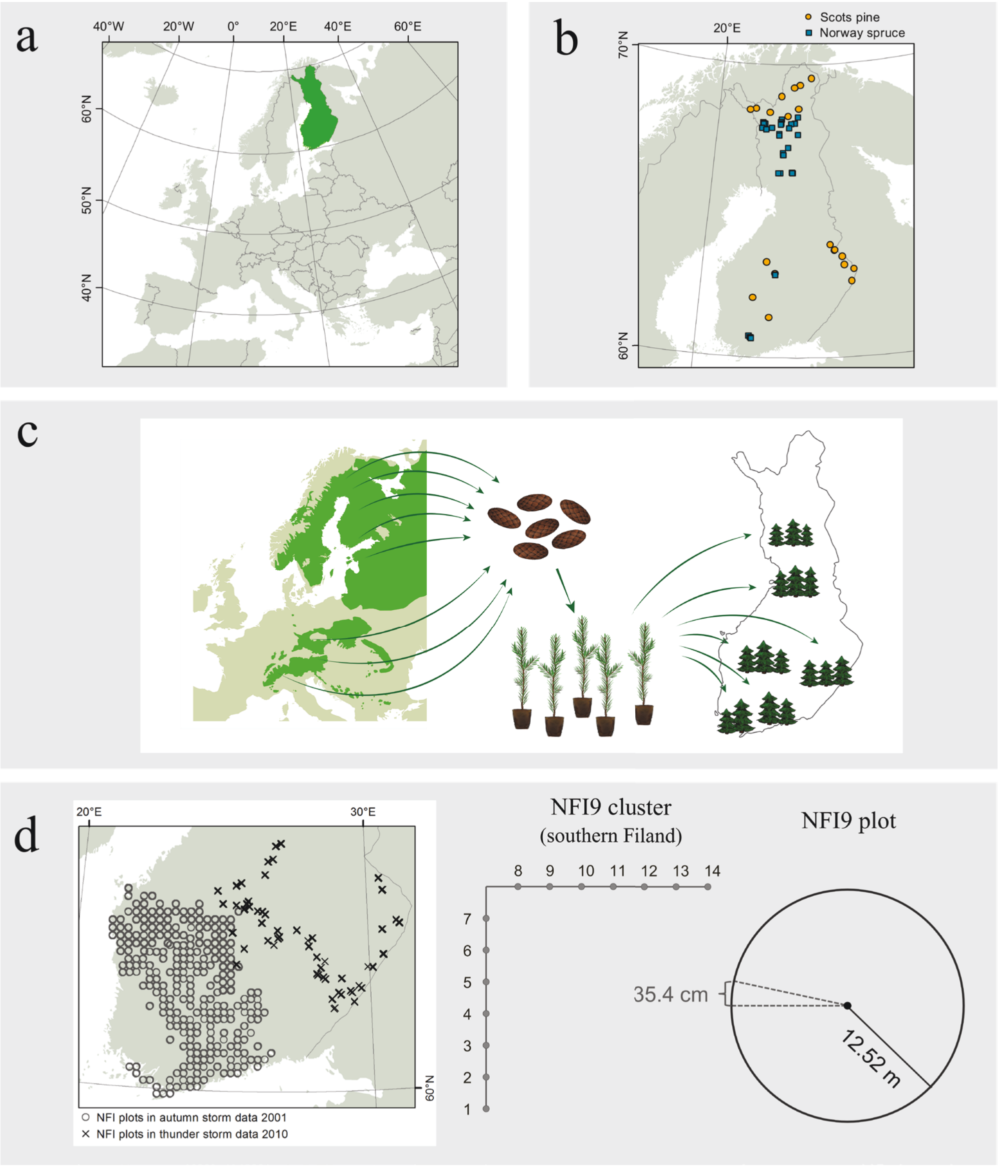

Figure 3. a) Location of the study area in Europe, b) locations of the study sites in unmanaged forests, used in paper II, c) Norway spruce provenance experiments used in paper I, d) NFI plots used in papers III and IV, structure of NFI cluster with 14 sample plots and illustration of angle count plot with restricted radius. Inclusion of trees in sampling depends on tree diameter and distance from plot center.

stand-level damage was documented (Viiri *et al.* 2011). The final data set contained 353 plots in 55 NFI clusters.

The storm damage data sets were combined with NFI field data measured from the plots before the storms. Therefore, data from the plots both before and after the storms were available. In the study area, the NFI sampling design is clustered, i.e. plots are located in clusters, which are placed in a rectangular grid. Plots in the 9th NFI are angle count plots (Bitterlich plots) where the plot radius in the study area is restricted to 12.52 m (Fig. 3d). In each NFI plot a large set of variables is recorded, describing trees, characteristics of the stand where the plot is located in, as well as the abiotic environment such as soil and topography (Tomppo *et al.* 2011).

