

Development of a universal height response model for transfer of Norway spruce (*Picea abies* L. Karst) in Fennoscandia

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A B S T R A C T

Norway spruce is a major industrial tree species in Fennoscandia and future productivity of the species must be secured by matching the variation in adaptation of the species with suitable sites for optimized performance. An appropriate transfer model for forest reproductive material (FRM) is crucial for regeneration of productive forests in the changing climatic conditions that are predicted to occur in Fennoscandia. We have developed a transfer model for prediction of height of Norway spruce in Norway, Sweden, and Finland, using data acquired from 438 progeny and provenance trials with 1919 genetic entries of local and transferred origins. Transfer of genetic material at a given site was expressed in terms of the difference in daylength (photoperiod) between the site and its origin. This variable best reflected the nonlinear response to transfer that has been commonly reported in previous studies. Apart from the transfer variable, the height prediction model included the age of material when height measurements were acquired, annual temperature sum over 5 °C, precipitation during the vegetation period, and interaction terms between test site and transfer variables. The results show that long northward transfers (4–5° latitude) seem to be optimal for relatively mild sites in southern parts of the countries where growing season is longer, and shorter northward transfers (2–4° latitude) for harsher northern sites with shorter growing seasons. The transfer model also predicts that southward transfers of Norway spruce would result in height growth reductions. The developed model provides foundations for development of common or national recommendations for genetically improving Norway spruce material in Fennoscandia.

1. Introduction

Climate and site properties, genetic background and phenotypic plasticity are major factors affecting growth of forest trees in their natural ranges (Kjær, 1996; Wang et al., 2010). Ongoing climate changes are very likely to affect trees' performance by changing growing conditions generally and increasing frequencies of sudden and extreme climatic events that might abruptly change the conditions, e.g., droughts (Alverson, 2000; Bergh et al., 2007; Bradshaw et al., 2000; Mann et al., 1998). Climatic changes are known to affect species' range boundaries, community compositions in ecosystems and biological phenomena affecting trees' growth, e.g., phenological patterns of both their own growth and development and those of associated organisms (Gömöry et al., 2012). Thus, to survive in their natural ranges, tree populations must adapt to climatic changes through phenotypic plasticity and genetic selection to the changes (Bradshaw et al., 2000; Gömöry et al., 2012).

Planned transfer of plants to new environments has been practiced in forestry for more than a 100 years (Aitken et al., 2008; Sáenz-Romero et al., 2021). This has been done to increase stand productivity, secure the availability of raw material for industry and in recent years to avoid problems caused by slow adaptation of local provenances to climatic changes i.e. assisted migration. Currently, assisted migration is advocated as a method to respond to rapid human-caused climate change in cases where local material might be suboptimal or threatened in the future.

Optimization of assisted migration has involved use of mathematical functions that predict phenotypes' performance using site or climatic variables related to planting sites and origins of transferred material at those sites (*ecodistance*-Matyas, 1994). The phenotypic performance has then been represented by measurement of trees' heights and survival in early rotation stages, up to ages of ca. 20 years. Measurements of height in genetic trials are almost always available as the trait has been used as a selection variable in most breeding programs intended to improve

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productivity. Strong correlations have been found between early measurements of height of Norway spruce and its productivity (Liziniewicz and Berlin, 2019; Liziniewicz et al., 2018). Another major advantage of height measurements is that they are often acquired using very similar techniques in trials all around the world. Important for productivity are also site characteristics such as soil and moisture properties, but they have rarely been possible to include in models because it is more challenging to gather consequent information describing them across larger regions.

The approach outlined above has been commonly applied, despite the ‘equal response to transfer’ limitation, i.e., the assumption that the responses of specific provenances will be the same at different sites (cf. Wang et al., 2010). Wang et al. (2010) overcame the drawbacks of the earlier approaches by modelling phenotypic performance with variables describing the planting site and origin of the genetic material simultaneously. In this solution, known as a universal response function (URF), variables used to describe the location of the planting site and genetic origin are sometimes replaced by the difference between these, e.g., the difference in latitude (Berlin et al., 2016). The models constructed in such a way are more flexible and can overcome the issue of the equal site response.

The developed transfer functions are often used to formulate species-specific guidelines for transfer of forest reproductive material (FRM). The guidelines are essential tools for optimizing the decisions of seed allocation in operational forestry concerning, i.e., delineation of deployment zones and seed transfer. The best seed sources are limited as there is substantial annual variation in seed production and intervals between mast years of most tree species, including Norway spruce (Lundströmer et al., 2020; Pukkala et al., 2010). Appropriate FRM transfer guidelines facilitate effective use of seed resources through the identification of optimally adapted seed sources for specific sites (Berlin, 2021; Lundströmer et al., 2020). However, ongoing and future climatic changes in Fennoscandia (and elsewhere) will have complex effects on forests, which will depend on relationships between local site conditions and origins of planted material, which in some cases will lead to sub-optimal adaptation, even if (for instance) the latitudinal transfer is close to ideal. At some forest sites, new climate conditions are predicted to improve growing conditions by, for example, increasing the length of vegetation periods through increases in temperature (Bergh et al., 2007). However, in other regions where spring frosts are an issue such increases in vegetation periods may exacerbate frost damage, causing quality defects and impairing tree growth (Langvall, 2011; Svystun et al., 2021). Thus, appropriate matching of seed sources and sites is important for supporting sustainable wood production (Ledig and Kitzmiller, 1992).

Norway spruce (*Picea abies* L. Karst) is an essential source of raw material for the forest based industry in Norway, Sweden, and Finland, with a growing stock of ca. 2800 mln m³ (Rytter et al. 2016). The growing conditions are favourable for spruce, and the species is more productive than other native species on a large proportion of the area (Ekö et al., 2008). There is a long tradition of transfer of Norway spruce provenances in Fennoscandia due to seed deficits and attempts to increase stand productivity (Myking et al. 2016). Stands planted with south-eastern European material are known to produce on average 6–10 % more volume than local material and are well adapted to conditions in southern Sweden (Persson and Persson, 1992). Large quantities of Norway spruce seeds from central and south-eastern Europe have traditionally been imported into southern parts of Norway and Sweden (Hannerz and Almäng, 1997; Jansen et al., 2017; Koskela et al., 2014; Myking et al., 2016) while smaller quantities of Swedish and Estonian seeds have been imported to southern Finland. The current guidelines in all three countries allow longer northward transfer to sites in southern than to northern regions. The recommended transfer distance declines with increases in latitude of the planting site. However, the recommendations have usually been based on limited evidence (Äijälä et al., 2019; Heikinheimo, 1949; Kroon and Rosvall, 2004; Persson and

Persson, 1992; Werner and Karlsson, 1982,) or practical experience. Thus, these models cannot incorporate data derived from new climate scenarios e.g., representative concentration pathway (RCP) scenarios. In older models climate variables, were often obtained by transformations of latitude and altitude rather than from currently available highly gridded climatic indices with a high temporal resolution (Kroon and Rosvall, 2004).

