Understanding the low-temperature limitations to forest growth through calibration of a forest dynamics model with tree-ring data

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Abstract

The sensitivity of altitudinal and latitudinal tree-line ecotones to climate change, particularly that of temperature, has received much attention. To improve our understanding of the factors affecting tree-line position, we used the spatially explicit dynamic forest model TreeMig. Although well-suited because of its landscape dynamics functions, TreeMig features a parabolic temperature growth response curve, which has recently been questioned, and the species parameters are not specifically calibrated for cold temperatures.

Our main goals were to improve the theoretical basis of the temperature growth response curve in the model and develop a method for deriving that curve’s parameters from tree-ring data. We replaced the parabola with an asymptotic curve, calibrated for the main species at the subalpine (Swiss Alps: Pinus cembra, Larix decidua, Picea abies) and boreal (Fennoscandia: Pinus sylvestris, Betula pubescens, P. abies) tree-lines.

After fitting new parameters, the growth curve matched observed tree-ring widths better. For the subalpine species, the minimum degree-day sum allowing growth (kDDMin) was lowered by around 100 degree-days; in the case of Larix, the maximum potential ring-width was increased to 5.19 mm. At the boreal tree-line, the kDDMin for P. sylvestris was lowered by 210 degree-days and its maximum ring-width increased to 2.943 mm; for Betula (new in the model) kDDMin was set to 325 degree-days and the maximum ring-width to 2.51 mm; the values from the only boreal sample site for Picea were similar to the subalpine ones, so the same parameters were used. However, adjusting the growth response alone did not improve the model’s output concerning species’ distributions and their relative importance at tree-line. Minimum winter temperature (MinWiT, mean of the coldest winter month), which controls seedling establishment in TreeMig, proved more important for determining distribution. Picea, P. sylvestris and Betula did not previously have minimum winter temperature limits, so these values were set to the 95th percentile of each species’ coldest MinWiT site (respectively −7, −11, −13).

In a case study for the Alps, the original and newly calibrated versions of TreeMig were compared with biomass data from the National Forest Inventory (NFI). Both models gave similar, reasonably realistic results.

In conclusion, this method of deriving temperature responses from tree-rings works well. However, regeneration and its underlying factors seem more important for controlling species’ distributions than previously thought. More research on regeneration ecology, especially at the upper limit of forests, is needed to improve predictions of tree-line responses to climate change further.

Keywords: TreeMig; Degree-day sum; Gap model; Gap dynamics; Minimum winter temperature; Tree-line; Growth; Establishment; Regeneration

1. Introduction

When analysing the effects of climate change, transition zones, such as the subalpine or boreal tree-line ecotones (as defined by Körner and Paulsen, 2004), are of particular interest because their fine balance, with species living at the extreme limit of their tolerance, makes them more sensitive to change (Theurillat and Guisan, 2001; Kullman, 2005). Furthermore, climate-induced timber-line shifts can significantly influence the global carbon budget (Solomon and Kirilenko, 1997; Neilson et al., 2005). Although other factors, such as wind, may also play a significant role (Esper and Schweingruber, 2004), temperature is believed to be the most important factor governing forest growth at tree-line (Körner, 1998; Jobbágy and
Dynamic forest gap models are often used to study the effects of climate change on the species composition and structure of forests under a range of change scenarios. In the original JABOWA forest gap model (Botkin et al., 1972) and many of its descendants, the temperature growth response curve (yearly diameter increment versus degree-day sum) has a parabolic shape. In some of these early models, the growth decline at higher temperatures (right-hand side of the parabola) can be interpreted as an indirect representation of drought, which is not modelled separately. However, the parabolic degree-day growth response curve was retained in many subsequent models, despite the introduction of drought as a separate variable. Although the shape of the curve may have little effect on species’ distributions under current climate, it can cause artificial die-back effects when the model is run under changing climate conditions (Bugmann, 2001). Several approaches have been used to replace the parabolic growth response curve by one which reflects the effect of temperature alone, such as an asymptotic function (e.g. Bugmann and Solomon, 2000; Lexer and Höninger, 2001).