2.3 Other data sets

The weather data used in the thesis were acquired from the Finnish Meteorological Institute (FMI). Daily temperatures and precipitation sums were used from weather stations close to the study sites (papers I and II, Table 1). In addition to the weather observations from the meteorological stations, we also used a 10 km grid data about temperature and rainfall (papers I, II), provided by the FMI (Venäläinen *et al.* 2005, Aalto *et al.* 2016).

To account for growth reductions resulting from intensive flowering and seed productions, seed crop data from long-term measurement sample plots in Norway spruce stands were used (Koski and Tallqvist 1978). The data set starts in the 1950s and contains seed counts at five stands in different parts of Finland. The years of intensive flowering (i.e., years preceding high seed crop) were included in the analysis of the provenance experiments (paper I).

Digital elevation models (DEM) from the National Land Survey of Finland (NLS) were used to extract variables describing topographical properties of the plots and the neighborhood of individual trees (papers III and IV). Two DEMs with different resolutions were used (Table 1). A 10 m resolution DEM (DEM10) is the highest resolution DEM available for the whole Finland (NLS 2017a), whereas a new 2 m resolution DEM (DEM2) is currently being produced and is estimated to cover the whole country by 2020 (NLS 2017b). DEM2 is based on laser scanning data with a point density of at least 0.5 points per square meter, whereas DEM10 is produced from contour lines, ground surface points digitized in a stereo workstation environment and elevational information in the objects of NLS Topographical database. The elevation accuracy is 0.3 meters in DEM2 and 1.4 meters in DEM10 (NLS 2017a, NLS 2017b).

Multi-source NFI data (MS-NFI), which combines NFI field measurements and satellite image data into a forest resource maps describing different forest attributes (Tomppo *et al.* 2008), was used for extracting independent variables in the stand-level storm damage model and as input data for a forest susceptibility map created based on the developed statistical models (paper III).

2.4 Methods

2.4.1 Methods in analyzing radial growth variation

A statistical modeling approach was used throughout the thesis. In the articles using tree-ring data (papers I and II), multiple linear models were used to examine how the interannual variation in climate related variables was connected to variation in radial growth.

In paper I, anomalous growth years in the provenance experiment data were identified with pointer year analysis, which compares the ring width in each year to the neighboring years and identifies years that show exceptionally low or high growth (Cropper 1979, Neuwirth *et al.* 2007). In addition, hierarchical clustering was used in paper I to study the differences in radial growth variance between provenances and experimental sites. In this method, the clusters are formed iteratively, starting with each object in its own cluster and then proceeding by combining the most similar pairs of clusters step by step (Everitt *et al.* 2011). Ward's minimum variance method was used in the pairing of the clusters and Euclidean distance was used as a measure of similarity between the RWI chronologies.

In paper II, three variables describing potential conditions of frost damage were formulated and calculated from meteorological data. The first variable described extreme cold minimum temperature during a winter (TMIN) and was defined as the lowest of the daily minimum temperatures between two growing season. The second variable described the sufficiency of frost hardiness level of needles in relation to the observed minimum temperatures (REL_TMIN) and it was calculated as the minimum difference between daily minimum temperature and the modelled frost hardiness level. The third variable described situations where lack of insulating snow cover was combined with freezing temperatures (FROSTSUM), and it was calculated as the frost sum of snowless days between two growing seasons. TMIN and REL_TMIN were calculated from weather station data and covered the same time period as the tree-ring data, excluding years 1927 and 1945. FROSTSUM was calculated from the FMI grid data, which only started from year 1961.

A dynamic needle frost hardiness model, developed for Scots pine by Leinonen (1996), was used to find events of insufficient frost hardiness levels (REL_TMIN variable in paper II). The model uses daily minimum and average temperature as well as night length to calculate frost hardiness, i.e. the temperature where 50% of needles are damaged (Fig. 4). Daily minimum temperature and night length are used to calculate the potential environment-induced change in frost hardiness. Daily mean temperature is used as input for annual cycle model designating the phenological phase the tree is in, which determines the level on which the environmental factors affect frost hardiness (hardening competence). For example, environmental control of frost hardiness is the strongest during rest phase in winter and the weakest during growing season. The daily target level of frost hardiness is defined from potential environment-induced change in hardening and hardening competence, and the daily value of frost hardiness approaches this target level with a delay.