In the future, Norway spruce will probably remain an important source of raw material for the forest industry in the region. However, allocation of suitable genetic resources to specific sites (or sets of sites with specific conditions) is necessary to secure sustainable volume production and stand stability. Currently, the national recommendations for Norway spruce transfer have been developed separately using country-specific materials. The aim of this study is to develop common transfer response models for height and survival for the entire Fennoscandia by gathering all the available phenotypic information. The developed models are also first steps towards formulation of climate-adapted deployment recommendations for Norway spruce for the countries and the region. The models are based on extensive data from provenance and progeny trials planted between 1930 and 2009 in Sweden, Norway, and Finland, and climate datasets with high spatial and temporal resolution.

2. Materials and methods

2.1. Field trial data

The data applied in the modelling reported here were collected during the last 80 years from 438 provenance and progeny trials of 115 experimental series located in Sweden, Finland, and Norway (Fig. 1, Table 1). From the progeny trials, neither data of tested plus-trees progenies nor clones were used, only unimproved check-lots. The planted material included various remotely transferred provenance material and local seed-lots (in both cases regarded as autochthonous material at source sites). The overlap of the material between the countries and series within the countries was generally very low.

The trials were established in different time periods and using different experimental designs, including both single- and multi-tree plots. The height of individual trees (H) was measured in each trial at different ages (Table 2). Tree height was measured in different years and not explicitly for the purpose of this study. In most cases measurements of individual trees were available, thus also enabling evaluation of tree survival rates (S) for each combination of genetic entry and field trial. However, for an experimental series with 158 multiple-tree plot trials established from 1930 to 1970 and compiled by Dietrichson (1977), neither individual tree height data nor numbers of trees representing each combination of entry and trial used to calculate mean values were available.

2.2. Data aggregation

Field trial data were analyzed in two steps. In the first step, single-tree data were aggregated and standardized due to their heterogeneity (e.g., different trial designs) This was done to homogenize the data and secure their quality. The aggregation and standardization were done by deriving least-squares (LS) means from the linear or linear mixed models fitted to the measurement data. In the second step, the URF models were developed based on the LS values obtained in step one.

In the step one, for the sites where individual measurements were available, raw data were analysed. In this analysis, the goal was to obtain a LS mean of height (H_{ij}) or survival (S_{ij}) for each genetic entry (j) within each genetic trial (i).

The following linear model was used for trials with replicated single plots:

$$Y_{kij} = \mu + B_k + G_j + \varepsilon_{kij}$$

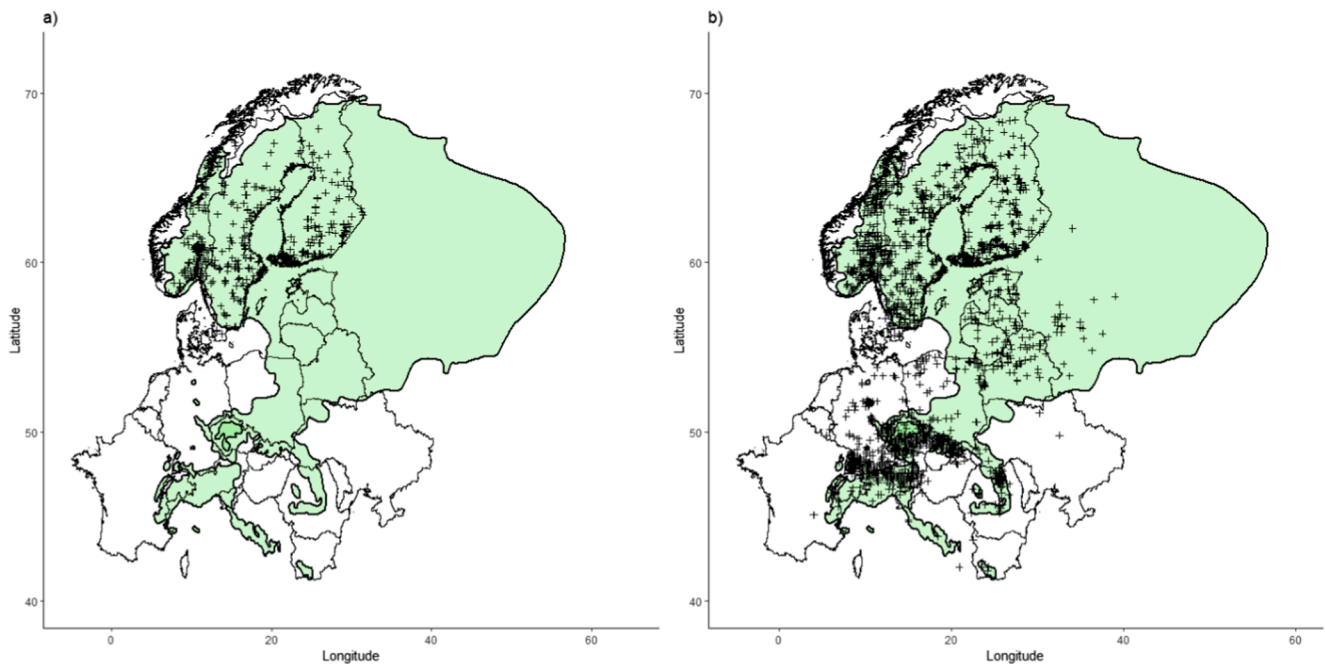


Fig. 1. Maps of a) available field trials and b) available genetic entries for the height model over current natural distribution (green) (Caudullo et al., 2017). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Summary of the geographic distribution of the sites and tested material used in the study.

Country	N	Mean lat.	Min. lat.	Max. lat.	Mean long.	Min. long.	Max. long.
Trials							
Sweden	142	60.9	55.8	67.0	16.1	11.7	23.6
Norway	169	60.6	58.2	69.7	10.8	7.1	19.5
Finland	127	62.1	59.9	67.9	25.7	19.8	31.4
Genetic entries							
Sweden	461	56.3	42	67.7	18.2	5.8	35.2
Norway	1003	53.6	41.8	66.4	13.7	4	39
Finland	455	58.4	43.8	68.4	24.0	8.3	30.7

The following linear mixed model was used for trials with multiple-tree plots:

$$Y_{kjl} = \mu + B_k + G_j + p_{kj} + \epsilon_{kjl}$$

In these models, Y is a dependent variable (height or survival), μ is a general trial mean, B is the fixed effect of the block k , G is a fixed effect of the genetic entry j , p is a random effect of the plot in block k for the genetic entry j , and ϵ is the residual error of the individual tree l within genetic entry j and block k . For height, single tree measurements were used according to the models above while for survival a results for a genetic entry at block/plot level was used and the l factor disappeared from the model. The models were fitted by either the GLM or MIXED procedures of the SAS STAT package (SAS Institute Inc. 2011).

