Forest Ecology and Management 493 (2021) 119252

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Model analysis of temperature impact on the Norway spruce provenance specific bud burst and associated risk of frost damage

Tetiana Svystun [a,*], Jenny Lundströmer [b], Mats Berlin [c], Johan Westin [d], Anna Maria Jönsson [a]

[a] Department of Physical Geography and Ecosystem Science, Lund University, SE-223 62 Lund, Sweden
[b] Department of Forest Genetics and Plant Physiology, Swedish University of Agricultural Science, SE-901 83 Umeå, Sweden
[c] Skogforsk (The Forestry Research Institute of Sweden), Uppsala Science Park, SE-751 83 Uppsala, Sweden
[d] Unit for Field-based Forest Research, Vindeln Experimental Forests, Svartbergets Field Station, SE-922 91 Vindeln, Sweden

ARTICLE INFO

Keywords:
Temperature response
Picea abies
Bud burst
Frost risk
Gridded climate data

ABSTRACT

The annual growth cycle of boreal trees is synchronized with seasonal changes in photoperiod and temperature. A warmer climate can lead to an earlier bud burst and increased risk of frost damage caused by temperature backlashes. In this study we analysed site- and provenance specific responses to interannual variation in temperature, using data from 18 Swedish and East-European provenances of Norway spruce (*Picea abies*), grown in three different sites in southern Sweden. The temperature sum requirements for bud burst, estimated from the provenance trials, were correlated with the provenance specific place of origin, in terms of latitudinal and longitudinal gradients. Frost damage had a significant effect on tree height development. Earlier timing of bud burst was linked to a higher risk of frost damage, with one of the sites being more prone to spring frost than the other two. The estimated provenance specific temperature sum requirements for bud burst were used to parametrize a temperature sum model of bud burst timing, which was then used together with the ensemble of gridded climate model data (RCP8.5) to assess the climate change impact on bud burst and associated risk of frost damage. In this respect, the simulated timing of bud burst and occurrence of frost events for the periods 2021–2050 and 2071–2100 were compared with 1989–2018. In response to a warmer climate, the total number of frost events in southern Sweden will decrease, while the number of frost events after bud burst will increase due to earlier bud burst timing. The provenance specific assessments of frost risk under climate change can be used for a selection of seed sources in Swedish forestry. In terms of selecting suitable provenances, knowledge on local climate conditions is of importance, as the gridded climate data may differ from local temperature conditions. A comparison with temperature logger data from ten different sites indicated that the gridded temperature data were a good proxy for the daily mean temperatures, but the gridded daily minimum temperatures tended to underestimate the local risk of frost events, in particular at the measurements 0.5 m above ground representing the height of newly established seedlings.

1. Introduction

The boreal bioclimatic zone covers a range of latitudes, with a mix of oceanic and continental conditions. As a result of local adaptation to seasonal changes in day length and temperature, the timing of phenological events, such as bud burst and bud set, of boreal trees varies between different provenances (Hänninen, 1990; Hänninen, 2016). The cell division and growth of the buds resume in spring after the break of winter dormancy. Some weeks following bud burst, the trees have fully differentiated shoots with needles spreading. During summer, the growth of trees continues and new buds for the next year are sprouted. In the autumn, the cell division slows down until it completely stops, and the tree enters dormancy to prepare for the dark and cold winter (Hänninen, 2016).

Trees of all sizes are sensitive to freezing temperatures while in active growth. The critical phase is the seasonal change from dormancy to active growth and vice versa (Christersson and Fircks, 1988; Sakai and Larcher, 1987). Trees that are not able to track the seasonal changes properly may show reduced or hampered growth. Typical spring frost events are often caused by radiation frosts that occur when cold air accumulates under conditions with clear skies and no wind, and they are often site specific (Hammersmith, 2014; Langvall, 2000). Spring frost

* Corresponding author.
E-mail address: tetiana.svystun@nateko.lu.se (T. Svystun).

https://doi.org/10.1016/j.foreco.2021.119252
Received 10 September 2020; Received in revised form 29 March 2021; Accepted 3 April 2021
Available online 30 April 2021

events due to radiation frost are most critical to young trees, often at tree heights below 2 m, but may also be harmful to larger trees (Augspurger, 2009). Frost damage can be reversible and non-reversible, with the latter being characterized by ice formation within the protoplast, resulting in needle losses and death of seedlings (Larcher, 1981; Weiser, 1970). In contrast, autumn frosts tend to be less of a problem compared to spring frost in large parts of southern Sweden, partly because the current year shoots are not as sensitive to frost at that time (Langlet, 1960; Skrøppa and Magnussen, 1993).

In Sweden, Norway spruce (*Picea abies*) is one of the most widespread and important tree species for both economic and ecological aspects. The spruce forest stands are predominately even-aged and managed with thinning and clear-cutting. In such forest practices spring frosts may locally be a major problem. Regeneration is commonly carried out by planting of seedlings, with the selection of plant material being influenced by expected growth and local risk of frost damage. The Swedish breeding populations and seed zones are divided into the northern and southern areas (Berlin et al., 2019; Rosvall, 2003). The border between northern and southern Sweden in this respect follows an east–west line between latitudes 60°N and 61°N, which divides the boreal from boreo-nemoral forests, also called *Limes Norrlandicus* (Fries, 1948). In the north of Sweden, a latitudinal transfer to the north from the local origin is recommended to take advantage of the higher growth capacity of the more southern provenances (Kroon and Rosvall, 2004; Rosvall and Ericsson, 1982). In the south of Sweden, plant material originating from East Europe is commonly used, due to a higher growth capacity and later timing of bud burst with lower risk of frost damage than the local provenances (Danusevicius and Persson, 1998; Persson and Persson, 1992; Werner and Karlsson, 1983).

The timing of bud burst can be estimated from a provenance specific temperature sum requirement (Hannerz, 1998). Provenances from the north have a generally lower temperature sum requirement than provenances from the south, an adaptation to a shorter growing season with later and faster temperature progression in spring. However, to break dormancy a period of exposure to chilling is needed (Nienstaedt, 1967; Worrall and Francois, 1967). Trees that have not been exposed to sufficient chilling may respond by delayed bud burst due to increased temperature sum requirement for bud burst (Hannerz et al., 2003; Heide, 1993; Man et al., 2017). In addition, photoperiod may interact with temperature during different stages of dormancy release to regulate the timing of bud burst (Basler and Körner, 2014; Kramer et al., 2017). Long photoperiods may compensate for a lack of chilling by reducing the temperature sum requirement to reach bud burst, but no photoperiod effect has been found when the chilling requirement was fulfilled (Heide, 1993; Myking and Heide, 1995). Absence of photoperiod effect on the timing of bud burst in some studies can be related to the experimental conditions of a constant photoperiod, which do not resemble the rate of photoperiod change under natural conditions. In contrast, under conditions of sufficient chilling, gradual shortening of the natural photoperiod was shown to delay bud burst, while continuous lengthening of the photoperiod advanced bud burst (Basler and Körner, 2014; Caffarra et al., 2011; Partanen et al., 1998).

A warmer climate will affect the duration of the boreal growing season and impose an earlier timing of bud burst. Phenological models driven by climate data can be applied to estimate the timing of bud burst and frost risk (Augspurger, 2013). The simplest bud burst models are based on the temperature sum accumulation (forcing) above a threshold value, modelled as linear or logistic functions. There are models including both chilling and temperature sum accumulations, occurring in sequence or in parallel (Hänninen, 1995; Linkosalo et al., 2008; Linkosalo and Hänninen, 2006). Photoperiod can be included as a starting day for the temperature sum accumulation, or as a dynamic variable modifying the temperature response, e.g. BC model (Blümel and Chmielewski, 2012). More complex models considering a combined effect of photoperiod, chilling and forcing, have also been introduced, e.g. the Promoter-inhibitor model (Schaber and Badeck, 2003), the Unified model (Chuine, 2000), and the DORMPHOT model (Caffarra et al., 2011). Temperature sum models are among the best performing models, and commonly outperform models accounting for chilling and photoperiod, though these factors can be of importance to consider if the requirements are not fulfilled (Linkosalo et al., 2008; Linkosalo and Hänninen, 2006; Olsson and Jönsson, 2015). Earlier studies have indicated that climate change may induce an increased risk of spring frost damage due to higher frequency of frost episodes during a vulnerable phase of shoot development (Bennie et al., 2010; Jönsson et al., 2004; Saxe et al., 2001). South Sweden is influenced by the fine balance between a reduced risk of frost due to a generally warmer climate and an increased risk caused by spring backlashes following an early bud burst (Jönsson and Bärring, 2011; Langvall, 2011a). Which process will dominate, depends on the degree of warming in combination with the provenance specific responses. Scenario assessments are thus needed to address the impacts of climate change, and the potential to mitigate an increased risk of frost damage via the selection of a suitable provenance.

The aim of this study was to analyse site- and provenance specific responses to seasonal changes in temperature conditions using data from three field sites with provenance trials in southern Sweden. We analysed the timing of bud burst and risk of spring frost damage under current and future climate conditions, as influenced by provenance specific temperature requirements. The climate change impact was assessed for southern Sweden, comparing two future periods 2021–2050 and 2071–2100 with the recent past, 1989–2018, using an ensemble of gridded climate model data representing RCP8.5. A temperature sum model was selected as the base model, and its validity was addressed by separately calculating chilling units and chilling days. In terms of selecting suitable provenances, local climate conditions are of importance, and gridded climate data may differ from the local temperature conditions (Olsson and Jönsson, 2015). Potential biases were depicted by comparing daily mean and minimum temperatures of gridded observed data with data from temperature loggers at ten different sites in southern Sweden.

2. Materials and methods

2.1. Field site descriptions

This study is based on data from three Norway spruce provenance trials established in the spring 2002 in southern Sweden in Sund (57.86°N, 15.23°E, 240 m a.s.l.), Toftaholm (57.03°N, 14.04°E, 155 m a.s.l.) and Skärsnäs (56.25°N, 14.39°E, 125 m a.s.l.) (Fig. 1). The trials were planted as single tree plots in a randomized block design with 25 replications and an initial spacing of 1,8 × 1,8 m. Seeds were collected from 6 Swedish provenances and 12 East-European provenances in the spring 2000 (Table 1). The seedlings were grown in the nursery at Skogforsk (Forestry Research Institute of Sweden) research station Ekebo for two years (2000–2001). The trial's establishment year, 2002, was considered as the first growth season. The provenances used (Table 1) are assumed to be autochthonous, though the background of the provenance Istebna is partly unclear.

2.2. Data on timing of bud burst, tree height and frost damage

Data from the field sites have been collected over the years by Skogforsk. The bud burst and shoot development were assessed in the spring of 2004, during the third growth season, for each individual tree according to Krutzsch scale (Krutzsch, 1973). The stage 0 was considered as corresponding to dormant bud, stage 3 to bud burst, and stage 8 to fully differentiated shoots with full-fledged basal needles. The observations were made on May 24, May 23, and May 21 in Toftaholm, Sund and Skärsnäs, respectively. The timing of the observations was selected to capture the whole span of phenologic variation (i.e. to enable monitoring of both early and late flushing provenances at the same time), aiming for the stages to be normally distributed (i.e. with a few

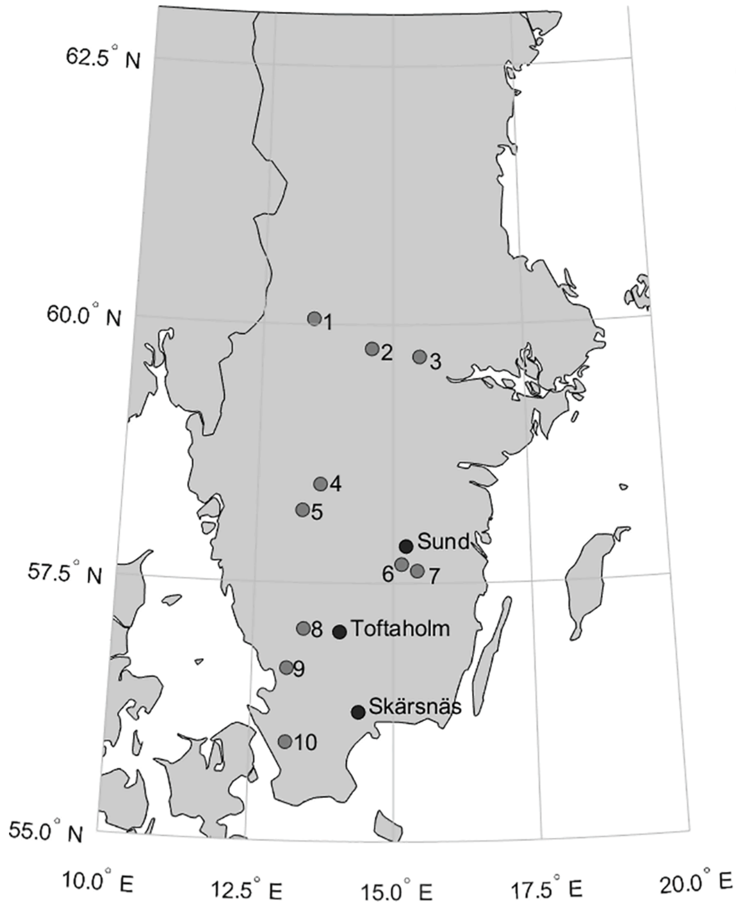

Fig. 1. Field sites with phenology assessments and temperature logger data in southern Sweden, years - data collected between these years.

observations in stages 0 and 8).