Some modifications were made to decrease the uncertainties related to the model and to use it for Norway spruce and different provenances of Scots pine. The time period included in the model was constrained to January to May instead of a full year in the original model (see similar approach in Hänninen *et al.* 2001). The model was also partly reparametrized for different Scots pine and Norway spruce provenances based on provenance test results on bud burst timing reported by Beuker (1994).

Potentially damaging frost conditions were identified using statistical theory of extreme value distributions (paper II). Two approaches to extreme value distributions were used in the analysis: 1) generalized extreme value distributions (GEV), that typically use a block maxima approach, where a single highest (or lowest) value within a time period is considered, and 2) peaks over threshold approach, where all values over (or under) a given threshold are considered. With a sufficiently high threshold the values exceeding the threshold have an approximate generalized Pareto (GP) distribution (Gaines and Denny 1993, Coles 2001, Katz *et al.* 2005). With GEV and GP distributions, a return level of 10 years was defined for the studied frost variables in paper II, which were then used for identifying years with exceptional frost conditions.

2.4.2 Methods in analyzing storm damage in trees and forest stands

Storm damage on stand-level and tree-level was analyzed in relation to stand and tree properties, forest management history, soil and topography. In the stand level models, the studied explanatory variables contained dominant species of the stand, stand age, basal area, mean diameter at breast height, wood decay in living trees, type and timing of the last cuttings, soil type, proximity of open stand borders and variables describing topography. In tree-level models, similar variables describing stand properties were used and, in addition, variables relating to tree properties (tree species and height) and finer scale topographical variables were considered.

In the parts of the thesis using storm damage data from NFI plots (papers III and IV) linear models were not sufficient, as they assume the response variable to be continuous and normally distributed, and assume all observations to be independent. These assumptions were not filled by the used data, as the studied response variable was binomial: damage or no damage in forest stand (paper III) or individual tree (paper IV). In addition, due to the hierarchical sampling design of the NFI the observations could not be seen as independent of each other. Therefore, generalized

Table 1. Descriptions of data used in the original articles included in the thesis (papers I to IV).

Data	Source	Paper I	Paper II	Paper III	Paper IV
Tree ring data from Heikinheimo's Norway spruce provenance tests	Luke	x			
Tree-ring data from unmanaged Norway spruce and Scots pine forests	Luke		x		
Finnish National Forest Inventory (NFI) data from 9th, 10th and 11th NFIs	Luke			x	x
Storm damage inventories at NFI plots after autumn storms in November 2001	Luke			x	x
Storm damage inventories at NFI plots after thunder storms in July-August 2010	Luke			x	
Multi-source NFI data 2009 and 2013	Luke			x	
Norway spruce seed crop data	Luke	x			
Meteorological data from the FMI weather stations and interpolated 10x10 km^2 grid (temperature, precipitation, snow cover, wind speed)	FMI	x	x		x
Digital elevation model, 10 meter resolution (DEM10)	NLS			x	x
Digital elevation model, 2 meter resolution (DEM2)	NLS				x

Luke – Natural Resources Institute Finland, FMI – Finnish Meteorological Institute,
NLS – National Land Survey of Finland

linear mixed models (GLMM) were used. The binomial response variable was modelled with a logit link function, so that the model output gave a probability of event, in this case, probability of storm damage in forest stand or individual tree. The hierarchical structure of the NFI data was taken into account by adding random intercept effects to the model for clusters (paper III) as well as for plots nested within clusters when individual trees were analyzed (paper IV).

The performance of the storm damage models was assessed with Receiver Operating Characteristic (ROC) curves and area under curve (AUC) values. Comparisons between different models were conducted with Akaike Information Criteria (AIC, Akaike 1974). To demonstrate predicted stand-level storm damage probabilities over rotation, stand simulations were calculated with the MOTTI simulator (Hynynen *et al.* 2002, 2005). Simulations were made in southern Finnish conditions (temperature sum 1252.8 dd) for Scots pine (sub-xeric site fertility class, established from seeds, number of stems 4000 per hectare at the start of the simulation) and Norway spruce (mesic site fertility class, established by planting seedlings, number of stems 1800 per hectare at the start of the simulation) stands with management operations following the recommendations (Äijälä *et al.* 2014) as well as for an otherwise similar Norway spruce stand but where no thinnings were made during the rotation.

The analyses in the thesis were conducted with R (R Core Team 2016) and SAS (SAS Institute Inc. 2017). Some of the GIS data processing and analysis was conducted in GIS programs ArcGIS (ESRI 2014) and QGIS (Quantum GIS Development Team 2016). The versions and other details about used software can be found in the original articles.