The LS means of the genetic entries obtained in the step one were

Table 2
Summary of arithmetic means describing the collected data used for modelling, where N is the total number of measured trees and ranges are given in brackets.

	Entries per trial	Trials per Entry	Establishment year	N*	Survival (%)	Height (m)	Age at survival assessment	Age at height assessment
Sweden	17 (4–98)	7.3 (2–71)	1977 (1941–2002)	196,772	79 (5–100)	2.7 (0.32 – 10.2)	15.4 (8 – 25)	14.2 (7–30)
Norway	16 (2–95)	7.7 (2–42)	1968 (1947–2009)	44,103	84 (10 – 100)	3.7 (0.25 – 10.0)	15.8 (6 – 33)	15.5 (6–33)
Finland	12 (2–36)	6.7 (2–35)	1971 (1930–2007)	161,124	79 (1–100)	3.45 (0.44 – 20.8)	16.4 (9 – 26)	16.8 (8–44)

*N – This is the number of stems monitored to acquire the survival data, the number of stems used to acquire the height data was even higher as tree number data were not available for 158 trials.

used for URF model development and the general distributions and characteristics of these means are shown in Fig. 2. The analysis in the step one resulted in 6709 unique observations for height and 4095 observations for survival. The difference is due to the fact that, the data collected in the trials compiled by Dietrichson (1977) could not be used in the calculation of LS means for survival as single tree measurements were not available. For this material, available mean height values for each entry and trial combination were used directly. These trials couldn't be used in a development of survival model.

2.3. Climate data

Two climate datasets were used to describe the climate of sites and genetic entries. Initially, 16 climatic indices describing the trial and genetic entry were derived from the climate dataset E-OBS (SMHI, Supplementary Table 1), a daily gridded land-only observational dataset over Europe. The dataset combines meteorological observations interpolated into high resolution (0.05) gridded data. The variables used to derive the indices were daily mean temperature, daily minimum temperature, daily maximum temperature, daily precipitation sum, daily averaged sea level air pressure and daily mean global radiation. The temporal resolution was six hours, and the dataset covered the years 1961–2017. The climatic data covered the whole range of trials and genetic entries included in the dataset used in the study. The E-OBS data set was initially used to identify variables that showed the strongest association with the effects of Norway spruce transfer.

The other climate dataset used in this study was derived from Version 4 of the CRU-TS monthly gridded multivariate climate dataset using a grid with the original resolution of ~ 0.5 (Harris et al., 2020). In

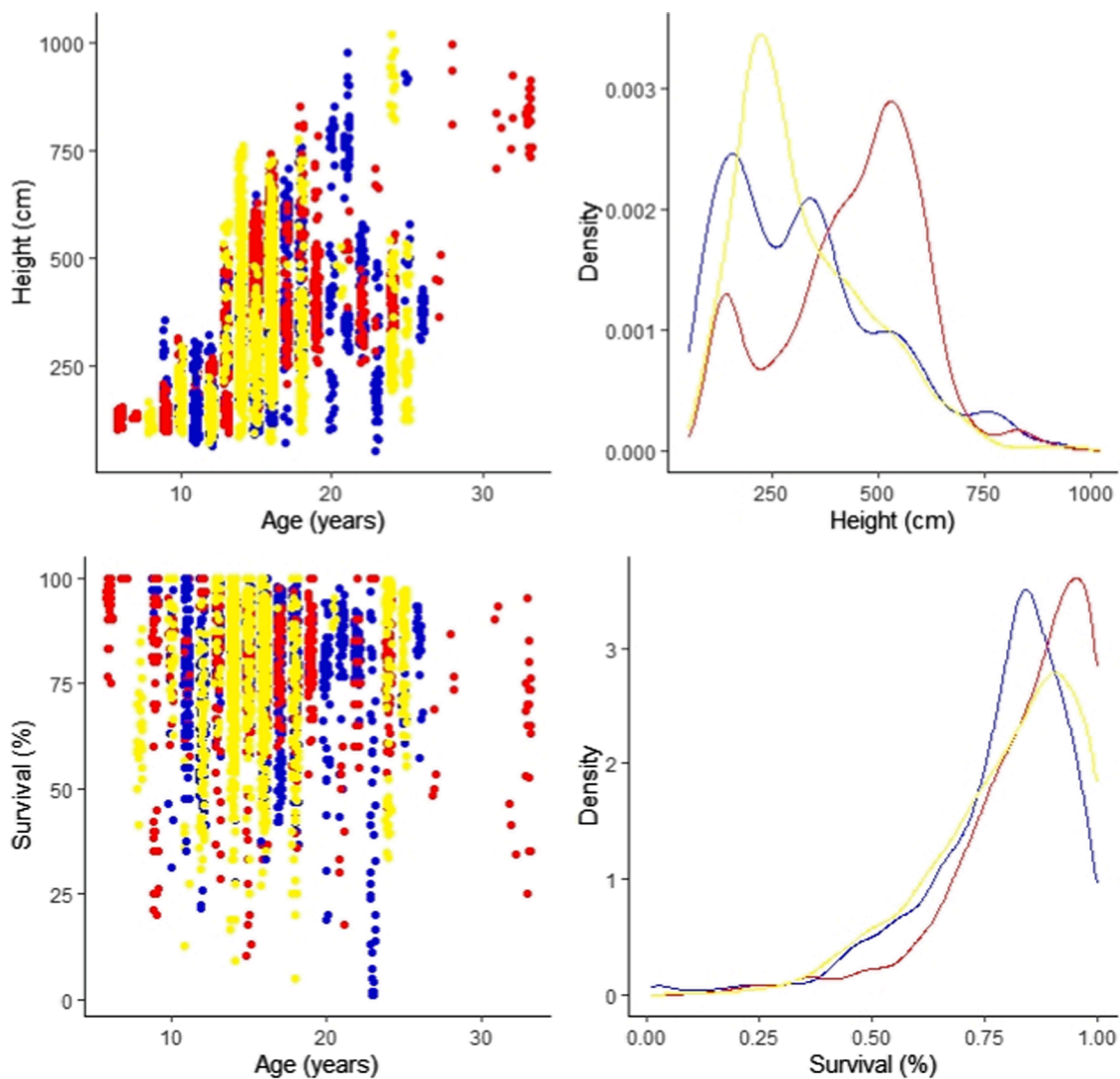


Fig. 2. Scatterplots (left panels) and distribution densities (right panels) of least-squares means estimates of the dependent variables of height (upper panels) and survival (lower panels) across tree age and countries: Finland (blue), Norway (red) and Sweden (yellow). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