Spring frost damage was noted at the same time as phenology observations in two of the sites, Toftaholm and Skärsnäs. The frost damage was assessed for each individual tree according to the binary scale of 0 (no damage) and 1 (damage) at the same time as phenology assessments. The tree was considered damaged when the apical shoot and at least 30% of all shoots from that year were visibly damaged, i.e. brown and dying. The dataset also included assessments of height growth in the autumn of 2007 (after 6 growth seasons) at all sites, and autumn of 2014 (after 13 growth seasons) at Toftaholm only.

2.3. Climate data

This study included three sets of climate data with information on both daily mean temperature and daily minimum temperature (details below). To link the field observations with observed temperature conditions, gridded observed temperature data (E-OBS) were used (Cornes et al., 2018), as none of the field sites with phenology assessments were equipped with temperature loggers. To discuss the potential influence of systematic and random differences between local climate conditions and gridded data, data from ten field sites with temperature loggers (Fig. 1) were compared with the corresponding gridded observed data.

To generate reference simulations and future projections of bud burst and risk of frost, we used gridded climate model data covering southern Sweden (Giorgi et al., 2009). The transient simulations, 1989–2100, were all based on bias corrected climate model data. That is, the climate model data provided had been adjusted using gridded observed climate data (MESAN 1989–2010) (Häggmark et al., 2000), to be fully representative of the regional climate conditions. The climate model data for this period are however still based on model simulations only. The data are thus not representative of the observed weather and could not be used in chronological comparisons with field data. The gridded observed data (E-OBS) were therefore used in all such comparisons.

2.3.1. Gridded observed temperature data

Gridded observed temperature data for the period 1989–2018 were derived from the European gridded observational dataset (E-OBS version 20e), with a spatial resolution of 0.1-degree regular latitude/longitude grid. E-OBS is generated from the interpolation of station-derived meteorological observations by the European Climate Assessment & Dataset (ECA&D) project. The E-OBS version 20e provides an improved estimation of interpolation uncertainty compared to the original E-OBS data set (Haylock et al., 2008) through calculating a 100-member ensemble of each daily field (Cornes et al., 2018).

2.3.2. Temperature logger data

From 2013, Skogforsk has installed temperature stations in all newly established tree breeding field sites. At each field site a temperature station consisting of two temperature loggers at 0.5 m and 1.8 m above ground was established at a central position of the trial. The loggers used are HOBO Water Temperature Pro v2 Data Logger - U22-001 from Onset Computer Corporation (US) and each logger was installed in a solar radiation shield (RS-1). The loggers assessed the temperature at both heights every 30 min. In this study, we compiled the data from ten field sites (Fig. 1) and calculated the site specific daily mean and minimum temperatures, to enable a comparison with the corresponding gridded observed dataset.

2.3.3. Climate model data

Climate model temperature data for the period 1989–2100 were

Table 1
Provenances included in this study, Swedish and East-European groups, with information on the latitude and longitude of the place of origin, and the country of origin.

Name	Group	Latitude (°N)	Longitude (°E)	Country of origin
Ängelsfors	Swedish	60.54	16.14	Sweden
Laxarby	Swedish	59.02	12.32	Sweden
Bollebygd	Swedish	57.71	12.5	Sweden
Ramkvilla	Swedish	57.2	14.85	Sweden
Emmaboda	Swedish	56.63	15.57	Sweden
Rezekne 1	East-European	56.5	27.35	Latvia
Hallaryd	Swedish	56.47	13.9	Sweden
Malta	East-European	56.25	27.25	Latvia
Istra	East-European	56.25	27.83	Latvia
Rezekne 2	East-European	56.08	27.42	Latvia
Svente	East-European	55.83	26.25	Latvia
Ignalina	East-European	55.4	26.38	Lithuania
Vitebsk	East-European	55.2	30.25	Belarus
Trakai	East-European	54.58	24.75	Lithuania
Punia	East-European	54.53	24.05	Lithuania
Minsk	East-European	53.9	27.55	Belarus
Bialystok	East-European	53.12	23.17	Poland
Istebna	East-European	49.57	18.89	Poland

obtained from CORDEX project, with a spatial resolution of 0.11-degree latitude/longitude in a rotated pole grid. To account for uncertainties associated with climate model data, three datasets were included (Table 2). The datasets consisted of data from one regional climate model SMHI-RCA4, that had been driven by CERFACS-CNRM-CM5, IPSL-CM5A-MR and M−MPI−ESM−LR global climate models, all representing concentration pathway RCP8.5, and bias adjusted with a distribution-based scaling method using data from MESAN 1989–2010 (Häggmark et al., 2000).

To capture a transient effect of temperature rise, the climate model data were split into three 30-year periods: 1989–2018 (reference period), 2021–2050 (near future) and 2071–2100 (far future). All variables were calculated for each climate model data set separately, and an average of the model output was used in this study.

2.3.4. Comparison of gridded observed temperature data and temperature logger data

To compare the gridded observed temperature data (representing the temperature at 2 m above ground) with the logger temperature data (0.5 and 1.8 m above ground), Cumulative Density Functions (CDFs) were created for the months of January to June, i.e. the time period of relevance for bud burst and spring frost events. This method, developed for the purpose of bias correction, provides a non-linear comparison of systematic differences between data sets (Brocca et al., 2011; Drusch et al., 2005). In this study, the gridded data were rescaled so that their CDF matches the CDF of the logger data, and then both were ranked and plotted against relative temperature (mean and minimum), to enable a visual comparison of datasets.

Table 2
Full names of the climate model datasets included in the study.

Dataset
tasAdjust_EUR-11_CNRM-CERFACS-CNRM-CM5_rcp85_r1i1p1_SMHI-RCA4_v1-SMHI-DBS45-MESAN-1989-2010_day
tasAdjust_EUR-11_IPSL-IPSL-CM5A-MR_rcp85_r1i1p1_SMHI-RCA4_v1-SMHI-DBS45-MESAN-1989-2010_day
tasAdjust_EUR-11_MPI-M-MPI-ESM-LR_rcp85_r1i1p1_SMHI-RCA4_v1a-SMHI-DBS45-MESAN-1989-2010_day

2.4. Analysis of temperature sum and chilling differences among sites and provenances

2.4.1. Calculation of temperature sums

For each individual tree, the temperature sum (TS) needed to reach bud burst was calculated as an accumulation of daily mean temperature above a threshold value (Eq. (1)):

$$TS = \sum_{t=t_0}^{t_1} \begin{cases} T_{mean}(t) - T_{\text{threshold}}, & \text{if} T_{mean}(t) \geq T_{\text{threshold}} \\ 0, & \text{if} T_{mean}(t) < T_{\text{threshold}} \end{cases} \tag{1}$$

where TS is the temperature sum requirement for bud burst (growing degree-days, GDD), $T_{mean}(t)$ is the daily mean temperature (°C) on day t, $T_{\text{threshold}}$ is the threshold temperature (°C), t_0 is the starting day for temperature sum accumulation, t_1 is the day of bud burst (day of the year, DOY). $T_{\text{threshold}}$ was set to +5 °C, as it has been found to be optimum for predicting the timing of bud burst in Norway spruce in Sweden (Hannerz, 1999). The choice of a starting day for the temperature sum accumulation within the first three month of the year in southern Sweden under current climate conditions has been shown to not significantly affect the calculations, as the contribution of this period to the temperature sum has been rather small (Hannerz, 1999). In our study, the starting day was set to January 1, to ensure that the climate change signal can be fully captured, as a starting day in March can be too restrictive. In addition, two ways of calculating the temperature sum were compared, starting from 1) January 1 and 2) onset of vegetation period (the first day of year after four consecutive days with a daily mean temperature above +5 °C). The average difference between two methods was small, 12 ± 6 GDD, and in all further analysis the temperature accumulated from January 1 was used.

2.4.2. Estimation of the date of bud burst

Since the dataset on bud burst and shoot development only included one observation of shoot development per tree, the date of bud burst (stage 3) had to be estimated for some trees, following the method in Hannerz (1999). This was done by using the temperature sum requirement of 40 GDD (+5 °C) per stage of shoot development. This value was obtained from the slope of the regression line of shoot development stages 2–6 (according to Krutszch scale) on temperature sum (Hannerz, 1999). For the trees observed that had not reached stage 3, the 40 GDD were multiplied by the number of stages remaining to reach stage 3, and the day of bud burst was calculated by adding the number of days needed to accumulate this to the date of observation. For the trees that had passed stage 3, the 40 GGD were multiplied by the number of stages exceeding the stage 3, and the day of bud burst was calculated by subtracting the time needed to accumulate this from the timing of observation. For shoot development stages below 2 and above 6, a linear approximation was assumed to be valid based on the figures of mean bud and shoot development presented by Langvall and Löfvenius (2019) for different sites representing a latitudinal gradient from 57°N to 64°N.

2.4.3. Calculation of chilling

To assess if the trees were exposed to a sufficient amount of chilling prior to the start of temperature sum accumulation (i.e. before January 1), the accumulation of chilling was calculated for autumn/ winter 2003 for each field site using two methods, i.e. as a number of chilling days (Eq. (2)) and a number of chilling units (Eq. (3)).

The number of chilling days (CD) was calculated as the number of days with a mean temperature below a threshold value (Cannell and Smith, 1983) (Eq. (2)):

$$CD = \sum_{t=t_0}^{t_1} \begin{cases} 1, & \text{if} T_{mean}(t) < T_{\text{threshold}} \\ 0, & \text{if} T_{mean}(t) \geq T_{\text{threshold}} \end{cases} \tag{2}$$

where CD is the number of chilling days, $T_{mean}(t)$ is the daily mean temperature (°C) on day t, $T_{\text{threshold}}$ is the threshold temperature (°C), t_0 is the starting day for chilling accumulation (September 1), t_1 is the last day for chilling accumulation (December 31). $T_{\text{threshold}}$ was set to +5 °C.

The number of chilling units (CU) was calculated according to the triangular function (Sarvas, 1974) (Eq. (3)):

$$CU = \sum_{t=t_0}^{t_1} \begin{cases} \dfrac{T_{mean}(t) - T_1}{T_{\text{opt}} - T_1}, & \text{if} T_1 \leq T_{mean}(t) \leq T_{opt} \\ \dfrac{T_2 - T_{mean}(t)}{T_2 - T_{\text{opt}}}, & \text{if} T_{opt} < T_{mean}(t) \leq T_2 \\ 0, & \text{otherwise} \end{cases} \tag{3}$$

where CU is the accumulated chilling units, T_1 is the minimum temperature threshold (°C), T_{opt} is the optimum temperature (°C), T_2 is the maximum temperature threshold (°C). $T_{mean}(t)$, t_0 and t_1 are the same as above (Eq. (2)). The parameter values developed by (Hänninen, 1990) for Finnish forest tree species, including Norway spruce, were used in the computations: $T_1 = -3.4$ °C, $T_{opt} = +3.5$ °C, $T_2 = +10.4$ °C.

Previous studies suggested that the chilling requirement for Norway spruce is between 20 and 40 chilling units or approximately the same number of chilling days (Hannerz, 1998; Hannerz et al., 2003; Hänninen, 1996). Hannerz et al. (2003) has found the chilling requirement to be lower for the northern Swedish provenances, representing continental type of response, intermediate for the southern Swedish provenance (Emmaboda), and higher for Belarus provenance (Vitebsk). In this study, the accumulated amount of chilling was separately compared with 40 chilling units and 40 chilling days, the upper limits of the chilling requirement, to ensure that the entire range of chilling requirements is fulfilled.