3. Results

3.1 Provenance differences in growth responses to climatic variation

In the cluster analysis, RWI chronologies were primarily grouped by site and subclusters were formed by provenance (paper I). In most cases Northern European and Central European provenances were clustered separately, but at the northernmost experimental sites Southern Finnish provenances were clustered together with Central European provenances.

The most distinct provenance differences in responses of RWI chronologies to weather conditions were found in winter and spring temperatures. The growth variation in northern provenances showed negative or non-significant correlations with winter and spring temperatures. In contrast, in southern provenances higher growth was associated with warmer winters. Same pattern was confirmed also in regression analysis where growing season weather conditions and years of intensive flowering were taken into account. No provenance differences were found in growth responses to growing season weather conditions.

In pointer year analysis, negative growth anomalies in years with cold winters (1956, 1966 and 1985) were identified only in Central European provenances. Other negative pointer years were found, for example, in intensive flowering years of Norway spruce (1973 and 1989) and in Northern Finland in year 1982 that had an exceptionally cold summer. However, these pointer years were found from both southern and northern provenances.

The main differences in growth variation were found between Central European provenances transferred north and the Northern European provenances. No differences were

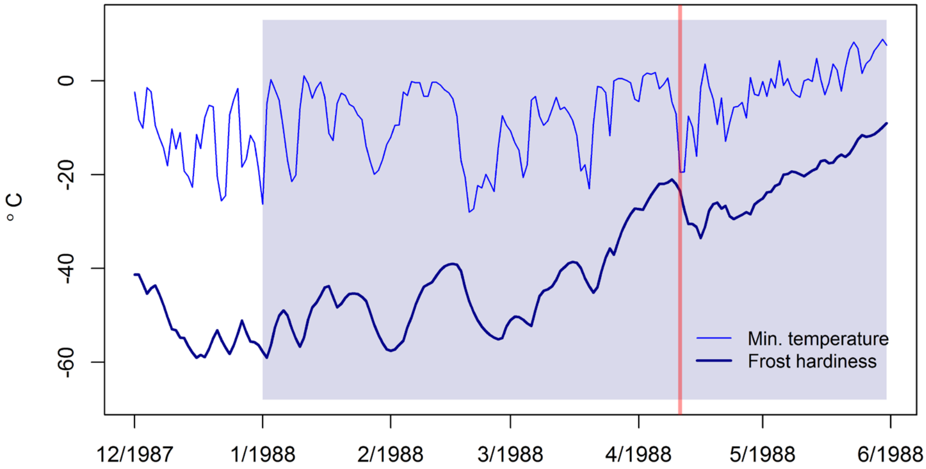

Figure 4. Example of variation in daily minimum temperature and modelled daily frost hardiness in the data, calculated for Jyväskylä weather station data. Red vertical line points the smallest difference between minimum temperature and frost hardiness. Only time period within the gray box was considered in the analysis (January to May).

detected in growth variation and its connection to weather variables between the Northern Finnish provenances transferred south and the Southern Finnish provenances growing in conditions similar to their origins.

3.2 Frost damage conditions and radial growth variation

The connections between RWI chronologies and the variables describing potential frost damage conditions were not very strong and varied between Norway spruce and Scots pine (paper II). For Norway spruce, years with exceptionally low winter temperature minima (TMIN) were associated with statistically significant increases in radial growth in Northern Finland. REL_TMIN variable, describing the events of insufficient frost hardiness levels, was associated with declines of radial growth at most of the sites, but this effect was significant in only few sites. Winters with high frost sum of snowless days (FROSTSUM) were also associated to lower radial growth at most sites and this effect was significant at sites located in Central Finland.

In Scots pine sites none of the studied variables were associated with statistically significant growth reductions. Instead, three sites in Southern and Central Finland showed significant positive coefficients with REL_TMIN, implying that years in which minimum temperature dropped close to modelled frost hardiness level were associated with higher radial growth.

3.3 Storm damage probability of stands and trees

Stand-level storm damage was shown to be related to stand characteristics, previous forest management operations as well as topography and soil type (paper III). The highest peaks of damage probability were found after thinnings and after regeneration cuttings. Differences between species were found, as damage probability increased with increasing basal area and stand average DBH in Norway spruce dominated stands but not in Scots pine stands (Fig. 5). Topographical variables were found to be significantly related to storm damage