this study, the data were downsampled following procedures developed by Marchi et al. (2020). The developed system is an online version of the ClimateEU (Marchi et al., 2020) and ClimateNA (Wang et al., 2016) software and implements a scale-free dynamic downscaling ('delta') method (Ramirez-Villegas and Jarvis, 2010), involving use of topographic data of the site (primarily altitude) to facilitate the process (Fréjaville and Benito Garzón, 2018; Moreno and Hasenauer, 2016). This can provide more than 100 climatic variables and indices for different research purposes. The CRU-TS dataset was limited to variables that were identified as significant in the model based on the EOBS climate dataset: the accumulated annual temperature sum above 5C (TS) and precipitation during the growing season, April-to-October (PREC). Again, the 1961–2017 period was used for deriving CRU-TS variables. Eventually, the scale-free CRU-TS dataset was used in the evaluation and selection of the final height model as the grid resolution of the E-OBS dataset was too coarse to properly simulate the climatic conditions in terrain with highly varying topography, e.g., the Norwegian alpine region where climatic conditions change quite rapidly with changes in altitude.

2.4. Model development

2.4.1. General model development

During the model development we followed the conceptualization proposed by Wang et al. (2010) of a universal response function (URF) that integrates individual response functions (environmental effect of test site) and genecology functions (genetic effect of provenance) into a single model. In this study, the genetic effect was represented by the transfer distance of a genetic entry, which was the difference between test site and then origin of the genetic entry (Berlin et al., 2016). Initially, field trials and genetic entries were associated with climate variables according to their geographical positions. Such a dataset was used to develop the models.

The general structure of the models was:

$$Y = \text{Test site effect} + \text{Transfer effect} + \text{Interaction} + \text{error}$$

The dependent variable (Y) was height (H), or survival (S) of a specific genetic origin recorded in a specific field trial at a specific age. The dependent variables were transformed with the natural logarithm and the logit transformation for height and survival models, respectively, to secure the homoscedasticity of the residuals.

The models were fitted with the *lme* function of the *nlme* package

(Pinheiro et al., 2016) in the R software (R Core Team 2016). In each case the error term was split into the random variation between sites (random error due to the experiment) and within sites (random error). For comparisons, the models were fitted with the ML argument, i.e., maximization of log-likelihood. In contrast, the REML argument (maximization of the restricted log-likelihood) was used for the final estimation of coefficients. To account for each genetic entry's varying number of information, a square-root of the tree number count measured at each experiment was used as a weight in the survival model but not for the height model (for which numbers of trees representing each combination of entry and trial used to calculate mean values were not available for all experiments).

The independent variables were selected based on: (i) their significance in the model, (ii) improvement of marginal R^2 (R^2_{marginal} , considering only fixed effects) calculated by the *piecewiseSEM* package of the R software (Lefcheck, 2019) when added to the model and the Akaike Information Criterion – AIC (Sakamoto et al., 1986), (iii) residuals' behaviour, (iv) model parsimony, (v) biological soundness and reliability in terms of correspondence with previous findings (Kroon and Rosvall, 2004; Persson and Persson, 1992). Such a strategy has been previously used in assessment of responses to transfers of Scots pine in northern Sweden and Finland by Berlin et al. (2016).

2.4.2. Choice of environmental variables

In the first step in the selection of environmental variables to include in the modelling, the 16 climatic indices from the E-OBS dataset (Supplementary Table 1) were tested to identify those with the strongest effects on height growth and survival of Norway spruce at the analysed sites. The accumulated annual temperature sum above 5C (TS) and precipitation during the growing season, defined as the months from April to October (PREC) were selected for further investigation as they met the described selection criteria. The reciprocal of measurement age (1/AGE) was used together with the climate variables at this stage of development. The transfer variable (ΔTRANS) was defined as the difference between specific site value and specific genetic origin value, so northward and southward transfers had positive and negative values, respectively. Initially, the difference in latitude between a planting site and the origin of genetic material (the ΔLAT variable) was used to represent the transfer.

Interactions between test site and transfer variables were only included for site variables found to be significant for the model without interaction (to limit the large numbers of available variables for testing). The final models were fitted with the data from the CRU-TS climatic dataset.

2.4.3. Choice of transfer variable

Several variables representing transfer of genetic material that were previously used in other studies were tested in the model in efforts to find a variable that accounts for the dynamic effects of transfer (Berlin et al., 2016; O'Neill et al., 2014; Ying and Yanchuk, 2006). In the model development, four transfer variables were tested and the models were compared with consideration of the criteria used in selection of the best initial model. The transfer variables were:

transfer in latitude (Model 1 - ΔLAT), transfer in terms of daylength (Model 2 - ΔDL), distance between locations of the trial and a genetic entry's origins defined by their latitude and longitude (Model 3 - ΔEUC) and transfer in terms of temperature sum (Model 4 - ΔTS). ΔDL was inferred from the latitudes of the field trials and genetic entries' origins, according to Forsythe et al. (1995) as implemented in the R package *geosphere* (Hijmans et al., 2017). Daylength has not been used in any previous efforts to develop transfer functions for FRM. However, the photoperiodic control of adaptive traits in Norway spruce has been well described, with clear demonstration that seedlings' bud set in late summer is controlled by night length (Dormling, 1973; Dormling et al., 1968; Heide, 1974). This direct control seems to diminish with age as the annual growth potential becomes predetermined and dependent on the

number of needle primordia developed in the preceding year, but the effect of photoperiod remains significant as it influences the period of primordia development (Ekberg et al., 1979). The optimal time of year for determining the variable ΔDL was assessed by testing ΔDL on Julian days in 17 five-day intervals from day 175 in a year (23rd of June) to day 230 (18th of August).

2.4.4. Other considerations

A categorical variable indicating the country (Norway, Sweden, Finland) of the field trial location was used to test whether there was a country effect in the final models. A significant country effect could, for instance, reflect problems in modelling, discrepancies in measurement methods across countries or *bona fide* differences in silvicultural practices. We did not expect to detect a significant country effect (which would have negated the possibility of developing a common model for the three Fennoscandian countries).

2.5. Model evaluation

To illustrate and evaluate the derived models' behaviour they were used to predict the optimal transfer distance for six hypothetical sites with defined latitude, altitude, temperature sum and precipitation sum in the vegetation period. The values represented averages for one degree latitude and longitude grid cells for the dataset used for model development e.g., latitude 59°N represented all field trials included in the dataset located between latitude 59°N and 59°99N. Two grid cells with the highest numbers of observations per cell were selected for each country, one in the southern part (latitude $\leq 63^\circ\text{N}$) and one in the northern part (latitude $> 63^\circ\text{N}$). The southern site represented sites with mild and climatically favourable growth conditions while the northern site represented sites with harsher conditions (Table 3). A common stand age of 20 years was used for predictions for all sites.