2.4.4. Statistical analysis

To compare the absolute temperature sum requirements of the individual trees (Eq. (1)), the effects of field site, provenance and block were analysed with two-way analysis of variance (ANOVA). In addition, we analysed the relative temperature requirements in a similar way, to account for that the use of gridded observed temperature data may induce artificial differences among sites, caused by biases between grid cell averages and local climate conditions. The relative temperature sums (delta GDD) were obtained by comparing the individual temperature sums with a base line, calculated as the mean value of the Ängelsfors provenance.

To explore the variation in temperature sum requirement along climatic gradients, two linear regression lines were derived with temperature sum requirement as a function of latitude and longitude of the provenance origin. A multiple linear regression was carried out to analyse the relationship with both latitude and longitude.

2.5. Analysis of frost risk differences among sites and provenances

2.5.1. Calculations of frost events

Frost risk was assessed by the occurrence of frost events, defined as days with minimum temperature below −2 °C and 0 °C. The threshold of −2 °C was chosen to represent the temperature at which plant cells start to freeze (Jönsson et al., 2004), as the freezing point of the cell sap is lowered by solutes (Larcher, 2003). The threshold of 0 °C was used for a comparison.

For each field site, site specific risk of frost was calculated as the annual average number of frost events occurring between January 1 and June 29 (DOY 180) over a 30-year period (1989–2018).

At each field site, provenance specific risk of frost was calculated as the cumulative number of spring frost events between bud burst and June 29 during 2002–2007 and 2002–2014, to be compared with the height measurements after 6 and 13 growth seasons, respectively, to enable a comparison with the data on frost damage. For those years, where no observations on bud burst were done, the timing of bud burst was estimated from the temperature sum requirement for bud burst (Eq. (1)).

For 2004, the year when frost damage assessments were made in Toftaholm and Skärsnäs, two measures of frost severity were calculated for each individual tree: the number of frost events during the frost susceptible period (defied as a period between bud burst and frost damage assessment day, to enable a comparison with the data on frost damage) and the lowest minimum temperature during the frost event.

2.5.2. Statistical analysis

To assess the impact of frost damage on tree height after 6 and 13 growth seasons, the average height of frost damaged trees was compared to the average height of non-damaged trees within the groups of Swedish and East-European provenances at Toftaholm and Skärsnäs. The significance of difference in height between frost-damaged and non-damaged trees and between the groups of Swedish and East-European provenances at an individual tree level was tested with two-way ANOVA. To analyse the influence of additional factors on height development, the effects of spring frost events, temperature sum requirement for bud burst (Eq. (1)), site, provenance, and block were tested at an individual tree level using ANCOVA (lm function in R).

To evaluate the relationship between frost damage and exposure to the lowest minimum temperature during the frost susceptible period, the Pearson's correlation was used.

2.6. Climate change impact assessment

To assess the climate change impact on tree's phenological responses and associated risk of frost damage under warmer climate conditions, the simulations of the timing of bud burst and occurrence of spring frost events were performed over 30-year periods using regional climate model data. All calculations were made for the three climate data sets separately, and the presented results represent ensemble averages.

The climate signal was expressed as the annual average number of frost events between January1 - June 29. The exposure to chilling before the start of temperature sum accumulation was examined by calculating the annual average number of chilling days (Eq. (2)) and chilling units (Eq. (3)) between September 1 - December 31. The date of bud burst was predicted by the temperature sum requirement for bud burst (Eq. (1)). The provenance specific risk of frost was assessed by calculating the cumulative number of spring frost events with threshold of −2 °C between bud burst and June 29 and the lowest minimum temperature during the frost event.

The outputs were illustrated by maps. For each field site and provenance trial the output variable value was calculated as the weighted average of each grid cell and the 8 surrounding grid cells, to get estimates representative of the regions. The climate change signal was calculated by comparing the near future (2021–2050) and far future (2071–2100) with the reference period (1989–2018). The results for southern Sweden for two contrasting Norway spruce provenances, Ängelsfors and Minsk, representing Swedish and East-European groups, respectively, were displayed in the result section, and results for the other 16 provenances are provided in Appendix S3 (Figs. C1-C16). Detailed results of simulations with the climate model data for each field site and provenance trial are provided in Appendix S3 (Tables C1-C4).

3. Results

3.1. Chilling and temperature sums differences among sites and provenances

The three sites had slightly different temperature conditions in autumn/winter 2003. However, the chilling requirement of 40 chilling units and 40 chilling days was met by the beginning of December at all sites. The accumulated number of chilling units was the same in Toftaholm and Sund, 60 units, but chilling expressed as chilling days was higher at Sund than at Toftaholm, 68 compared with 63 days. Skärsnäs had a slightly less amount of chilling compared to the other sites, 57 chilling units and 48 chilling days.

There were only minor differences in the provenance specific temperature sum requirement for bud burst between the sites (Table 3). The earliest and latest bud burst took place at 133–243 GDDs at Sund, 131–257 GDDs at Skärsnäs, and 132–266 GDDs at Toftaholm. Northern provenances had in general lower temperature sum requirements compared to more southern provenances, with Laxarby having the lowest temperature sum, and Minsk and Punia the highest. Istebna, the southernmost provenance, deviated from the latitudinal pattern with a temperature sum requirement close to the general average. A two-way ANOVA revealed significant effects of field site ($p < 0.05$) and provenance ($p < 0.001$) on the absolute temperature sums required for bud burst, with no significant block effect. When re-calculated based on relative temperature sums, the temperature differences among sites were removed, and only the provenance effect turned out as significant ($p < 0.001$). The absolute temperature sums, calculated as the average of the three sites, were used in all further analysis.

There was a clear difference between the two groups of Swedish and East-European provenances, with the latter having higher temperature sum requirement determined by the more southern latitudinal origin

Table 3
Mean temperature sum requirements for bud burst, expressed as growing degree days (GDD) above + 5 °C, and standard deviation for different Norway spruce provenances.

Provenance	Toftaholm		Sund		Skärsnäs	
	No. of trees	GDD	No. of trees	GDD	No. of trees	GDD
Ängelsfors	36	159 ± 57	38	153 ± 43	48	154 ± 49
Laxarby	35	132 ± 48	39	133 ± 43	46	131 ± 45
Bollebygd	42	154 ± 54	41	151 ± 53	49	157 ± 56
Ramkvilla	39	159 ± 45	39	142 ± 37	47	154 ± 45
Emmaboda	30	193 ± 56	38	181 ± 56	49	189 ± 61
Rezekne 1	35	198 ± 62	34	200 ± 60	49	199 ± 66
Hallaryd	34	156 ± 65	28	174 ± 53	43	136 ± 43
Malta	34	240 ± 38	35	216 ± 40	49	227 ± 53
Istra	40	234 ± 56	36	219 ± 49	47	224 ± 57
Rezekne 2	35	208 ± 60	32	193 ± 55	46	200 ± 50
Svente	32	224 ± 53	25	227 ± 44	31	214 ± 56
Ignalina	30	233 ± 52	25	237 ± 36	42	240 ± 56
Vitebsk	33	224 ± 52	36	223 ± 45	47	230 ± 49
Trakai	34	244 ± 42	35	220 ± 48	45	234 ± 57
Punia	31	259 ± 36	31	243 ± 27	47	257 ± 43
Minsk	30	266 ± 32	30	240 ± 27	45	251 ± 33
Bialystok	32	230 ± 61	33	237 ± 35	44	242 ± 53
Istebna	27	201 ± 78	32	206 ± 56	41	221 ± 66
Average		206		200		203

(Fig. 2). Within the East-European group, provenances with more continental origin usually exhibited lower temperature sum requirement compared to those closer to coast. Istebna, a provenance from the mountain range area of southern Poland, stands out in terms of having an intermediate requirement in combination with the lowest latitude of origin. There were significant correlations between the provenance-specific temperature sum requirement for bud burst and the latitudinal ($R^2 = 0.43$, $p < 0.001$, Fig. A1a) and longitudinal ($R^2 = 0.71$, $p < 0.0001$, Fig. A1b) gradients, and with both latitude and longitude ($R^2 = 0.84$, $p < 0.001$) in a multiple linear regression.

3.2. Frost risk differences among sites and provenances

At all sites, the number of frost events continuously decreased as the day of the year progressed and the accumulated temperature sum increased (Fig. 3). Toftaholm had more late frost events compared to the other sites, especially at threshold 0 °C. Laxarby, the provenance with the earliest bud burst, was more likely to experience frost damage in Toftaholm than in Sund or Skärsnäs. At the average timing of bud burst, the number of frost events was close to zero at Sund and Skärsnäs, whereas Toftaholm displayed a risk of frost events below 0 °C.

Spring frost events after bud burst below 0 °C were more frequent than below −2 °C at all three field sites during all growth seasons (Table 4). The trees experienced the highest number of spring frost events in Toftaholm, and fewer events in Sund. In Skärnäs, the trees rarely experienced any spring frost event. Due to an earlier timing of bud burst, Swedish provenances experienced more spring frost events than the East-European provenances. Laxarby was most exposed to spring frost, followed by Hallaryd, Bollebygd, Änglesfors and Ramkvilla. Minsk, Punia, and Trakai were least exposed to spring frost.

The average tree height after 6 growth seasons for Sund, Toftaholm and Skärsnäs was 205 cm, 238 cm and 254 cm, respectively, and 687 cm after 13 growth seasons for Toftaholm. The average height of frost damaged trees was lower compared to non-damaged trees for Swedish and East-European provenance groups at Toftaholm and Skärsnäs after 6 growth seasons, and at Toftaholm after 13 growth seasons (Fig. A2). Both factors, the frost damage and provenance group had a significant effect on height, with $p < 0.0001$ and $p < 0.05$, respectively. Tree height and cumulative number of spring frost events after 6 growth seasons displayed a significant relation, when data from all sites at threshold −2 °C were analysed separately for Swedish and East-European provenances (Table 5). In Toftaholm, the site that was most frost prone, significant relations were observed for Swedish provenances after 6 growth seasons at both thresholds, and for all provenances after 13 seasons. In most cases the relations were positive, negative effect was displayed for Toftaholm after 13 growth seasons. When analysing the effect of temperature sum at timing of bud burst on tree height, similar significant relations were observed, although the model coefficients mainly displayed the opposite sign.

The provenances with most frost-damaged trees in the spring of 2004 in Toftaholm were Ängelsfors, Ramkvilla, Bollebygd, Laxarby and Hallaryd (Table 6). During the frost susceptible period, the same provenances experienced more frost events compared to the others at both thresholds. Also in Skärsnäs, with less severe frost events than Toftaholm, the Swedish provenances were more frost-damaged than the East-European provenances. The correlation between exposure to the lowest minimum temperature during frost susceptible period and occurrence of frost damage was −0.31 in Toftaholm and 0.04 in Skärsnäs, indicating that the selection of provenance is more critical at frost prone sites. This was further explored by plotting the percentage of frost-damaged trees in Toftaholm versus the provenance specific temperature sum requirement (Fig. 4). Provenances with lower temperature sums had higher percentage of frost-damaged trees.