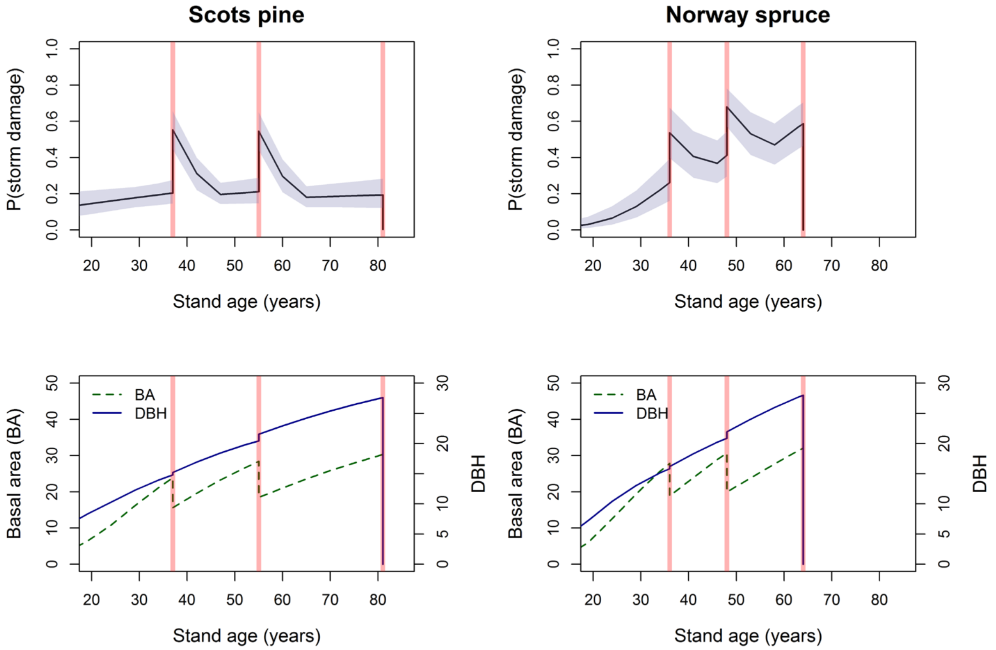

Figure 5. Modelled probability of storm damage (upper row) for stand simulations following the Finnish forest management recommendations for Scots pine and Norway spruce, and the simulated values for basal area (BA, m2/ha) and average diameter at breast height (DBH, cm) (lower row). The red vertical lines mark the conducted forest management operations (two thinnings and final felling) and the grey shadings in the upper row plots represent the bootstrapped 95% confidence intervals. In final felling all trees were assumed to be cut, therefore the damage probability drops to 0.

probability: the interaction term of slope steepness and slope direction (wind / shelter) was statistically significant.

In tree-level models, the best model contained variables describing the type of the tree species (conifer or deciduous), tree height, wood decay in living trees in the same stand, recent regeneration cuttings and proximity of open stand border, as well as slope steepness calculated from high-resolution DEM. The interaction between tree type and tree height showed that damage probability increased with height for conifers but decreased with height for deciduous trees. The ability of the model to separate damage cases from no-damage was satisfactory (AUC=0.70).

3.4 Effect of storm type on damage probability on stand-level

Models with similar predictor variables were fitted separately to both the autumn storm data set and the thunder storm data set (paper III). In both cases, the models were able to discriminate between damaged and non-damaged plots on a satisfactory level (AUC_{autumn}=0.724, $AUC_{thunder}$=0.808). The model fitted with the autumn storm data set was used to predict damage probability in the thunder storm data set. With the thunder storm data set, the discriminatory ability of the autumn storm model was lower (AUC=0.675) and slightly below 0.7, which is often used as a threshold for acceptable discrimination (Hosmer *et al.* 2013).

In the autumn storm model most explanatory variables or their interaction terms were statistically significant ($p < 0.05$, except variables describing wood decay in living trees and proximity of open area), whereas in the thunder storm model the statistically significant variables were related to recent cuttings, wind-side topographical position and wood decay in living trees.

3.5 Fine-scaled topographical data in modeling damage probability

In the tree-level study, the comparison of models containing different variable groups was done with AIC and AIC weights (paper IV). Slope steepness calculated from the high-resolution DEM2 and, thus, describing topography in the proximity of the tree, was included in the best model together with the variables describing tree properties and forest stand properties. The AIC weights showed a clear difference between the best model and the other models (w_i=0.48 for the best model and w_i=0.19 for the second best model, that also contained coarser scale topographical variable in addition to the variables in the best model).

4. Discussion

4.1 Drivers of radial growth variation

4.1.1 Provenance differences

The largest differences in radial growth variation were found between the Central European and Northern European Norway spruce provenances (paper I). This reflects the large geographical distance between the tree origins, but is also in accordance with the genetic division of European Norway spruce populations, resulting from the dispersal patterns after the last ice age (Lagercrantz and Ryman 1990, Morgenstern 1996, Vendramin *et al.* 2000). However, not all results in paper I followed the division between Central and Northern European populations. In the northernmost sites, Southern Finnish provenances were clustered together with Central European provenances instead of the geographically and most likely also genetically closer Northern Finnish provenances. This may be a result of clinal variation within the Finnish Norway spruce populations. Many features such as timing of bud set in autumn and growth initiation in spring have been shown to vary with latitude within north European populations of Norway spruce (Aitken and Hannerz 2001, Chen *et al.* 2012). Transferring the Southern Finnish provenances to north, to conditions they had not been adapted to, is perhaps reflected to the growth variation in a same way as the longer transfer north experienced by the Central European provenances.