3. Results

3.1. Final height model

The final height model was Model 2 and it included the reciprocal of age (1/AGE), the daylength transfer variable in linear (ΔDL) and quadratic (ΔDL^2) forms and its quadratic interaction with the temperature sum ($\Delta\text{DL}^2 \times \text{TS}$), precipitation in linear (PREC) and quadratic (PREC²) forms, and TS in a linear form (Table 4). The R^2_{marginal} value of the final model was 0.62 (Table 4). The effect of country was not significant ($p > 0.05$) when added to the final model (result not shown).

3.2. Transfer effect variable

The test of transfer variables showed that transfer expressed as the difference in daylength (ΔDL – Model 2), in hours on the 205th Julian day of the year, resulted in a slightly higher marginal R^2 (Table 4) and more negative AIC than models with ΔLAT (Model 1). The Model 4 with ΔTS as a transfer variable provided opposite signs for the transfer

Table 3

Typical values of accumulated annual temperature sum above 5C (TS) and precipitation sum during the growing period from April to October (PREC) for southern (mild) and northern (harsh) sites in Norway, Sweden, and Finland (1961–2017).

Country	Site	Latitude (°)	Altitude (m)	TS (day °C)	PREC (mm)
Norway	Mild	59	165	1321	568
	Harsh	64	82	832	573
Sweden	Mild	58	107	1500	406
	Harsh	64	408	770	396
Finland	Mild	61	40	1305	391
	Harsh	65	100	965	346

Table 4

Comparison of the height model performance with indicated transfer effect variables (Δ TRANS, the difference in values between locations of trials and genetic entries' origins) and: difference in daylength on the 205th Julian day of the year (Δ DL – Model 1), latitudinal distance (Δ LAT – Model 2), Euclidean distance in coordinate degrees (Δ EUC – Model 3), and difference in temperature sum (Δ TS – Model 4) between the locations. Standard errors of coefficient estimates are given in brackets just for selected model (Model 2).

Variable ¹	Term type ²	Model 1 (Δ LAT)	Model 2 (Δ DL) ³	Model 3 (Δ EUC)	Model 4 (Δ TS)
Intercept		4.4384	4.4830 (0.32) ⁴	4.5043	4.4173
1/AGE	S	-22.7365	-22.7952 (0.96)	-22.6002	-22.6241
Δ TRANS	T	0.0272	0.0637 (0.002)	0.0022	-0.0001
Δ TRANS ²	T	-0.0026	-0.0210 (0.002)	-0.0016	-2.30×10^{-7}
PREC	S	0.0052	0.0053 (0.0011)	0.0052	0.0053
PREC ²	S	-4.23×10^{-6}	-4.28×10^{-6} (1.12×10^{-6})	-4.16×10^{-6}	-4.27×10^{-6}
TS	S	0.0011	0.001071 (0.000091)	0.001063	0.001110
Δ TRANS ² \times TS	I	2.83×10^{-7}	-8.51×10^{-6} (3.05×10^{-6})	1.11×10^{-6}	1.36×10^{-10}
R ² marginal		0.617	0.621	0.616	0.607
AIC		-7243.85	-7262.24	-6409.01	-6488.21

¹ AGE – stand age, DL – daylength, PREC – sum of precipitation during the vegetation period, TS – sum of daily temperatures over 5C during the vegetation period, Δ TRANS indicates the difference between locations of a field trial location and origin of a genetic entry in the trial.

² S – site variables, T – transfer variables, I – interactions.

³ MODEL 2 (Δ DL) is a best and recommended model of the effect of Norway spruce transfer in Scandinavia with the natural logarithm of height as the dependent variable. Fitted to maximise the restricted maximum likelihood (“REML”).

⁴ Values in italics are significant at 0.05 level.

coefficients (Δ TRANS) and significantly lower negative AIC. The Model 3 with Δ EUC had slightly lower prediction capacity defined by the marginal R² and AIC fit statistics (Table 4).

3.3. Model biological performance

The optimal transfer distances calculated with the final model (Model 2) using daylength as the transfer variable (Table 5) differed substantially between mild southern sites and harsh northern sites. The optimal transfer distances, in terms of latitude, decreased with increasing latitude and for both site types a northward transfer was optimal, i.e., improved height growth. The average optimum transfers for southern and northern sites were ranged from 4.8° to 3.7° and 3.7° to 3.4° latitude, respectively, (Table 5, Fig. 3).

The Model 2 including Δ DL also indicated shorter optimum transfers to all the typical planting sites than the second-best model, with Δ LAT – Model 1 (Table 5). This pattern was particularly clear for harsh northern sites, where the optimum transfer distance was on average 2.6 shorter for Δ DL than for Δ LAT. The difference between models including Δ DL and Δ LAT was greatest at harsh sites in Finland with a 3.1° latitude optimum transfer difference between Δ LAT and Δ DL. At milder southern sites this difference in optimum transfer was only 1.8° on average. According to the final model, an optimal transfer of genetic materials will increase height growth by ca. 3.2 % at southern fertile sites while the gain at harsher sites will be ca 3.6 % (Table 5).

Table 5

Optimal origin of forest reproductive material in terms of latitude for planting at typical sites in Norway, Sweden and Finland based on the height model with the transfer variables Δ LAT (latitude transfer – Model 1) or Δ DL (daylength transfer – Model 2). The optimal transfer distance (difference between optimal latitude of site latitude and genetic origin) in each case is shown in brackets in the optimal origin columns. Relative gain in height (Gain H) predicted with the height model including Δ DL at the age of 20 years.