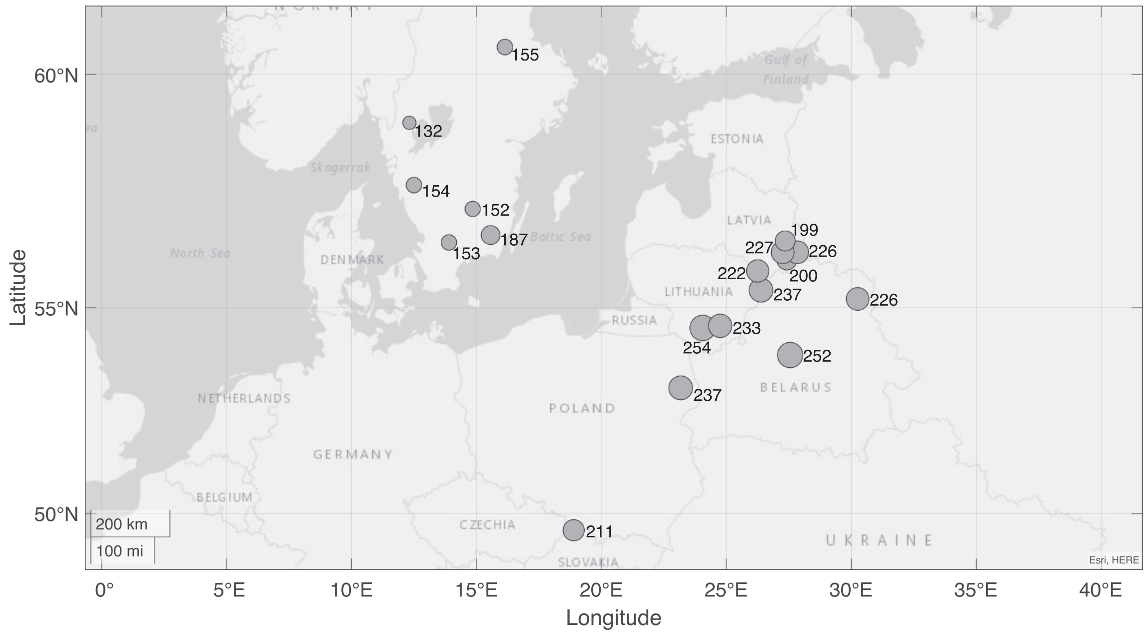

Fig. 2. Provenance-specific temperature sum requirements for bud burst. Each symbol represents the provenance, with numbers representing the average temperature sum of the three field sites, expressed as growing degree days above +5 °C.

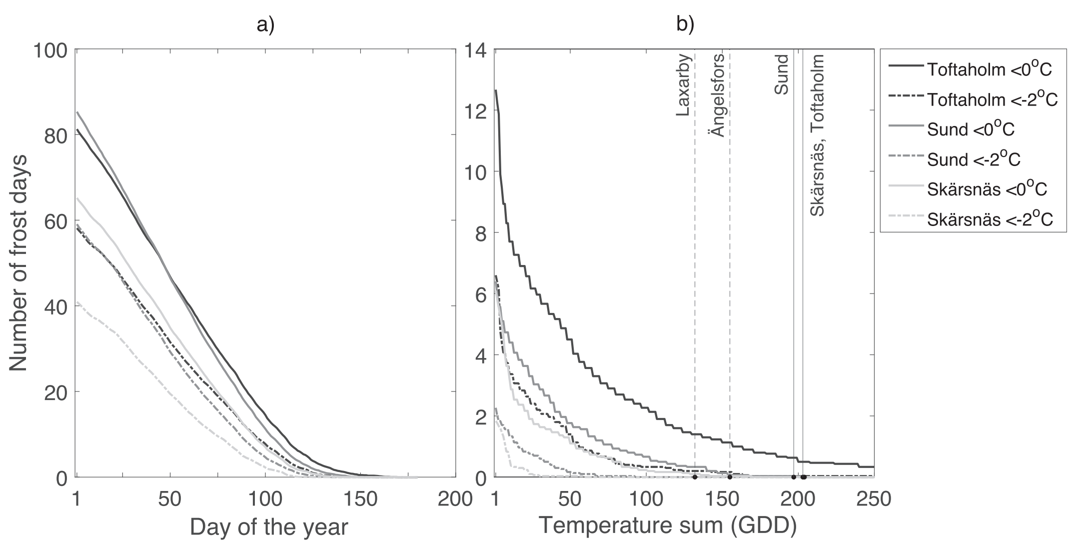

Fig. 3. The annual average number of frost events between January 1 - June 29 (DOY 180) below 0 °C and −2 °C over 30 years (1989–2018), calculated from EOBS data: a) in relation to the day of the year, b) in relation to the accumulated temperature sum, expressed as growing degree days (GDD) above +5 °C. Dashed vertical lines indicate the average temperature sum required for bud burst in two different provenances: Laxarby (with the earliest date of bud burst) and Ängelsfors (most northern origin). Solid vertical lines indicate the average temperature sum required for bud burst at the three different sites, given all individual trees.

3.3. Analysis of gridded observed temperature data and data from temperature loggers

A comparison between ten site specific CDFs of gridded temperature data and logger data at 0.5 m and 1.8 m indicated that gridded data were a good approximation of the mean temperature at all sites (Figs. B1-B10). The comparison between gridded and observed minimum temperature indicated that the gridded observed data tended to overestimate the local minimum temperature, i.e. warmer than observed (Figs. B12-B20), in particular in comparison with the 0.5 m logger. Only for one out of ten sites, Edebäck, did the gridded observed data provide an underestimate of the minimum temperature compared to local observations (Fig. B11). In appendix, results from January to June are shown, as this period is of relevance for calculating the onset of vegetation period and bud burst. Similar results were however obtained also for July to December.

3.4. Climate change impact assessments

For the reference period 1989–2018, the number of frost events between January 1 - June 29 increased along the latitudinal gradient of Sweden (Fig. 5), ranging between 30 and 130 events per year below 0 °C, and between 25 and 120 events per year below −2 °C. The number of frost events will decrease in response to climate change. A decrease within the range of 5–20 frost events per year was projected for the near future, 2021–2050, with a relatively homogeneous pattern across southern Sweden. A reduction of 25–50 events per year below 0 °C and by 15–50 events per year below −2 °C was projected for the end of the

Table 4
Provenance specific frost risk, i.e. cumulative number of spring frost events below 0 °C and −2 °C occurring between bud burst and June 29 (DOY 180) during 6 and 13 growth seasons (GS) at the three different field sites.

Provenance	Toftaholm				Sund				Skärsnäs			
	6 GS		13 GS		6 GS		13 GS		6 GS		13 GS	
	<0 °C	<−2 °C	<0 °C	<−2 °C	<0 °C	<−2 °C	<0 °C	<−2 °C	<0 °C	<−2 °C	<0 °C	<−2 °C
Ängelsfors	13.3	2.3	31.2	9.3	2.7	0.3	7.3	1.1	0.5	0.2	3.4	0.4
Laxarby	17.1	3.2	41.6	13.3	4.2	0.5	11.6	2.2	0.8	0.2	5.8	0.6
Bollebygd	14.0	2.5	33.0	10.0	3.3	0.4	9.1	1.7	0.5	0.1	3.9	0.4
Ramkvilla	12.5	1.7	29.0	7.8	3.3	0.3	8.9	1.2	0.3	0.0	3.1	0.2
Emmaboda	8.1	1.0	19.9	4.9	2.0	0.2	5.2	0.8	0.1	0.0	2.0	0.1
Rezekne 1	8.2	1.1	20.0	5.2	1.4	0.2	3.9	0.7	0.3	0.1	2.3	0.2
Hallaryd	14.2	2.7	33.5	10.4	2.4	0.6	6.6	2.0	0.7	0.2	4.8	0.5
Malta	3.2	0.2	9.0	1.8	0.5	0.0	1.2	0.0	0.1	0.0	0.8	0.1
Istra	4.5	0.5	12.2	2.9	0.7	0.0	1.7	0.1	0.1	0.0	0.9	0.1
Rezekne 2	6.9	0.7	17.0	4.1	1.4	0.2	3.9	0.6	0.1	0.0	1.0	0.1
Svente	5.2	0.5	13.1	3.0	0.5	0.0	1.3	0.2	0.0	0.0	0.7	0.0
Ignalina	4.1	0.4	11.6	2.6	0.2	0.0	0.6	0.0	0.0	0.0	0.6	0.0
Vitebsk	4.8	0.4	12.8	2.8	0.5	0.0	1.3	0.1	0.0	0.0	0.3	0.0
Trakai	3.1	0.1	8.4	1.5	0.6	0.0	1.5	0.1	0.1	0.0	0.8	0.1
Punia	2.3	0.1	7.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0
Minsk	1.8	0.0	6.3	1.1	0.1	0.0	0.2	0.0	0.0	0.0	0.1	0.0
Bialystok	5.1	0.7	13.7	3.7	0.3	0.0	0.6	0.0	0.0	0.0	0.5	0.0
Istebna	9.1	1.8	23.0	7.2	1.1	0.1	3.1	0.5	0.2	0.0	1.3	0.1
Average	7.6	1.1	19.0	5.2	1.4	0.2	3.8	0.6	0.2	0.0	1.8	0.2

Table 5
ANCOVA table describing the relation between tree height and exposure to spring frost events (FE) occurring between bud burst and June 29 (DOY 180), growing degree days (GDD) at timing of bud burst (BB) and provenance (prov.). Model significance (*p*-values) and coefficients (COEFF) for all provenances, Swedish provenances (Swe) and East-European provenances (EE) after 6 growth seasons (GS) at all sites and Toftaholm, the most frost prone site, and after 13 growth seasons at Toftaholm only.

Site	Data (prov.)	No. of GS	Spring FE < 0 °C		GDD at BB		Prov.	Spring FE < -2 °C		GDD at BB		Prov.
			p	COEFF	*p*	COEFF	*p*	*p*	COEFF	*p*	COEFF	*p*
All	All	6	n.s.		<0.01	−0.08	<0.0001	n.s.		<0.001	−0.05	<0.0001
	Swe		n.s.		<0.001	−0.14	<0.0001	<0.05	1.26	<0.001	−0.14	<0.0001
	EE		n.s.		n.s.		<0.0001	<0.01	2.0	<0.05	−0.001	<0.0001
Toftaholm	All	6	n.s.		<0.001	0.16	<0.0001	n.s.		<0.0001	0.1	<0.0001
	Swe		<0.01	0.83	n.s.		<0.001	<0.01	0.92	n.s.	−0.06	<0.001
	EE		n.s.		n.s.		<0.001	n.s.		<0.05	0.16	<0.001
Toftaholm	All	13	<0.001	−0.03	n.s.		<0.0001	<0.01	0.03	<0.01	0.02	<0.0001
	Swe		n.s.		n.s.		n.s.	n.s.		n.s.		n.s.
	EE		n.s.		n.s.		<0.01	n.s.		n.s.		<0.01

Table 6
Percentage of frost-damaged trees for each provenance in spring 2004 (the third growth season) in Toftaholm and Skärsnäs in comparison with different measures of frost severity. The number of frost events (FE) and the lowest minimum temperature are calculated for the frost susceptible period (between bud burst and frost damage assessment date), an average value for each provenance, based on 33 and 45 individual observations per provenance in Toftaholm and Skärsnäs, respectively, is displayed.

Provenance	Toftaholm				Skärsnäs			
	Frost-damaged trees (%)	T min (°C)	FE		Frost-damaged trees (%)	T min (°C)	FE	
			<0 °C	<−2 °C			<0 °C	<−2 °C
Ängelsfors	42	−2.42	3.6	1.3	2	1.64	0.0	0.0
Laxarby	32	−2.77	4.2	1.4	2	1.60	0.0	0.0
Bollebygd	36	−2.12	3.3	1.2	10	1.69	0.0	0.0
Ramkvilla	41	−2.39	3.3	1.0	9	1.79	0.0	0.0
Emmaboda	20	−1.06	2.0	0.6	8	1.84	0.0	0.0
Rezekne 1	24	−1.88	2.8	0.9	4	1.67	0.0	0.0
Hallaryd	29	−2.47	3.8	1.5	5	1.64	0.0	0.0
Malta	6	−0.36	1.0	0.3	2	1.84	0.0	0.0
Istra	5	−1.36	2.1	0.6	0	1.84	0.0	0.0
Rezekne 2	21	−1.59	2.4	0.7	0	1.84	0.0	0.0
Svente	16	−1.75	2.4	0.7	0	1.84	0.0	0.0
Ignalina	3	−0.73	1.6	0.4	0	1.84	0.0	0.0
Vitebsk	9	−1.02	1.8	0.5	0	1.84	0.0	0.0
Trakai	9	−0.63	1.2	0.4	2	1.84	0.0	0.0
Punia	0	−0.78	1.3	0.4	0	1.84	0.0	0.0
Minsk	0	0.12	0.5	0.2	0	1.84	0.0	0.0
Bialystok	6	−1.89	2.9	1.0	2	1.84	0.0	0.0
Istebna	22	−2.69	4.2	1.6	0	1.70	0.0	0.0

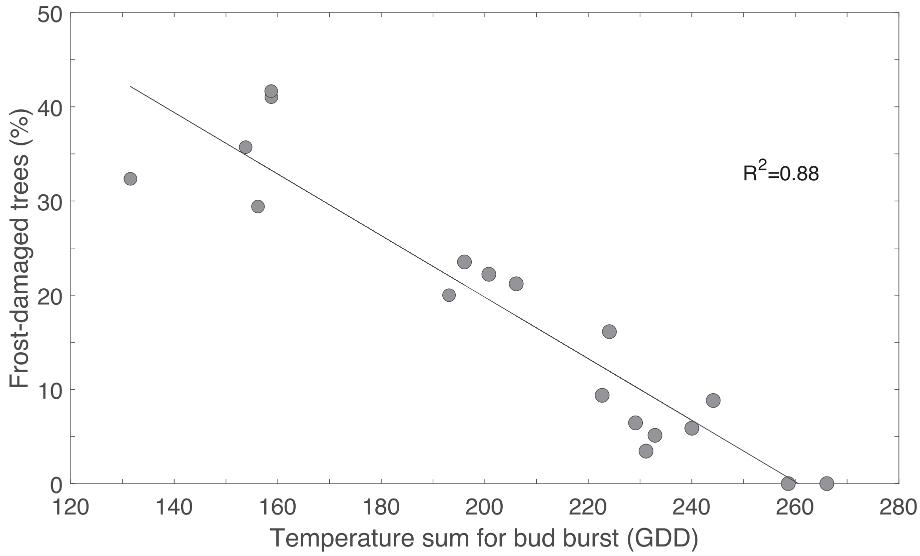

Fig. 4. Percentage of frost-damaged trees for each provenance, recorded in spring 2004 in Toftaholm, in relation to the provenance specific temperature sum requirement for bud burst, expressed as growing degree days (GDD) above +5 °C. Grey line is the regression line.