The main provenance differences in the relationship of growth variation and weather conditions were found for winter and spring time temperatures. Years with cold winters were associated with anomalous growth declines in the results (paper I). Weaker adaptation of southern provenances to low temperatures seems to be the main reason for this. Frost damage in southern provenances has been documented at the experiments after harsh winters (Heikinheimo 1949, Hagman 1986, Hänninen *et al.* 2001). Southern provenances of Norway spruce have shown weaker tolerance to frost desiccation in seedlings (Danusevicius *et al.* 1999), as well as weaker and later induced autumn frost hardiness (Beuker *et al.* 1998, Westin *et al.* 2000, Hannerz and Westin 2005).

No provenances differences were found in the growth responses to growing season weather conditions (paper I). A likely explanation is the type of the experimental sites, as all experiments were located in rather moist areas where water shortages are rare. Therefore, possible provenance differences in drought tolerance would not be revealed in the results.

4.1.2 Tree growth variation and potential frost damage effects

While provenances transferred north from their origins experienced frost damage and growth declines in years with cold winters (paper I), local provenances growing in natural forests did not show lower radial growth after winters with low minimum temperatures (paper II). In fact, radial growth of Norway spruce in northern Finland seemed to be higher in years with exceptionally cold winters. While this pattern is consistent with previous research (e.g., Jonsson 1969, Miina 2000, Mäkinen *et al.* 2000), the reasons for cold winters being associated with higher growth are not clear. A potential explanation could be respiratory losses during warm winters and springs, if trees initiate photosynthetic activity before sufficient availability of light for photosynthetic production (Skre and Nes 1996, Miina 2000, Linkosalo *et al.* 2014). However, more research would be needed to understand whether this correlative pattern is truly related to winter time conditions.

The results in paper II showed signs of decreased growth in Norway spruce after events of insufficient frost hardiness (Fig. 4) and after years with high frost sum of snowless days. However, the growth decline was observed at only some of the Norway spruce sites, while many sites showed no statistically significant connection to the studied variables. Therefore, conclusions about the results should be done with caution. In any case, the results suggest that considering only temperature is unlikely to be sufficient in studying winter temperature effects on tree growth. Instead, understanding the effects of changing temperature and snow conditions in relation to tree physiology and phenology is needed.

The differences between Norway spruce and Scots pine in responses to potential frost damage events in paper II were consistent with earlier results. Previous studies connecting Scots pine tree-ring data and winter time conditions have generally not found statistically significant connections (Jonsson 1969, Miina 2000). The species differences are most likely related to winter time physiology. For example, lower levels of frost hardiness in buds have been reported for Norway spruce than for Scots pine (Beuker *et al.* 1998) and photosynthesis in Norway spruce has been shown to be reactivated more readily with increasing temperatures (Linkosalo *et al.* 2014).

4.2 Storm damage

4.2.1 Factors driving storm damage probability of stands and trees

On stand-level, stand characteristics and forest management were strongly related to stand-level damage probability (paper III, Fig. 5). Increasing damage probability after thinnings and regeneration cuttings as well as higher damage probability in Norway spruce dominated stands was consistent with previous studies (e.g., Lohmander and Helles 1987, Peltola *et al.* 1999, Dobbertin 2002, Valinger and Fridman 2011).

Topography was found to contribute in predicting the storm damage probability on both stand- and tree-levels (papers III and IV). The importance of topographical variables is particularly interesting because of the small variation in topography in the study area. Several previous studies that found no connections between topographical variables and storm damage attributed this to low variability in topography in the study area (Anyomi and Ruel 2015, Saarinen *et al.* 2016).

Our results suggest that taking wind direction into consideration was essential in defining meaningful topographical variables for stand-level damage probability models (paper III). Slope direction was significant in both stand-level models and in the autumn storm model the interaction of slope steepness and direction was significant. Similar to our results, Hanewinkel *et al.* (2014) also found steeper lee side slopes to be associated with lower damage probability.