Country	Site	Latitude	Optimal origin – Model 1 (Δ LAT)	Optimal origin – Model 2 (Δ DL)	Gain H (%)
Norway	Mild	59	52.9 (6.1)	54.2 (4.8)	3.2
	Harsh	64	58.3 (5.7)	60.7 (3.3)	3.7
Sweden	Mild	58	51.8 (6.2)	54.5 (4.5)	3.1
	Harsh	64	58.3 (5.7)	60.6 (3.4)	3.8
Finland	Mild	62	56.0 (6.0)	58.3 (3.7)	3.2
	Harsh	65	59.2 (5.8)	62.3 (2.7)	3.5

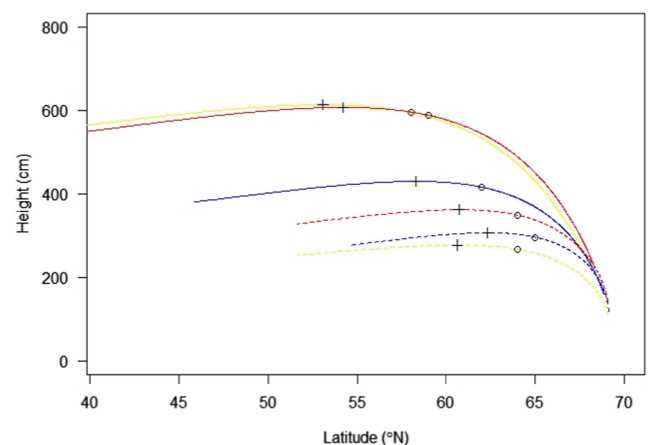


Fig. 3. Tree height in cm at age 20 years as a function of transfer in daylength (Model 2) described in terms of latitude for six typical sites in Norway (red), Sweden (yellow) and blue (Finland). The solid lines represent heights at mild sites (Table 3), and dashed lines represent heights at harsh sites. Black circles indicate site locations while black crosses indicate optimal choices of genetic origins for the sites. Each curve was drawn for a daylength transfer range between -4.6 and 3 h. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.4. Survival model

The analytical approach used to develop the height model was also used to develop a survival rate model. Despite extensive analytical work, the best model developed for the gathered material had poor predictive quality (the marginal R² never exceeded 0.13). The model did not behave in an ecologically sound way for southern sites in any of the countries, i.e., curves derived from the model were flat for long transfers both northward and southward. In addition, the survival model did not perform well for either the whole available dataset or parts of the dataset defined by different minimum heights and different latitudes. Finally, both model predictions and the underlying dataset (Fig. 2) indicated that the survival rate was generally high (>75 %), implying that even a robust survival model would have limited practical value. The best survival model is presented in the supplementary material (Supplementary material 2).

4. Discussion

4.1. Data

The developed height model is a first attempt to develop a universal response function (URF) for Norway spruce for a specific but geographically large European region. Previously, different provenance-specific response functions or site-specific transfer functions have been reported for growth-related traits in Europe (Beuker et al., 1998; Gömöry et al., 2012; Kapeller et al., 2012; Kroon and Rosvall, 2004; Schueler et al., 2013), but no function integrating both has been developed. The previous functions have been based on common garden experiments which have generally been established with small numbers of replicated experiments and limited variety of genetic materials. Kroon and Rosvall (2004) developed transfer functions for northern Sweden based on data obtained from eight common garden experiments containing material from eight Swedish breeding populations. Persson and Persson (1992) used only three IUFRO provenance trials located in Sweden with 1100 provenances. The use of a single progeny or provenance trial series has also been a common feature of models developed in North America (Farjat et al., 2015; Wang et al., 2010).

The greatest novelty of this study was use of a large dataset to develop a URF jointly for three Nordic countries, including data on genetic entries from a large part of the Norway spruce distribution in Europe transferred to 438 experimental trials in Fennoscandia. The experimental trials include both provenance trials and unimproved stand checklots in progeny trials from several series that have been prepared and aggregated for a joint analysis (cf. Berlin et al., 2016). The experimental trials were located across Norway spruce's range in Norway, Sweden, and Finland. Use of such a dataset provides a high degree of confidence that the derived URF models will correctly predict heights of transferred Norway spruce. A possible limitation is underrepresentation of long transfer from the south to extremely northern sites, as transfers to southern sites were performed from a greater span of geographical areas than transfers to the northern sites. Long transfers from north to south were also underrepresented in the analysed dataset.

In the study, climate indices obtained from two climatic datasets (EOBS and CRU-TS) were used to model the height and survival rate of Norway spruce. Two important differences between the datasets lie in their temporal and spatial resolution. The CRU-TS dataset featured monthly data with the original grid resolution of ~ 0.5 but could be freely downscaled to any given spatial point as topographic data (e.g., altitude) were used to facilitate the process (Ramirez-Villegas and Jarvis, 2010; Moreno and Hasenauer, 2016; Fréjaville and Benito Garzón, 2018). In contrast, the E-OBS dataset was based on daily observations at a coarser spatial resolution (5.5×5.5 km) and did not account for the variation in topography and local climate as well as the CRU-TS dataset, especially in Norway. Furthermore, the CRU-TS climatic dataset has been used as a baseline for the development of several future climate scenarios using the CMIP5 datasets (see, for example, Hallingbäck et al., 2021) that will allow further studies on Norway spruce performance under expected future global climate change. There were indications that the E-OBS dataset could provide better estimations of certain climatic variables, like temperature sum, due to its higher temporal resolution. Nevertheless, for this study the overall advantages of using the CRU-TS climatic dataset outweighed those of E-OBS and CRU-TS was ultimately chosen for the final development of the presented URF models.

As the data were collected over a considerable time span, and by different scientific institutes, it was not possible to obtain additional standardised and objectively assessed site characteristics, that could have improved the models' quality. For instance, site variables such as soil type, depth, moisture, and local microsite variation are known to affect Norway spruce growth, but they were not included as it was not possible to obtain such data in a systematic way. However, there is considerable potential for improving the estimation of site quality with

respect to Norway spruce in Sweden using climatic and site variables that could be obtained from the national GIS models (Mason et al., 2018). Further improvements of digital tools for measuring terrain parameters, such as slope, exposure, and soil humidity, might also enhance the models. Standardised and objective assessments of abiotic or biotic induced defects could not be included in the models for the same reason.

4.2. The developed model

The general form of the model, i.e., universal response function conceptualised on lodgepole pine by Wang et al (2010), has been used in similar study for Scots pine (Berlin et al., 2016). This is a convenient approach for predicting consequences of genetic material transfers that allows the formulation of FRM deployment recommendations with consideration of anticipated climatic changes. The final model included site-specific variables represented by climatic parameters, i.e., annual temperature sum (TS) and growing season precipitation (PREC), an indicator of transfer distance (represented as the difference in daylength between locations of a planting site and origins of a genetic entry at that site) and interaction terms that introduced additional dynamic properties to improve model performance.

Changes in variables that are expected to influence Norway spruce growth in coming decades most strongly include increases in temperatures and changes in precipitation patterns (Lévesque et al., 2013; van der Maaten-Theunissen et al., 2013). Hence, both variables were included in the developed models, which will allow us to study Norway spruce responses to climatic changes. The temperature sum (TS) variable has been used as a driver in models of height growth and mortality of Norway spruce in northern Sweden (Kroon and Rosvall, 2004), and Scots pine in northern Sweden and Finland (Berlin et al., 2016). In addition, Mason et al. (2018) found that use of a cumulative modified radiation sum significantly improved site index prediction for Norway spruce in Sweden. Precipitation is also well-recognised as a key climatic factor for Norway spruce growth (Munster-Swendsen, 1987; Rybníček et al., 2012). However, the effect of precipitation has not been previously considered in Norway spruce transfer modelling.