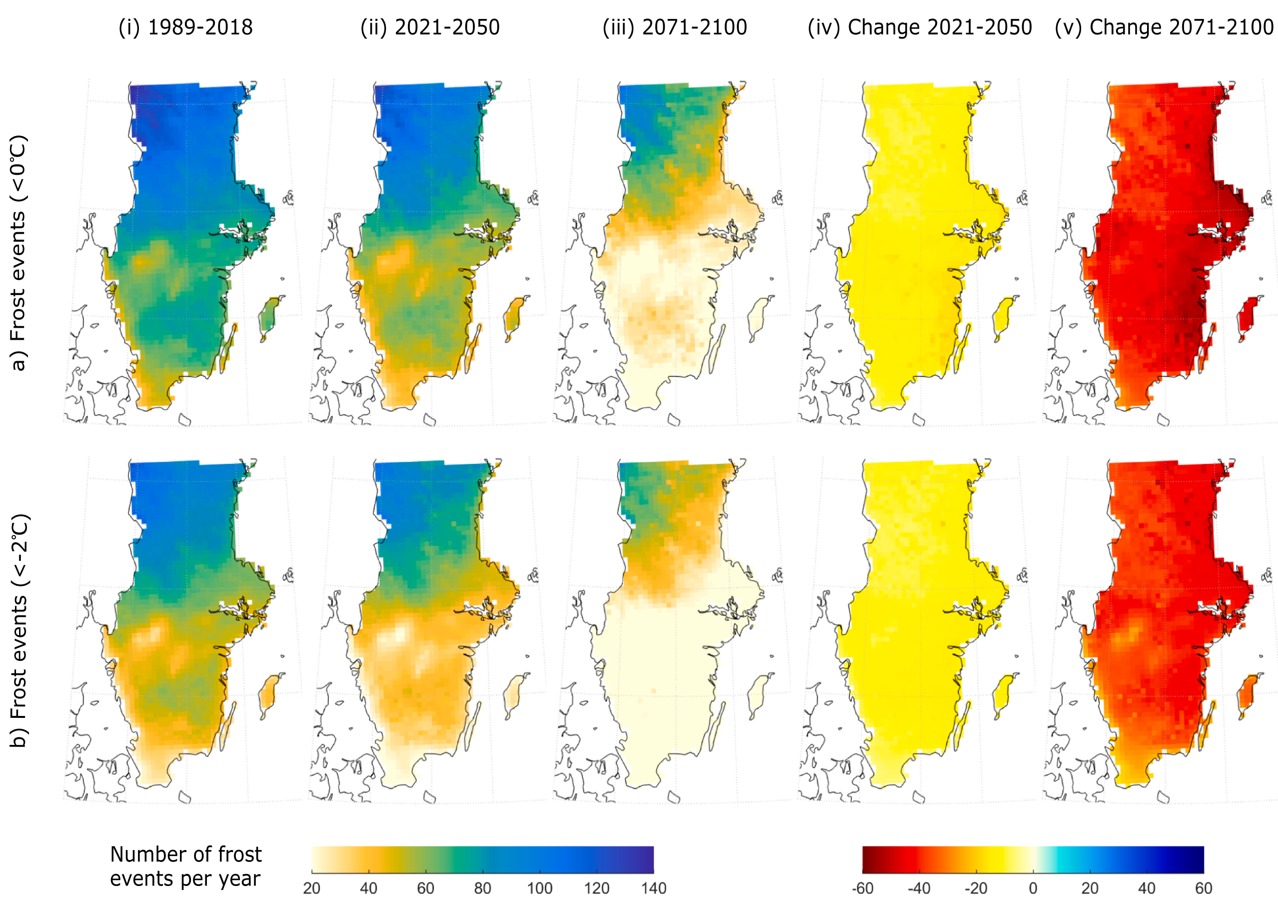

Fig. 5. The annual average number of frost events between January 1 - June 29 (DOY 180) below (a) 0 °C and (b) −2 °C in southern Sweden. The results are based on temperature data from three climate models representing RCP8.5. Three time periods were assessed (i) 1989–2018, (ii) 2021–2050, (iii) 2071–2100. The climate change signal was expressed as the difference between time periods, (iv) 2021–2050 and 1989–2018, (v) 2071–2100 and 1989–2018.

century, according to RCP8.5, with the eastern parts of the study area displaying the most pronounced change.

During the reference period, the number of chilling days and chilling units (calculated from September 1 till December 31) varied between 55 and 110 and 40–60 per year, respectively, over a major part of Sweden (Fig. 6). The chilling days increased gradually from the south to north, while the chilling units were more evenly distributed over the study area. The model simulations indicated that a warmer climate will be associated with a reduction in chilling days. Southern parts of the study area will likely be experiencing a more pronounced reduction than

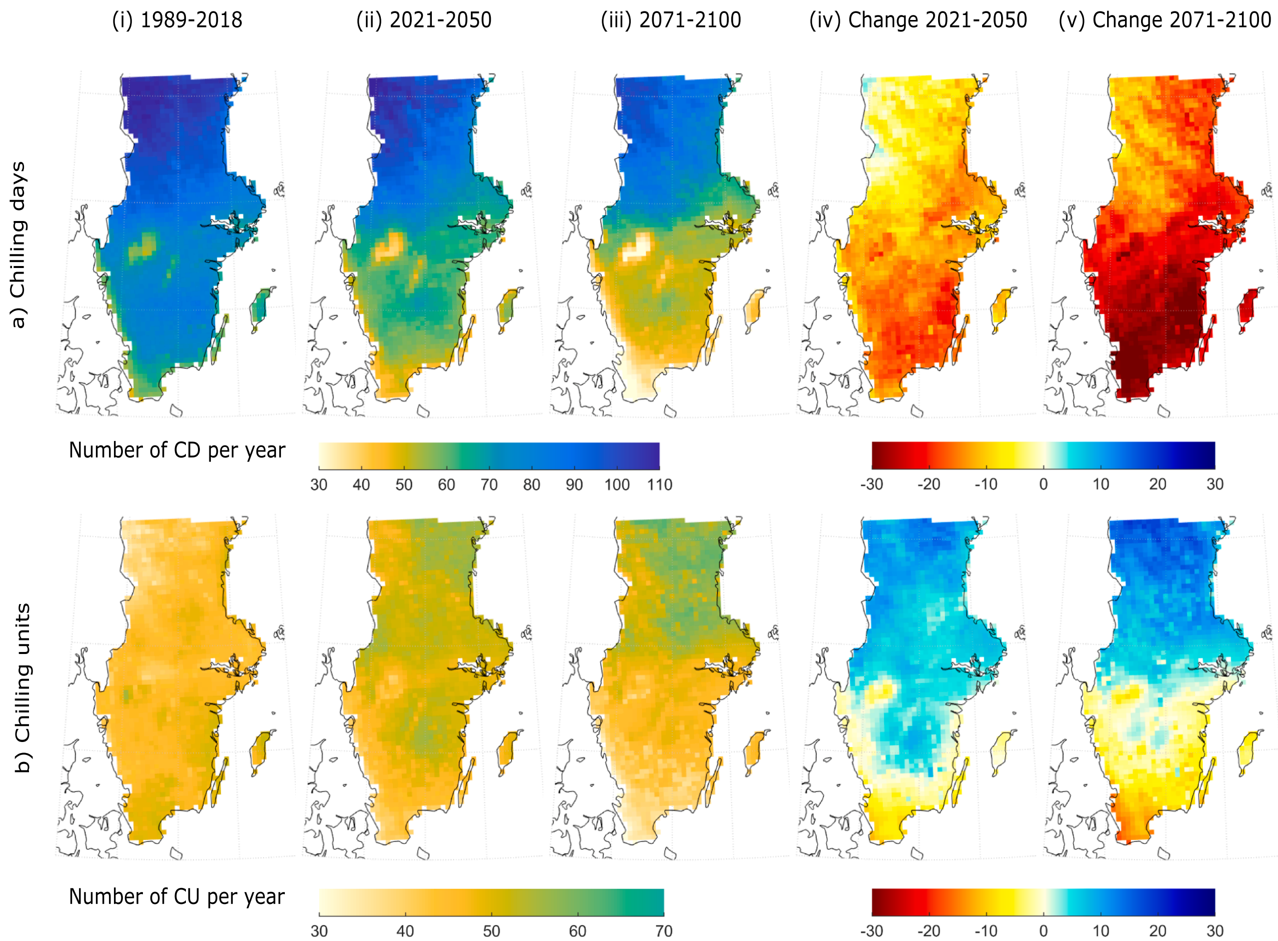

Fig. 6. (a) The annual average number of chilling days and (b) the annual average number of chilling units, representing the period September 1 till December 31, in southern Sweden. The results are based on temperature data from three climate models representing RCP8.5. Three time periods were assessed (i) 1989–2018, (ii) 2021–2050, (iii) 2071–2100. The climate change signal was expressed as the difference between time periods, (iv) 2021–2050 and 1989–2018, (v) 2071–2100 and 1989–2018.

northern parts, up to 30 chilling days per year in the far future. The chilling units displayed a mixed pattern of change in response to a warmer climate, with a decrease of up to10 chilling units per year in the south, and an increase of up to 15 chilling units per year towards the north in the far future. The chilling requirement of 40 chilling units and 40 chilling days was fulfilled in all years during the reference period and the near future. During the far future, in 30–40% of years the accumulated amount of chilling over the southern coastal areas (which corresponds to approximately 4% of gridcells) will be slightly lower than 40 chilling units or chilling days, i.e. 35 ± 2 chilling days and 38 ± 1 chilling units.

The timing of bud burst occurred predominantly in May and June (DOY 120–180) in 1989–2018, following a latitudinal gradient (Fig. 7a). For all provenances, the model simulations indicated a similar direction of change in response to a warmer climate (Fig. 7a, Figs. C1a-C16a). Bud burst was projected to occur about 10 days earlier in most parts of the study area in 2021–2050 compared with 1989–2018. This corresponds to DOY 130–160 for the Ängelsfors provenance and DOY 140–175 for Minsk. RCP8.5 assumes a stronger climate change signal in 2071–2100, corresponding to about 30 days earlier bud burst over a major part of southern Sweden, and up to 60 days earlier along the western coast. This corresponds to DOY 120–135 for the Ängelsfors provenance and DOY 130–140 for Minsk.

The exposure to spring frost varied between 0 and 17 spring frost events per 30 years among provenances for the period 1989–2018, with an average of 7 frost events (Fig. 7b). Provenances from northern latitudes were more exposed to spring frost events compared to those from southern latitudes (Fig. 7b, Figs. C1b-C16b). The earliest provenance may experience a substantially increased risk of frost exposure, for Ängelsfors up to 9 and 29 events for the periods of 2021–2050 and 2071–2100, respectively. The corresponding numbers for Minsk are 11–20 and 5 events.