On tree-level, tree properties were the most important single variable group affecting damage probability, while also stand level variables and topography were included in the best model. The difference between Norway spruce and Scots pine was not significant in the tree-level study and they were therefore grouped into one class. The storm damage in our data set contained both wind and snow damage and this may have reduced the difference between the two conifer species, as spruce is considered to be more vulnerable to wind (Dobbertin 2002, Valinger and Fridman 2011) and the crown shape of pines may expose them to snow damage (Nykänen *et al.* 1997). It is also possible that the deciduous trees in the data have been mostly damaged by snow, as the damaged deciduous trees were smaller than average.

In contrast to the stand-level results, slope direction was not statistically significant in the tree-level model (paper IV). This may be due to the high local variability of slope direction in the high-resolution DEM. Slope direction calculated from the DEM2, which describes only the close environment of the tree, may not reflect the wind exposure as well as the same variable calculated from DEM10, where the slope direction is averaged over a larger area. However, fine-scale slope steepness, calculated from DEM2 was found to significantly decrease the damage probability in the tree-level model. This effect may be related to locations with high slope steepness being associated with more variable topography and being therefore more sheltered from wind. In addition, high-resolution slope steepness may be correlated to other variables than wind that are related to storm damage. For example, topography is related to soil properties, which in turn affect the support trees have against uprooting (Peltola *et al.* 1999, Mitchell 2013).

4.2.2 Differences between storm types

Same factors were related to storm damage probability in both autumn cyclones and summer thunder storms (paper III). Models with similar independent variables were able to discriminate between damaged and non-damaged stands in both data sets and the autumn storm model had some discrimination ability also in the thunder storm data set. This indicates that same factors can be used in assessing forest vulnerability to storm damage also in thunder storms. The factors driving the similar responses in the two data sets are most likely related to the variables with low p-values also in the thunder storm data, i.e. forest management history and topography.

While the results showed that similar variables in general were related to damage probability, the analysis did not allow for detecting finer differences between the storm types. For example, during the summer thunder storms deciduous trees had leaves and were therefore subject to larger wind loads than during autumn storms. Thus, the damage probability of deciduous trees should be higher during summer thunder storms. However, this difference cannot be seen in our results because, due to the smaller size of the data set and the dominance of coniferous species in the study area, there were only few storm damaged stands dominated by broad-leaved trees in the thunder storm data.

The difference in sample size between the data sets also complicates the interpretation of the model coefficient estimates and their p-values. Because the sample size in the autumn storm data set (n=1722) is much larger than in the thunder storm data set (n=353), the p-values are not comparable between the models and complexity of the model makes many coefficient estimates in the thunder storm model uncertain.

4.2.3 Fine-scaled topographical information in modeling storm damage probability

The results demonstrated that tree-level storm damage models can be improved by adding topographical variables calculated from high-resolution DEMs. The fine-scale topographical variables also performed better than the variables calculated from the lower resolution DEM10. This indicates that the topographical environment in the close proximity of a tree significantly affects the tree's damage probability in storm. On the other hand, the high-resolution DEM2 produced from laser scanning data also has higher elevational accuracy than the older DEM10. This may also partly explain the better performance of the high-resolution topographical variables in the model comparison.

Recent studies by Jung & Schindler (2016) and Venäläinen *et al.* (2017) have used topographical information to produce higher resolution wind data for assessing the forest wind damage risk. However, our results call for accounting for topographical variation at even higher resolution, as these studies only use a resolution of tens of meters (50 m and 20 m, respectively).

4.3 Methodological considerations

Paper II presented a more ambitious methodological approach in the thesis by combining frost hardiness modelling with tree-ring data and utilizing novel statistical methods of extreme value distributions. Yet, the results also demonstrate the challenges in using long time-series of tree-rings and meteorological records. Little data about observed damage or tree physiology is available for the studied sites and the used frost hardiness model contains a lot of uncertainties. The statistical approach in paper II used statistical distributions of extreme values to define biologically meaningful extreme conditions. However, this approach does not overcome the challenge of having only few years of truly exceptional conditions in the data, as 'extreme events' by definition do not occur frequently. In addition, a categorization of years into "normal" and "extreme" was used in the analysis, even though categorization of continuous variables can be problematic from the methodological point of view (see Harrell 2015).

The thesis was conducted using mainly already existing experiments and data sets. This enabled the use of extensive data sets and long-term provenance experiments with mature trees but also made me dependent on the previous decisions on data collection and experiment design. This problem is maybe the most prominent in the provenance experiments (paper I). Even though the old provenance experiments provide a unique data set, the design of the experiments planned already in the 1920s does not meet the modern standards of experiment design. The plots did not have replicates, i.e. there is only one plot for each provenance per site, and at some sites the plot were not randomized but the provenances were arranged in latitudinal order. In addition, the information about the used seed material lacks details, especially for the non-Finnish provenances (Heikinheimo 1949, Beuker 1996). These issues add uncertainties to the results and make the interpretation of the results more challenging. However, similar trends in the results at all experimental sites support the conclusion that the observed growth reactions were indeed a result of provenance differences and not, for example, caused by variation in environmental conditions between the plots.