4.3. Selection of transfer variable

The environmental variable selected for indication of the FRM transfer (the difference in a daylength on the 205th Julian day of the year) differed from the variables used in other studies concerning estimation of transfer limits. In other studies, the transfer distance was commonly represented by a difference in latitude (Berlin et al., 2016), difference in temperature sum (Beuker et al., 1998; Gömöry et al., 2012; O'Neill et al., 2014) or transformations of latitude and longitude. The effect of latitudinal transfer is supposed to be strengthened by testing, and ultimately the inclusion of influential interaction terms should ensure the flexibility of the functions over different latitudes, according to Berlin et al. (2016). However, the differences in optimal transfer between mild southern sites and harsh northern sites were small (ca. 0.3) when difference in latitude was used as the transfer variable. So, the predicted optimal transfers for northern harsh sites were almost as long as for the southern mild sites, which conflicts with practical experience and several previous studies of material in Sweden and Norway (Kroon and Rosvall, 2004; Persson and Persson, 1992; Skrøppa and Steffenrem 2019; Skrøppa and Steffenrem 2020). For example, Kroon and Rosvall (2004) found that local material provided outstanding performance at the harsh sites in northern Sweden, while for northern coastal sites with a slightly milder climate, the optimal latitudinal transfer for height was 4.3. The height models based on latitudinal transfers (Δ LAT) developed in this study indicate that long northward transfers of 5.7–5.8 would be optimal, even for target sites in northern Fennoscandia. The lack of a shortening of the optimal transfer distance with increasing latitude in this study appears to be associated with the essentially linear relationship between latitude and distances in the north–south direction.

As an alternative to latitude, solar daylength (and thus night length) has highly non-linear relationships with north–south distances and latitude. Thus, daylength cannot be properly represented by latitude and its quadratic transformation in URF models. When the difference in daylength between locations of a field trial and origin of a genetic entry was used as the transfer variable instead of latitude, the non-linear dynamic properties of the model were improved as well as the overall statistical fit. The predicted optimal transfer distances differed significantly between southern milder sites (4.4–4.8 northward transfer) and northern harsher sites (2.7–3.4 northward transfer), as expected from practice. The night length also has proven importance for the timing of several adaptive traits related to growth and performance of Norway spruce, particularly growth cessation and bud set in late summer, in controlled experimental conditions (Dormling, 1973; Dormling et al., 1968; Heide, 1974). The seedlings of provenances originating from central Europe cease growth and develop buds when the night length reaches 6–7 h in late summer, while provenances from northern Sweden reach the same developmental stage when night lengths are 2–3 h. There is also a coastal-continental trend as Norwegian provenances at the same latitude as Northern Sweden need a 4–5-hour night to reach the same developmental stage (Ekberg, et al. 1979, Heide 1974, Kohmann 1996). Thus, to reach 21 h daylength at latitude 69° the upper geographic limit of the dataset used in this study, a Julian day around day 211 (30th of July) should be reasonable. For the final models, Julian day 205 (24 July) was selected as it provided the highest significance over the tested variables and fit statistics used.

4.4. Model performance

The developed transfer models provide predictions for the performance of both domestic seed sources and imported European provenances in the three Fennoscandic countries. Such functions are essential to fully exploit the existing genetic diversity in operational seed orchards without developing a separate function for each of the material types. Most of the seed orchards in Norway, Finland and northern Sweden have been established with domestic Norway spruce trees selected in natural forests. However, in southern and central Sweden most of the seed-orchards that have been developed from the ongoing breeding program contain material with a mixture of genetic origins as there has been a long-term tradition of importing seeds (Hannerz and Almäng, 1997; Myking et al., 2016). The plus-trees were selected in operational plantations with little or no prior knowledge of their genetic backgrounds. More recently, however, genomic analysis of the Swedish Norway spruce breeding population has revealed that it has high genetic diversity with individuals from seven population clusters originating from various regions throughout Europe (Chen et al., 2019).

For height, the final model developed in this study followed earlier observed patterns, indicating that height increases in response to a northward transfer in Sweden and this effect decreases with increasing latitude of the planting site (Heikinheimo, 1949; Kroon and Rosvall, 2004; Oleksyn et al., 2001; Persson and Persson, 1992). The transfer patterns in these studies were mostly presumed as they were based on analysis of significantly less material (Persson and Persson, 1992) or covered a limited geographical area (Kroon and Rosvall, 2004). The statistically best model developed in the study presented here fully agrees with these indications.

The material transferred from optimal locations to representative sites performed ca. 3 % better in terms of height growth than local material in southern, milder sites in all countries. As height and diameter growth are usually well correlated, due to allometric relations, as described for example by Hallingbäck et al. (2010), this gain could be extrapolated in all three dimensions, which would then correspond to a gain in volume growth of ~ 9 %. Although speculative, such an extrapolation roughly agrees with the 6–10 % gain in volume per hectare over rotations that has been commonly used as an average effect of FRM transfer of non-local (Eastern European) seed sources to Sweden

(Jansson et al., 2013; Rosvall et al., 2001). It should also be mentioned that the height model predicts losses in height with southward transfer of Norway spruce (of ca. 3 % to mild sites and ca. 7 % to harsh sites) that should be treated with care in development of FRM guidelines.

The tested survival rate models had poor predictive ability and cannot be recommended for practical use. The raw data showed that survival rates were high at sites in the southern parts of all countries and most of the northern sites. Moreover, the few recorded cases of high mortality were likely due to other factors, not with provenance transfer and adaptation *per se* (pine-weevil, drought, competition with weeds, poor planting positions, or waterlogging). With the available data it was not possible to reliably associate any mortality with a specific material transfer to an experimental site. This is consistent with findings and claims that Norway spruce has highly plastic responses to changes in various environmental factors and indicates that future climate change will not necessarily cause Norway spruce mortality in the regeneration phase but rather later when the stands become fully closed and ready for other management treatments, such as thinnings (Berlin et al. 2015, Liepe, 2022).

4.5. Comparisons with current transfer regulations

The optimal transfers predicted by the height model deviate from the current recommendations for FRM transfer in Norway and Finland but are largely in line with available recommendations for Sweden. In Sweden, transfers of material from Baltic countries, Belarus and western Russia have been recommended up to latitude 62N (Regeringskansliet, 1979). However, the origin of transferred material is limited to no further north than latitude 56N. Transfers from the central Belarus area (e.g., the Minsk and Vitebsk region, latitude ~ 54N) that have been more productive than local southern Swedish provenances are allowed for sites located south of latitude 60N. South of this latitude, transfers up to 8° of latitude are allowed with consideration of changes of local elevation. The optimum transfer for a mild southern site in southern Sweden is ca. 4.5 according to the developed height model, which partly confirms that the previously developed recommendations have not caused maladaptation in the Swedish Norway spruce stands and rather supported their high productivity. However, extreme transfer distances need to be more carefully considered.