During the reference period, the spring frost events were associated with lower temperatures in the north of the study area than in the south (Fig. 8, Figs. C1c-C16c). The exposure to low temperatures differed among provenances, with the early bursting Ängelsfors being more exposed to frost episodes than late bursting Minsk (Fig. 8). Future projections illustrated that larger parts of the study area will be exposed to spring frost events, along with trends toward less cold events in the northern parts and colder events in the southern parts.

4. Discussion

In southern Sweden, the rotation period of Norway spruce is 60–90 years (Skogsstyrelsen, 2020), which means that trees currently planted will be exposed to a different climate. In a future climate, the risk of frost damage caused by spring frost events will potentially increase (Jönsson and Bärring, 2004; Langvall, 2011b). Recommendations of suitable seed sources for deployment need to gradually consider the potential of growth and frost avoidance in the current as well as future climate conditions. To this end, we analysed the provenance specific timing of bud burst in relation to the risk of spring frost damage, using a

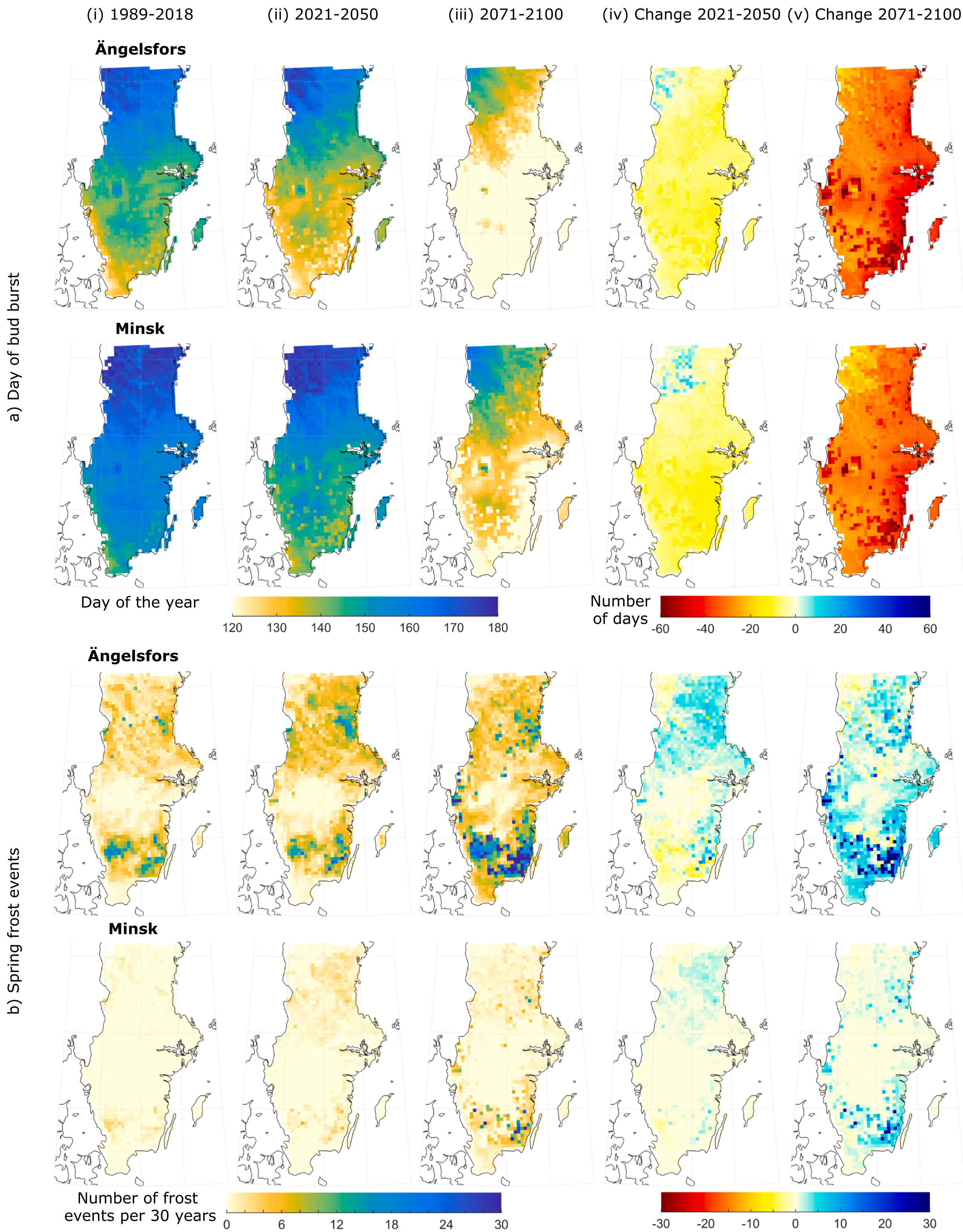

Fig. 7. (a) The average day of bud burst and (b) the cumulative number of spring frost events over 30 years with the threshold of −2 °C calculated from the day of bud burst till June 29 (DOY 180) in southern Sweden. The simulations represent the earliest and latest Norway spruce provenances assessed in this study. Results for the other provenances can be found in Appendix S3. The results are based on temperature data from three climate models representing RCP8.5. Three time periods were assessed (i) 1989–2018, (ii) 2021–2050, (iii) 2071–2100. The climate change signal was expressed as the difference between time periods, (iv) 2021–2050 and 1989–2018, (v) 2071–2100 and 1989–2018.

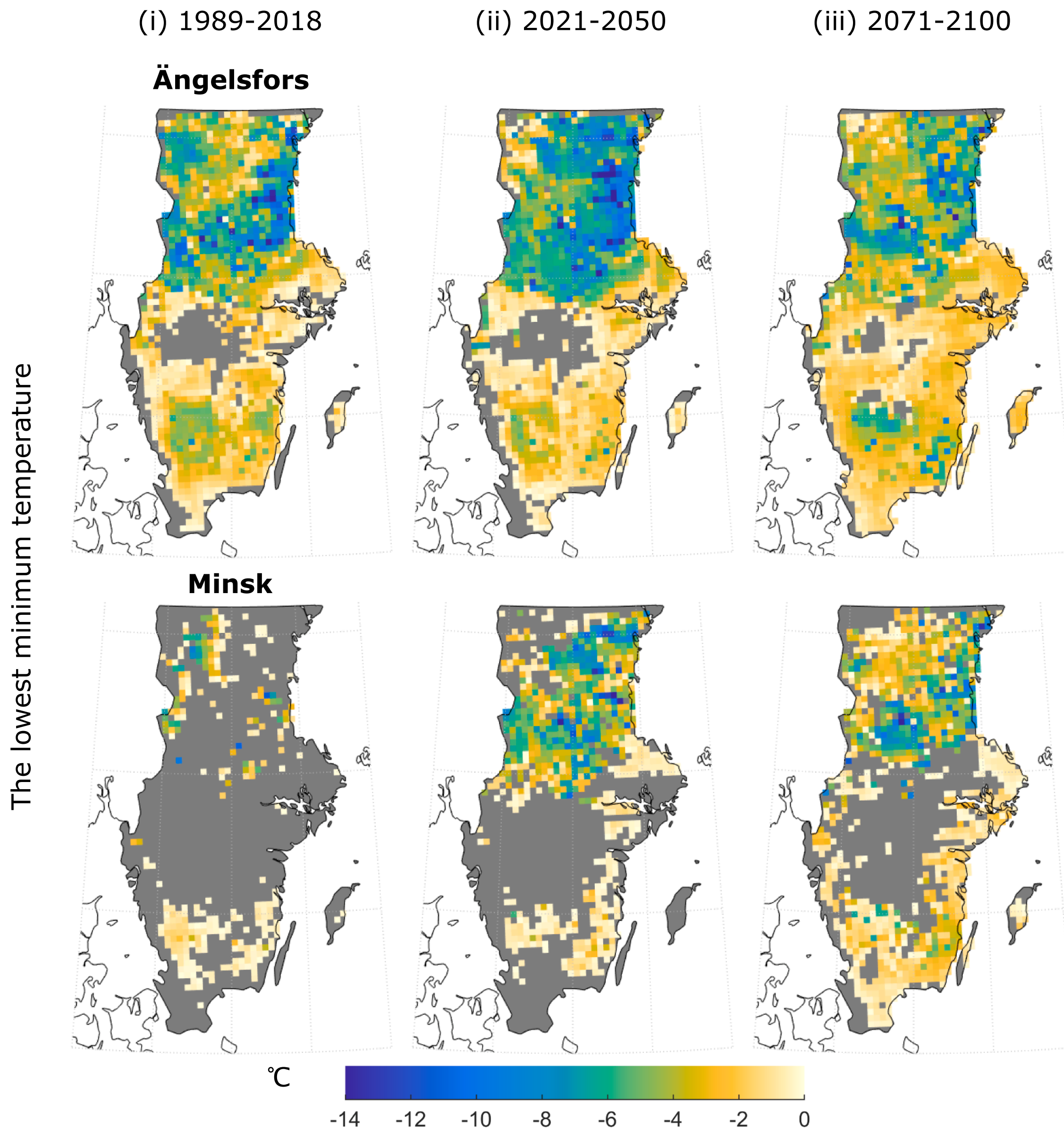

Fig. 8. The lowest minimum temperature during a spring frost event (between the day of bud burst and June 29, DOY 180) in southern Sweden for the earliest and latest Norway spruce provenances assessed in this study. Results for the other provenances can be found in Appendix S3. The results are based on temperature data from three climate models representing RCP8.5. Three time periods were assessed (i) 1989–2018, (ii) 2021–2050, (iii) 2071–2100. The grid cells without any spring frost event are displayed in grey.

combination of statistical methods and phenological modelling approaches.

Phenological models attempt to describe the interaction between temperature and photoperiod in release of dormancy and regulation of the timing of bud burst. The common temperature sum model has been demonstrated to give the most robust predictions under current climate conditions, outperforming chilling-forcing models and more complex photoperiod-chilling-forcing models (Hannerz, 1999; Linkosalo et al., 2008; Olsson and Jönsson, 2014). The photoperiod has been suggested to have a role in enabling the initiation of bud burst in Norway spruce (Partanen et al., 2001), with development before the winter solstice being restricted (Partanen et al., 1998; Partanen et al., 2001). This is in line with having January 1 as a starting date for temperature sum calculations. The photoperiod may further influence the temperature response. A phenology model assuming enhanced temperature response by photoperiod when days become longer (Blümel and Chmielewski, 2012) has been found to be as good as the temperature-sum model in simulating the timing of bud burst of Norway Spruce (Olsson and Jönsson, 2014; Olsson and Jönsson, 2015). In this study, the simpler of the two models was used, as information on provenance-specific responses to photoperiod in spring is lacking. The separate calculation of chilling units and chilling days also indicated that the temperature sum model with January 1 as the starting day was to be considered as reliable for all provenances assessed, under both current and future climate conditions. However, in an even warmer climate associated with a potential lack of chilling, models with a chilling component should be included. The temperature sum requirement for bud burst is then usually assumed to increase with the decreasing amount of chilling (Heide, 1993; Kramer et al., 2017; Man et al., 2017).

4.1. *Temperature sum differences among sites and provenances*

In this study, the estimated temperature sum requirement for bud burst was associated with model assumptions and uncertainties. The significant effect of provenance on the absolute temperature sum requirement for bud burst of the individual tree indicated provenance differentiation in this trait. There were no major differences in the phenological responses among three field sites, the potential differences between sites attributed to the usage of gridded observed temperature data were accounted for by analysing relative temperature sums. This in turn removed the effect of site on the temperature sum requirement for bud burst, which enables the generalization of the provenance specific temperature sums (expressed as an average value of three sites) for an arbitrary site.

The provenance differentiation in the timing of bud burst along climatic gradients was demonstrated by strong significant correlations between temperature sum requirements for bud burst and latitude and longitude. Spruce trees from East Europe require a higher thermal sum before bud burst compared to spruce trees from northern Sweden, as the seasonal temperature progression in the north occurs later and faster, in response to the returning day light (Jönsson and Bärring, 2011). The effect of latitude was confounded with the longitudinal gradient, i.e. within the East-European group provenances with more continental origin tended to have lower temperature sum requirement compared to those from western parts, influenced by oceanic conditions. Latitude and longitude should be considered as a proxy for climatic conditions, with latitude representing the onset of warm temperatures in spring and differences in photoperiod, while longitude indicating the likelihood of warm spells occurring in winter (Eysteinsson et al., 2009).