Apart from the shape of the curve, the other prerequisite for a realistic model is the set of parameters defining the curve’s boundaries (minimum, asymptote) for each species. In most gap models, these parameters were estimated by matching species’ distribution maps (which represent the realised niche) to isotherm maps (e.g. Botkin et al., 1972) or taken from literature sources (e.g. Kienast, 1987; Bugmann, 1994), which may also contain values derived from distribution maps (e.g. Prentice and Helmisaaari, 1991). The difficulty lies in finding the parameters for potential, rather than realised growth: model curves aim to express the former, i.e. growth along temperature or other gradients with no reduction due to competition and shading (which is modelled separately in gap models). However, potential growth is rarely observed in the field and experiments under controlled conditions are difficult with large, long-lived species such as trees. Loehle and LeBlanc (1996) suggest using dendroclimatic analysis to improve the climate response functions in forest simulation models. Although tree-rings are an expression of realised rather than potential growth, if one factor (in this case temperature) primarily influences the response, potential growth can be estimated provided enough data is available so that the rings representing the highest observed growth rates, found under a combination of no shade and the best site conditions (nutrients, water), can be filtered out.

Another aspect of forest response to temperature is the establishment and survival of seedlings. There have been studies of the effects of temperature on regeneration at tree-line, for instance in the mountains of North America (Lloyd and Graumlich, 1997; Germino et al., 2002), the Southern Urals (Moiseev et al., 2004) or Scandinavia (Kullman, 1986, 2005), but only a few in the Alps (Motta and Nola, 2001). The values for the minimum winter temperature allowing recruitment in a species vary greatly amongst authors (e.g. Kienast, 1987; Prentice and Helmisaaari, 1991; Bugmann, 1994). The minimum winter temperature is the limit below which actual damage is caused to the trees and it can be represented by the coldest month’s mean temperature, as a surrogate for the absolute minimum temperature (Sykes et al., 1996). On the other hand, some species have winter chilling requirements. These are mostly related to the length of the chilling season, although the maximum temperature of the coldest month has also been used as a measure of winter chilling. A longer chilling season is thought to protect species with a low tolerance to late frost by delaying bud-burst, in deciduous species, chilling may also be necessary to trigger abscission (Sykes et al., 1996).

The spatially explicit dynamic forest model TreeMig (Lischke, 2005; Lischke et al., 2006) is well adapted to simulating the effects of climate change, as it includes processes for landscape dynamics (e.g. seed production and dispersal) as well as the usual climate-dependent forest population processes (e.g. growth, competition, mortality). It is also designed to be flexible and its parameters can be adapted for different applications. TreeMig is derived from the distribution based model DisCForM (Lischke et al., 1998), itself scaled-up from an early version of the gap model ForClim (Bugmann, 1994, 1996), and uses the traditional parabolic growth response curve with ForClim’s parameter set. The impact of low temperatures on forests is also included as a minimum winter temperature limit on regeneration in the model, but TreeMig, like most of its gap model predecessors, does not address the issue of winter chilling requirements (Price et al., 2001).

In their review of the suitability of forest models for assessing the effects of climate change, Loehle and LeBlanc (1996) concluded that dynamic forest models were the best solution, provided some improvements were made. These included realistic reproduction and dispersal functions, based on the trees present in the model, and competition for light, all of which have been addressed in the TreeMig model (Lischke and Löfler, 2006). The other aspects requiring improvement were the growth-response functions, in particular the replacement of the temperature–response parabola by a curve representing the fundamental niche (Hutchinson, 1957) of each species, and mortality functions, including disturbance regimes.

The growth parameters in ForClim, also used in TreeMig, were originally derived for Central European forests in general (Bugmann, 1994), but not specifically adapted to studying the sensitive tree-line ecotone under climate change. The aim of the present study was to improve our understanding of tree growth and species’ distributions in response to temperature, therefore providing a better basis for the formulation and parameterization of the TreeMig model. In particular, we wanted to (1) take into account criticisms of the shape of the temperature-related growth function (Loehle and LeBlanc, 1996; Bugmann and Solomon, 2000), (2) capture the physiological limitations to growth for the main tree-line species through the use of
tree-ring data (Loehle and LeBlanc, 1996), (3) calibrate TreeMig for Alpine and Fennoscandian tree-line species and (4) evaluate the new model in a case study in the Alps.

2. Material and methods

To calibrate the temperature response in TreeMig, we used dendrochronological (ring-width) data for the three main subalpine tree-line species at locations throughout the Swiss Alps, collected from various literature sources (Fig. 1 and Table 1). Preference was given to sites (or groups of neighbouring sites) for which data had been collected at different altitudes, although some isolated sites were included to increase the range of altitudes and climatic regions in the dataset. A gradient was necessary to fit the curve, as we did not know in advance how far the influence of temperature would extend. However, none of our sites were situated in the lowlands (Table 1; minimum = 1200 m) and the shape of response curve used was designed to minimise the influence of other factors, which take over when temperatures become non-limiting. The species were: European larch (Larix decidua), Norway spruce (Picea abies) and Swiss stone pine (Pinus cembra).