According to regulations for reforestation within the natural range of Norway spruce in Norway, a transfer of up to 200 km is allowed. This corresponds to ca. 2° latitudinal transfer and there is practically no use of continental provenances within the natural range of Norway spruce today. According to the new model presented here, production could be potentially increased in the mild southern sites by using provenances from Eastern regions of Europe, central Poland, and central Germany. However, such long transfers have only been recommended into the oceanic climatic region on the west coast, as summarized by Øyen (2007). In Eastern Norway, the experiences with the adaptation and stem quality of provenances from central Europe have been negative (Skrøppa et al. 1993), while improved FRM selected from provenances of Eastern European origin has shown very promising development (Skrøppa and Steffenrem 2016). According to regulations for Finland, transfers from Estonia are allowed to the southernmost part of the country, approximately to 61°N. This transfer limit is quite short compared with the Swedish recommendations and is due to observations of spring frost damage in Finland.

The lack of consistency between the developed functions and national recommendations is at least partially due to a more restrictive management practice to reduce late-summer frost risk and drought occurrence, that were not explicitly considered in development of the models as a landscape coverage of data does not exist. In addition, it is challenging to include such phenomena in predictive models because of their stochastic nature (Seidel et al., 2019).

4.6. Future challenges

The presented height model was developed for unimproved seed lots transferred to and within Fennoscandia. Formal validation procedure of the model on the improved material currently used in all the concerned countries is needed. Hayatgheibi et al. (2020) found that transfer models for height and survival rate of Scots pine in northern Sweden and Finland can predict these parameters very well for improved genetic material in 1.5 generation Scots pine seed orchards, i.e. orchards with only selected and tested plus trees. However, there are considerable differences in the biology of Norway spruce and Scots pine e.g., light demand, suitability of different soil types, growth rhythm and damaging agents. Therefore, our model should be subjected to similar validation procedures before they are implemented for improved FRM.

Spring frost is known to have negative effects on the growth and development of Norway spruce (Langvall et al. 2001; Langvall, 2011; Lundströmer, 2021; Svystun et al., 2021; Skråppa and Steffenrem 2016). Some frost indicators in the original 16 climatic variables (Supplementary Table 1) were tested but none of them were significant. There are predictions that frequencies of frosts in spring will decrease as average temperatures are predicted to increase, but the increases in temperature might also cause the trees to initiate growth earlier in the spring. If so, the trees may be more vulnerable to damage by frosts, which are more likely to occur at earlier dates in the year. The potential scale of effects of frost damage on height performance of the analysed material is also unknown, and such effects could not have been explicitly included in the modelling presented here. However, there are evidence that Norway spruce populations from warmer origins are flushing later than local or more northern materials (Beuker, 1994; Skråppa and Steffenrem, 2019, 2020; Solvin and Steffenrem, 2019; Svystun et al., 2021). Nevertheless, it is known that frost damage impairs the growth and quality of the plants, rather than killing them (Langvall et al. 2001; Svystun et al., 2021), thus risks associated with frost have been considered in further recommendations in each of the countries.

Factors other than frost affecting Norway spruce growth are much more poorly recognised. Fungal diseases related to transfer of plant material have been threatening Scots pine (Uotila, 1985) and broadleaf species, e.g., European ash (*Fraxinus excelsior*). In addition, Norway spruce populations originating from areas that are appropriate and recommended sources of material for southern Sweden (Belarus and Ukraine) has been regarded as susceptible to fungal attacks in Finland (Napola, 2014). However, no evidence of increases in fungal threats due to transfer has been observed for Norway spruce in either Sweden or Norway.

There are observations indicating that some Norway spruce provenances might be more prone to stem cracks, spike knot occurrence. However, there is no systematic evidence about genetic background of the problem and major setbacks associated with transfer (Myking et al. 2016). The provenances tested in Fennoscandia have not been distinguished in respect to such damage.

Extensive drought periods during the vegetation period have affected Fennoscandia several times in the last five years, causing substantial mortality in young Norway spruce plantations and impairing the vitality of older stands, thereby fostering outbreaks of the bark beetle (*Ips typographus*). Due to climate change, such calamitous events are predicted to occur more often in this region (IPCC 2021). The developed height model will not be able to account for effects of such abrupt events as it has been based on long-term observations of climatic variables and consider just first half of a rotation for a typical Norway spruce stand in Fennoscandia which is usually between 60 and 100 years long. Thus, additional constraints for sites that are particularly prone to drought events must be implemented in the practical recommendations and decision support systems.

Careful analysis of the prediction uncertainties under different climate scenarios is necessary before implementation of the model in practice. For Scots pine models (Berlin et al., 2016), Hallingbäck et al.

(2021) developed a framework that can be used to analyse effects of climate change and quantify uncertainties that will be helpful for development of robust recommendations for Norway spruce in Fennoscandia.

5. Conclusions

The developed transfer functions are based on large amounts of diverse and widely planted empirical material and provide the best currently possible predictions of height for all Norway spruce provenances in Fennoscandia. They provide good foundations for formulation of common deployment recommendations in the region, which might ultimately lead to development of a common market for seeds and seedlings. The developed functions can differentiate provenances only in respect to their growth. Other aspects related for example to flushing time and frost risk, growth rhythm and quality properties need to be additionally considered.

Measurement age, annual temperature sum, precipitation during the vegetation period, genetic material transfer and altitude were identified as the most important variables influencing height performance of young Norway spruce in Fennoscandia. It should be noted that the analysed stands' were much younger than practical rotation ages of Norway spruce stands, so the effects of transfer on stand productivity at other ages warrant attention, although height is known to be a good indicator of stand productivity.

The transfer variable based on the difference in daylength between locations of planting sites and origins of planted material provided the best representation of the growth of the transferred genetic material, both statistically and biologically. The non-linear nature of daylength as a transfer variable is consistent with the reduction in optimal transfer length with increasing latitude that has been frequently observed in practice, and patterns observed in previous physiological studies.

The results indicate that long northward transfers to southern milder sites in Fennoscandia can have positive effects on height growth of Norway spruce, while for harsher northern sites, the optimum northward transfer is shorter. Northward transfers are predicted to provide greater height growth than use of local material but the predicted gain in height growth was relatively small (ca. 3 %). Findings and observations in other studies, e.g., the outstanding performance of certain Belarusian provenances in southern Sweden, must be considered for development of practical recommendations.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: All authors reports financial support was provided by European Union.

Data availability

The data that has been used is confidential.

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Appendix A. Supplementary data

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