Despite the uncertainty related to temperature sum requirement estimation based on single year observations, the sites average values and the range of the accumulated temperature sums at bud burst were close to the value estimated by Langvall and Löfvenius (2019) for Asa site (i.e. 200 GDD on average with the range 146–246 GDD), located at approximately the same latitude as sites in our study, 57°N. The variation among the provenances in the temperature sum requirement for bud burst was within the ranges observed by earlier studies (Beuker, 1994; Hannerz, 1999; Hannerz et al., 2003). Compared to the provenance specific values estimated by Hannerz (1994) from the studies in Uppsala and Brunsberg, the temperature sum requirement in our study was similar for the northern Swedish provenances, but about 70 and 90 GDD higher for the Belarus provenances, Vitebsk and Minsk, respectively. To explain these differences, we compared the previous chilling exposure between the studies. However, in relation to the specific years with observations, the differences in the amount of chilling between sites in our study and Uppsala/ Brunsberg were small, with the standard deviation of 4 chilling units and 11 chilling days. In addition, by comparing mean monthly temperatures in April-May of the year of bud burst assessments at different sites, no relation between spring temperatures and the temperature sum for bud burst was found. Due to the latitudinal differences between Uppsala/ Brunsberg (60°N) and sites in our study (57°N), the variation in temperature sums required to reach bud burst can be attributed to the effect of photoperiod on the temperature sum requirement, i.e. faster increase of photoperiod after the spring equinox at 60°N may promote earlier bud burst compared to lower latitudes (Caffarra et al., 2011; Olsson and Jönsson, 2014).

4.2. Frost risk differences among sites and provenances

The likelihood of a frost event generally decreased as the accumulated temperature sum increased. The local risk of frost was dependent on the climate conditions at each field site, with the southernmost site Skärsnäs being the least frost prone. Since the sites are in southern Sweden and to some extent are influenced by oceanic conditions from the Baltic Sea and the Atlantic Ocean, the risk of occurrence of more severe frost events below −2 °C was close to zero even at the earliest timing of bud burst.

The risk of frost damage during a given year is influenced by several factors, the ambient temperature influences the rate of dehardening, development and bud burst, and a local frost episode must occur for the tree to get damaged (Augspurger, 2013). Frost damage had a major impact on Norway spruce height development, while genetic provenance specific differences seemed to have an additional effect on the variation in height between individual trees. The start of the growing season, as defined by timing of bud burst, thereby being related to the risk of frost damage, can further modify the tree height development, with the positive and negative model coefficients indicating a fine balance between the two factors frost events and growing degree days at bud burst. The positive effect of growing degree days on height was expected, since later bud burst is usually associated with later growth cessation, thereby longer growing season. Later start of the growing season is also linked to a lower risk of frost damage. However, a negative effect of growing degree days on height may be related to a very late bud burst, linked to a higher risk of autumn frost instead, creating a hampered growth (Hannerz et al., 1999). The stochastic nature of frost events may be the reason behind why the expected negative relation between frost events (0 °C) and height was detectable only after 13 years at the most frost prone site, Toftaholm. A possible explanation for the positive relation between frost events (mainly −2 °C) and height is that these were rare events, so in most years an early onset may provide a growth benefit. An additional explanation is that the analysis was only based on the living trees, excluding seedlings that have died in previous seasons, e.g. due to severe frost damage. Early provenances with lower temperature sum requirement for bud burst, including Swedish group and Istebna provenance, had higher percentage of frost-damaged trees, as they had been exposed to lower temperatures and more frequent frost events during the frost susceptible period. This relationship has been seen before, when trees with later bud burst suffered from less frost (Danusevicius and Persson, 1998; Hannerz, 1994; Werner and Karlsson, 1983).

Comparison between temperature loggers and gridded data (E-OBS) indicated that it is possible to use gridded mean temperature if data from temperature loggers in the sites are not available. However, due to the different datasets properties (gridded data have in general lower variability and fewer extremes than point measurements) (Director and Bornn, 2015), the gridded data tended to overestimate the minimum temperature, especially at 0.5 m, and this has to be taken into account when interpreting the results. Thus, no direct link between the percentage of frost-damage trees in Skärsnäs and different measures of frost severity during frost susceptible period (Table 6) could be explained by likely lower than calculated the actual minimum temperature experienced by the young seedlings and higher frequency of frost events.

4.3. Climate change impact assessment

In this study the climate change impact on tree's phenological responses and the associated risk of frost damage was assessed according to RCP8.5 concentration pathway, which is characterised by the highest increase in global mean temperature by 2100. However, similar temperature changes are expected under RCP4.5, 6.0 and 8.5 by the mid-century. Thus, by analysing the output of RCP8.5 at different time periods enables to capture a transient effect of temperature rise and to consider all RCPs. The climate model data were indicated to overestimate the minimum temperature, as the site specific numbers of frost events for the period 1989–2018 were generally about 5–11 events lower when calculated from climate model data (Table C1) than E-OBS data (Fig. 3a).

In response to a warmer climate, an overall reduction of frost events between January 1 and June 29 was projected in southern Sweden. Different parts of the study area will be affected slightly differently, with regions in the north having more spring frost events than in the south. There will also be local differences, as one site can be more frost prone because of e.g. the topography of the site. The magnitude of projected changes in the timing of bud burst is in line with Olsson et al. (2017), which also used the RCP8.5 concentration pathway. Due to earlier bud burst, all Norway spruce provenances assessed in this study will experience an increased risk of frost damage, as indicated by an increased frequency and severity of frost events following bud burst. An increased risk of frost damage to boreal trees associated with earlier timing of bud burst and lower level of frost hardiness in a warmer climate has been suggested by previous studies (Hänninen, 1991; Kellomaki et al., 1995; Leinonen, 1996). Other studies indicated that future changes in frost damage in response to phenological changes will differ between species and populations (Hänninen, 2016; Morin and Chuine, 2014). In our study, the difference in frost risk between early and late bursting provenances will remain, i.e. Ängelsfors provenance will experience more spring frost events with lower minimum temperature compared to later bursting Minsk. Considering the overestimation of the minimum temperature by the climate model data, the future projections presented here are more likely to underestimate the local risk of frost.

4.4. Progress towards deployment recommendations

Future projections covering the 21st century and a strong climate change signal (e.g. RCP 8.5) are useful for detecting and quantifying spatial and temporal trends in risk of frost damage. Due to the inherent uncertainties associated with future projections, and that young seedlings that are more susceptible to lethal frost damage than older trees, the provenance specific deployment recommendations should be based on the near-future simulations only. When choosing a robust strategy for the selection of plant material, several aspects need to be considered. For a secondary tree species like Norway spruce spring frost events tend to be more frequent in forest practices using even-aged forest stands, clear-cutting and planting without large sheltering trees. To reduce damage due to spring frost events under such conditions, frost prone site need to be identified and planted with seed sources with late bud burst (Hannerz et al., 1999; Persson and Persson, 1992). The recommendation is in general not associated with a trade off in terms of a lower growth potential, as the late bursting trees usually also have a later bud set and can use the whole growing season.

In this study, we showed that the provenance specific risk of being exposed to spring frost events can be quantified and predicted for an arbitrary site (at the grid cell level resolution) in southern Sweden. This information could be included in current systems for deployment recommendations like Plantval (Skogforsk, 2020), to provide information on what plant material to deploy in case you have a frost prone site and still get a high gain in growth with low or no losses due to spring frost events. This study is based on provenance trials, however, the dominating source of forest regeneration material used in Sweden are seed orchard material. To further apply the results to seed orchard material, a link between growth rhythm (i.e. timing of bud burst) of provenances and seed orchards is needed, as the susceptibility to spring frost events may differ between the forest regeneration material groups (Hannerz and Westin, 2000). The trials used in our study together with three more trials in the same trial series contain material from currently available seed orchards that could be used to establish such a link.

4.5. Implications for breeding and selection

The Swedish breeding program for Norway spruce is divided into 22 sub-populations, each defined by an adaptation profile consisting of a combination of temperature and light conditions, and where a few also have a specialized objective including phenology to resist frost (Danell, 1991; Danell, 1993). The provenances in this study provide a good representative sample of the founders of the breeding sub-populations, especially with regards to growth rhythm. Each sub-population is genetically evaluated at four different sites, covering and going slightly beyond the adaptation profile, to enable the selection of genotypes with a stable performance across all sites (Rosvall, 2011). Thus, the selection of sites should ideally be based on the environmental and climatic conditions belonging to the adaptation profile of the sub-population in question. In southern Sweden, several sub-populations are to be adapted to withstand damages of late spring frosts and therefore at least one of the four test sites should be "frost prone" to provide performance under such conditions. As this depends on both the material used and the site conditions, an analysis like the one conducted in this study could improve the selection of sites and consequently improve the selection for those sub-populations.

5. Conclusions

In this study we demonstrated that the estimated provenance specific temperature sum requirements for bud burst can be used to calculate the risk of spring frost events for an arbitrary site in southern Sweden, to provide guidance on the selection of a suitable seed material. Frost damage had a main effect on tree growth, with provenance specific differences and the start of the growing season being additional factors influencing the tree height development. Provenances with earlier timing of bud burst experienced a higher risk of frost damage, which is in agreement with earlier studies.

The model projections representing RCP8.5 indicated a decrease in the total number of frost events in southern Sweden in response to a warmer climate, while an earlier timing of bud burst will be associated with an increased frequency and severity of spring frost events following bud burst. The gridded daily minimum temperatures tended to overestimate the local temperature data, indicating that the risk of frost damage can be higher than calculated.

To apply the results of the study to seed orchard material, a link between growth rhythm of provenances and seed orchards is needed. Future modelling studies using provenance and seed orchard materials in the same trials may elaborate the development of such a link.

CRediT authorship contribution statement

Tetiana Svystun: Methodology, Formal analysis, Writing - original draft, Visualization. **Jenny Lundströmer:** Formal analysis, Writing - original draft, Visualization. **Mats Berlin:** Conceptualization, Data curation, Writing - review & editing. **Johan Westin:** Data curation, Writing - review & editing. **Anna Maria Jönsson:** Conceptualization, Methodology, Writing - review & editing, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This study has received funding via the project "Understanding the environmental regulation of annual growth cycle in trees", supported by Knut och Alice Wallenbergs stiftelse, and from the European Union's Horizon 2020 Programme for Research & Innovation under grant agreement No 773383 (B4EST).

The study is a contribution to the Research School of Forest Genetics, Biotechnology and Breeding.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119252.

References

Augspurger, C.K., 2009. Spring 2007 warmth and frost: phenology, damage and refoliation in a temperate deciduous forest. Funct. Ecol. 23 (6), 1031–1039.
Augspurger, C.K., 2013. Reconstructing patterns of temperature, phenology, and frost damage over 124 years: spring damage risk is increasing. Ecology 94 (1), 41–50.