Storm damage in forests is stochastic in nature, which makes the modeling of the phenomenon challenging. This can be seen also in this thesis, as the performance of the models, measured by AUC, did not rise much higher than the 0.7 threshold for acceptable discrimination of damage events from non-damage, and in some occasions was even below this threshold. In addition, the AUC was in most cases calculated with the same data that was used for model fitting. Thus, before using the models in practical applications more rigorous testing of the model performance should be carried out by using cross-validation and independent test data.

In this thesis storm damage was modelled empirically using statistical modeling methods. While statistical approaches are common (e.g., Lohmander and Helles 1987, Valinger and Fridman 1999, Jalkanen and Mattila 2000, Schmidt *et al.* 2010) mechanistic models as well as hybrid models combining empirical and mechanistic approaches are gaining popularity, as they aim to describe the physical processes behind wind damage in trees, and are therefore less restricted to the conditions of the original data set (Peltola *et al.* 1999, Gardiner *et al.* 2000, Gardiner *et al.* 2008). In future research, both statistical and mechanistic approaches are needed to improve the understanding of boreal disturbance regime and its future changes.

4.4 Future perspectives

As the climate change effects are most pronounced in winter time, understanding of mechanisms of how temperatures outside of growing season affect trees becomes increasingly important. While growth variation responded to winter temperatures in Central European provenances transferred far north (paper I), this type of simple temperature variable was not sufficient in describing the conditions affecting local provenances in natural forests (paper II). Therefore, information about tree phenology and physiology needs to be included in future studies of outside growing-season weather effects on tree growth. As long time-series of observational data on tree phenology and physiology are rarely available for study sites, utilization of modelling is the natural approach for this. However, at least in the case of frost hardiness models, more work is still required for the parametrization of models for different species, provenances as well as different tree organs and tissues (Hänninen 2016).

The storm damage part of the thesis concentrated on forest susceptibility to damage. However, a comprehensive understanding of storm damage risk would require accounting for more factors. More detailed information about the exposure of forests to wind should be included, for example, by utilizing new resources describing the high-resolution extreme wind speeds produced by Venäläinen *et al.* (2017). In addition, information about the length of soil frost period and its future changes should be included for calculating spatial risk estimates of storm damage. More research would also be needed to find the best way to include fine-scale topographical variation in storm damage studies.

The results of the thesis provide insight into how forests and trees respond to weather events. The research on climate sensitivity of forests should be used to define the best forest management practices under changing climatic conditions (Gardiner and Quine 2000, Heinonen *et al.* 2009, Zubizarreta-Gerendiain *et al.* 2017) and this information should be included in decision support systems (Olofsson and Blennow 2005, Hanewinkel *et al.* 2011) and effectively communicated to stakeholders (Lindner *et al.* 2014).

5. Conclusions

In this thesis extensive data sets of tree radial growth and forest storm damage were used to study the effects of weather conditions on radial growth and the factors predisposing forests to storm disturbances. The results provide insight into modeling of climate effects on boreal forests and illustrate how between- and within-species differences mediate the impact climate has on tree growth and forest disturbance.

The following conclusions can be drawn from the thesis:

- Provenance has an evident effect on radial growth variation in Norway spruce. When grown in northern European climatic conditions, provenances differ most in their growth response to winter temperature, as adaptation to winter temperatures in weaker in Central European than in Northern European provenances.
- In case of local provenances in natural forests, using only temperature variables in studying potential frost damage effects on trees is not adequate. Instead, considering factors such as tree phenology and snow cover is needed. In addition to modeling approaches and tree-ring data used in the thesis, further physiological and experimental research is needed to understand how tree growth is affected by conditions outside of growing season.
- Stand-level damage probability is affected by stand characteristics and previous management operations. On tree-level, damage probability is connected to the type of the tree species (conifer or deciduous) and tree height as well as recent changes in wind exposure and wood decay in the stand. In addition, topography is connected to storm damage probability on both stand and individual tree level.
- Storm damage probability in autumn storms and summer thunder storms are affected by similar factors, and the similarities are clearest in the effects of forest management history and topography. However, the analysis was not able to detect all differences between the storm types due to the limitations of the data. This concerns especially the differences of damage risk in deciduous trees between winter and summer.
- High-resolution topographic information can be used to improve the models of tree-level storm damage probability.

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