Basler, D., Körner, C., 2014. Photoperiod and temperature responses of bud swelling and bud burst in four temperate forest tree species. Tree Physiol. 34 (4), 377–388.
Bennie, J., Kubin, E., Wiltshire, A., Huntley, B., Baxter, R., 2010. Predicting spatial and temporal patterns of bud-burst and spring frost risk in north-west Europe: the implications of local adaptation to climate. Glob. Change Biol. 16 (5), 1503–1514.
Berlin, M., Jansson, G., Högberg, K.A., Helmersson, A., 2019. Analysis of non-additive genetic effects in Norway spruce. Tree Genet. Genomes 15 (3 (Article 42)), 17.
Beuker, E., 1994. Adaptation to climatic changes of the timing of bud burst in populations of Pinus sylvestris L. and Picea abies (L.) Karst. Tree Physiol. 14 (7-8-9), 961–970.
Blümel, K., Chmielewski, F.-M., 2012. Shortcomings of classical phenological forcing models and a way to overcome them. Agric. For. Meteorol. 164, 10–19.
Brocca, L., et al., 2011. Soil moisture estimation through ASCAT and AMSR-E sensors: an intercomparison and validation study across Europe. Remote Sens. Environ. 115 (12), 3390–3408.
Caffarra, A., Donnelly, A., Chuine, I., Jones, M.B., 2011. Modelling the timing of Betula pubescens budburst. I. Temperature and photoperiod: a conceptual model. Climate Res. 46 (2), 147–157.
Cannell, M.G.R., Smith, R.I., 1983. Thermal time, chill days and prediction of budburst in Picea sitchensis. J. Appl. Ecol. 20 (3), 951–963.
Christersson, L., Fircks, H.A.v., 1988. Injuries to conifer seedlings caused by simulated summer frost and winter desiccation, 22. Silva Fennica, pp. 195–201.
Chuine, I., 2000. A united model for budburst of trees. J. Theor. Biol. 2007, 337–347.
Cornes, R.C., van der Schrier, G., van den Besselaar, E.J., Jones, P.D., 2018. An ensemble version of the E-OBS temperature and precipitation data sets. J. Geophys. Res.Atmos. 123 (17), 9391–9409.
Danell, Ö., 1991. Survey of past, current and future Swedish forest tree breeding. Silva Fennica 25, 241–247.
Danell, Ö., 1993. Breeding programmes in Sweden. Corrected reprint from: Lee, S.J. (Ed.). Progeny testing and breeding strategies, Proceedings of the Nordic group of tree breeding, October 1993, 184 pp. Edinburgh: Forestry Commission, pp. 1–25.
Danusevicius, D., Persson, B., 1998. Phenology of natural Swedish populations of Picea abies as compared with introduced seed sources. Forest Genetics 5 (4), 211–220.
Director, H., Bornn, L., 2015. Connecting point-level and gridded moments in the analysis of climate data. J. Clim. 28 (9), 3496–3510.
Drusch, M., Wood, E.F., Gao, H., 2005. Observation operators for the direct assimilation of TRMM microwave imager retrieved soil moisture. Geophys. Res. Lett. 32 (15).
Eysteinsson, T., Karlman, L., Fries, A., Martinsson, O., Skulason, B., 2009. Variation in spring and autumn frost tolerance among provenances of Russian larches (Larix Mill.). Scand. J. For. Res. 24 (2), 100–110.
Fries, M., 1948. Limes norrlandicus-studier. En växtgeografisk gränsfråga historisk belyst och exemplifierad. Sven. Bot. Tidskr. 42 (1), 51–69.
Giorgi, F., Jones, C. and Asrar, G.R., 2009. Addressing Climate Information Needs at the Regional Level: The CORDEX Framework. World Meteorological Organization (WMO) Bulletin, vol. 58, no. 3, pp. 175.
Häggmark, L., Ivarsson, K.-I., Gollvik, S., Olofsson, P.-O., 2000. Mesan, an operational mesoscale analysis system. Tellus A: Dyn. Meteorol. Oceanogr. 52 (1), 2–20.
Hammersmith, S., 2014. Cold Air Accumulation and the Grower's Guide to Frost Protection. Westbow Press.
Hannerz, M., 1994. Predicting the risk of frost occurrence after budburst of Norway spruce in Sweden. Silva Fennica 28 (4), 243–249.
Hannerz, M., 1998. Genetic and seasonal variation in hardiness and growth rhythm in boreal and temperate conifers – a review and annotated bibliography (Report no. 2 1998, SkogForsk – Forestry Research Institute of Sweden). "", Uppsala, 140 pp.
Hannerz, M., 1999. Evaluation of temperature models for predicting bud burst in Norway spruce. Can. J. For. Res. 29 (1), 9–19.
Hannerz, M., Ekberg, I., Norell, L., 2003. Variation in chilling requirements for completing bud rest between provenances of Norway spruce. Silvae Genetica 52 (3/4), 161–168.
Hannerz, M., Sonesson, J., Ekberg, I., 1999. Genetic correlations between growth and growth rhythm observed in a short-term test and performance in long-term field trials of Norway spruce. Can. J. Forest Res. 29, 768–778.
Hannerz, M., Westin, J., 2000. Growth cessation and autumn-frost hardiness in one-year-old Picea abies progenies from seed orchards and natural stands. Scand. J. For. Res. 15 (3), 309–317.
Hänninen, H., 1990. Modelling bud dormancy release in trees from cool and temperate regions. Acta Forestalia Fennica 213, 47 pp.
Hänninen, H., 1991. Does climatic warming increase the risk of frost damage in northern trees? Plant, Cell Environ. 14 (5), 449–454.
Hänninen, H., 1995. Effects of climatic change on trees from cool and temperate regions: an ecophysiological approach to modelling of bud burst phenology. Can. J. Bot. 73 (2), 183–199.
Hänninen, H., 1996. Effects of climatic warming on northern trees: testing the frost damage hypothesis with meteorological data from provenance transfer experiments. Scand. J. For. Res. 11 (1–4), 17–25.
Hänninen, H., 2016. Boreal and temperate trees in a changing climate. Biometeorology. Springer, Dordrecht.
Haylock, M., et al., 2008. A European daily high-resolution gridded data set of surface temperature and precipitation for 1950–2006. J. Geophys. Res.: Atmos. 113 (D20).
Heide, O., 1993. Daylength and thermal time responses of budburst during dormancy release in some northern deciduous trees. Physiol. Plant. 88 (4), 531–540.
Jönsson, A.M., Bärring, L., 2004. Climate change and the effect of temperature backlashes causing frost damage in Picea abies. Global Planet. Change 44, 195–207.
Jönsson, A.M., Bärring, L., 2011. Ensemble analysis of frost damage on vegetation caused by spring backlashes in a warmer Europe. Natl. Hazards Earth Syst. Sci. 11 (2), 401–418.
Jönsson, A.M., Linderson, M.-L., Stjernquist, I., Schlyter, P., Bärring, L., 2004. Climate change and the effect of temperature backlashes causing frost damage in Picea abies. Global Planet. Change 44 (1–4), 195–207.
Kellomaki, S., Hanninen, H., Kolstrom, M., 1995. Computations on frost damage to Scots pine under climatic warming in boreal conditions. Ecol. Appl. 5 (1), 42–52.
Kramer, K., et al., 2017. Chilling and forcing requirements for foliage bud burst of European beech (Fagus sylvatica L.) differ between provenances and are phenotypically plastic. Agric. For. Meteorol. 234, 172–181.
Kroon, J., Rosvall, O., 2004. Optimal produktion vid nordförflyttning av gran i norra Sverige. Skogforsk, Redogörelse nr 5 (5), 24.
Krutzsch, P., 1973. Norway Spruce Development of Buds., IUFRO S2.02.11. International Union of Forest Research Organization, Vienna.
Langlet, O., 1960. Mellaneuropeiska granprovenienser i svenskt skogsbruk, 80. Uppsatser/Statens skogsforskningsinstitut.
Langvall, O., 2000. Interactions between near-ground temperature and radiation, silvicultural treatments and frost damage to Norway spruce, Dissertation, Sc. Silvestria 140, Swedish Univ Agric Sc.
Langvall, O., 2011a. Impact of climate change, seedling type and provenance on the risk of damage to Norway spruce (Picea abies (L.) Karst.) seedlings in Sweden due to early summer frosts. Scand. J. For. Res. 26 (S11), 56–63.
Langvall, O., 2011b. Impact of climate change, seedling type and provenance on the risk of damage to Norway spruce (Picea abies(L.) Karst.) seedlings in Sweden due to early summer frosts. Scand. J. For. Res. 26 (S11), 56–63.
Langvall, O., Löfvenius, M.O., 2019. Long-term standardized forest phenology in Sweden: a climate change indicator. Int. J. Biometeorol. 1–11.
Larcher, W., 1981. Effects of low temperature stress and frost injury on plant productivity. Physiol. Process. Limit. Plant Prod. 253–269.
Larcher, W., 2003. Physiological Plant Ecology: Ecophysiology and Stress Physiology of Functional Groups. Springer Science & Business Media.
Leinonen, I., 1996. A simulation model for the annual frost hardiness and freeze damage of Scots pine. Ann. Bot. 78 (6), 687–693.
Linkosalo, T., Lappalainen, H.K., Hari, P., 2008. A comparison of phenological models of leaf bud burst and flowering of boreal trees using independent observations. Tree Physiol. 28 (12), 1873–1882.
Linkosalo, T.H.R., Hänninen, H., 2006. Models of the spring phenology of boreal and temperate trees: is there something missing? Tree Physiol. 26.
Man, R., Lu, P., Dang, Q.-L., 2017. Insufficient chilling effects vary among boreal tree species and chilling duration. Front. Plant Sci. 8, 1354.
Morin, X., Chuine, I., 2014. Will tree species experience increased frost damage due to climate change because of changes in leaf phenology? Can. J. For. Res. 44 (12), 1555–1565.
Myking, T., Heide, O.M., 1995. Dormancy release and chilling requirement of buds of latitudinal ecotypes of Betula pendula and B. pubescens. Tree Physiol. 15 (11), 697–704.
Nienstaedt, H., 1967. Chilling requirements in seven Picea species. Silva Genet. 16, 65–68.
Olsson, C., Jönsson, A.M., 2014. Process-based models not always better than empirical models for simulating budburst of Norway spruce and birch in Europe. Glob. Change Biol. 20 (11), 3492–3507.
Olsson, C., Jönsson, A.M., 2015. Budburst model performance: The effect of the spatial resolution of temperature data sets. Agric. For. Meteorol. 200, 302–312.
Olsson, C., Olin, S., Lindström, J., Jönsson, A.M., 2017. Trends and uncertainties in budburst projections of Norway spruce in Northern Europe. Ecol. Evol. 7 (23), 9954–9969.
Partanen, J., Koski, V., Hänninen, H., 1998. Effects of photoperiod and temperature on the timing of bud burst in Norway spruce (Picea abies). Tree Physiol. 18 (12), 811–816.
Partanen, J., Leinonen, I., Repo, T., 2001. Effect of accumulated duration of the light period on bud burst in Norway spruce (Picea abies) of varying ages. Silva Fennica 35 (1), 111–117.
Persson, A. and Persson B. 1992. Survival, growth and quality of Norway spruce (*Picea abies* (L.) Karst.) provenances at the three Swedish sites of the IUFRO 1964/68 provenance experiment. Swedish University of Agricultural Sciences, Dept. of Forest Yield Research, Report No. 29, 67 pp.
Rosvall, O., 2003. Zon- och ägarvisa plantagearealer för tredje omgången fröplantager i Sverige. Skogforsk, Arbetsrapport Nr 549, 42 pp(549).
Rosvall, O., 2011. Review of the Swedish tree breeding programme. Skogforsk, Gävle Offset, Gävle, 84 pp.
Rosvall, O., Ericsson, T., 1982. Förflyttningseffekter i norrländska granprovieniensförsök / Transfer effects of Picea abies in northern Sweden, Årsbok 1981 (Föreningen skogsträdsförädling och Institutet för skogsförbättring). Uppsala 85–117.
Sakai, A., Larcher, W., 1987. Frost Survival of Plants. Responses and Adaptation to Freezing Stress. Springer-Verlag.
Sarvas, R., 1974. Investigations on the annual cycle of development of forest trees.II. Autumn dormancy and winter dormancy. Commun. Instituti Forestalis Fenniae 76 (3), 1–101.
Saxe, H., Cannell, M.G.R., Johnsen, O., Ryan, M.G.R., Vourlitis, G., 2001. Tree and forest functioning in response to global warming. New Phytol. 149 (3), 369–400.
Schaber, J., Badeck, F.-W., 2003. Physiology-based phenology models for forest tree species in Germany. Int. J. Biometeorol. 47 (4), 193–201.
Skogforsk, 2020. PlantVal - Gran (Planters guide). Skogforsk, Forestry Research Institute of Sweden. https://www.skogforsk.se/produkter-och-evenemang/verktyg/plantval-gran.
Skogsstyrelsen, 2020. Skogsvårds lagstiftningen.
Skrøppa, T., Magnussen, S., 1993. Provenance Variation in shoot growth components of Norway Spruce. Silvae Genet. 42 (2/3), 111–120.

Weiser, C., 1970. Cold resistance and injury in woody plants: knowledge of hardy plant adaptations to freezing stress may help us to reduce winter damage. Science 169 (3952), 1269–1278.

Werner, M. and Karlsson, B., 1983. Resultat från 1969 års granproveniensserie i syd- och mellansverige, Årsbok 1982 (Föreningen skogsträdsförädling och Institutet för skogsförbättring). Uppsala, pp. 90–158.

Worrall, J.M., Francois, 1967. Environmental and genetic control of dormancy in Picea abies. Physiol. Plant. 20 (3), 733–745.