Similarly, the temperature–response curves of Scots pine (Pinus sylvestris), Downy birch (Betula pubescens) and Norway spruce (P. abies) were calibrated using dendrochronological data from the boreal tree-line in Fennoscandia, with sites all situated above the arctic circle (Table 1). A separate calibration was necessary, as the species compositions of both tree-lines differ: L. decidua and P. cembra do not occur in Fennoscandia, while P. sylvestris and, to a lesser extent, B. pubescens are present in the Alps but do not form the tree-line. Even when a species is present in both regions, like P. abies, a separate calibration may be necessary if different ecotypes were involved.

2.1. Climate data processing

The climate data for the different tree-ring collection sites was derived from mapping daily minimum and maximum temperatures ($T_{\text{min}}, T_{\text{max}}$), using the DAYMET simulation model (Thornton et al., 1997), which was specifically developed for complex terrain such as mountain ranges. In this model, all the stations in a defined neighbourhood contribute to predict the local temperature through a distance-weighted regression which follows a Gaussian curve. For Switzerland, the available maps cover a 38-year time-span

Fig. 1. Location of the tree-ring-width data sites in the Alps. The symbols indicate the species sampled at each site. The numbers refer to those in Table 1, which contains information on the sites and datasets used. The black square shows the extent of the case study area in the Upper Engadine (Switzerland).
Mean monthly temperatures \( T_{\text{mm}} \) for each site were calculated from the daily minimum and maximum values (Eq. (1), with \( n \) the number of days in the month in question). The minimum winter temperature (MinWiT) for each year \( y \) was then calculated as the lowest of the mean monthly temperatures for the three winter months (Eq. (2)).

\[
T_{\text{mm}} = \frac{\sum (T_{\text{min}} + T_{\text{max}})/2}{n}
\]

\[
\text{MinWiT}_y = \min(T_{\text{mm}, \text{Dec}}, T_{\text{mm}, \text{Jan}}, T_{\text{mm}, \text{Feb}})
\]

The methods for calculating degree-day sum and minimum winter temperature follow those described by Bugmann (1994) for the ForClim model, which are also used in TreeMig. However, we applied the sine-wave method for degree-day sum directly to daily temperatures, rather than use monthly values and an empirical correction factor, by definition only applicable to the region for which it was derived, which might diminish the portability of the model.

### 2.2. Growth curves and parameter adjustment

First, we examined the calibration of the temperature constraints on tree growth, particularly near its cold-induced limit. To achieve this, for each site and species (Table 1), all the tree-ring-width values falling within the time-span of the climate data were assigned their corresponding degree-day sum. The ring-widths were then sorted according to this sum and grouped into 25 degree-day “windows”. In each window, we calculated the mean of the 10% largest ring-widths. As all the ring-widths for a given degree-day sum value have the same temperature constraint, it can be supposed that those showing sub-optimal growth are the result of additional constraints (e.g. shade, drought), whereas the largest ring-widths are constrained by temperature only. Fig. 2 shows an example for \( P. \) abies at site no. 9 (Grindelwald S2); the mean values (■) correspond to one data series on that species’ plot (Fig. 3b). This procedure was repeated for each of the sites and species in Table 1, to obtain the temperature-related potential growth of each site/species combination. The reason for using the 10% largest ring-widths, rather than the single largest value, is that individual trees have inherently different growth potentials and the overall maximum ring-width only reflects the potential of the fittest tree. Additionally, it buffers the effect of local temperature peculiarities, which are not captured by the climate maps we used and could lead to over-optimistic results if the largest ring-widths alone were taken into consideration. A percentage of the largest values should therefore give a more realistic estimate of the average growth potential in a tree population.

The potential growth values at all the sites for one species were plotted together (Fig. 3). The original parabolic growth curve of TreeMig and the asymptotic curve (Eq. (3)), proposed by Bugmann and Solomon (2000) and used in the model ForClim V2.9, were also plotted.

\[
g_{\text{DDGF}} = \max(1 - \exp((k_{\text{DDMin}} - u_{\text{DD}}) \cdot a), 0)
\]
According to this equation, the growth response to degree-day sum (gDDGFs) is a function of the minimum degree-day sum allowing growth for species \(s\) (kDDMin\(_s\)), the current degree-day sum (uDD) and a parameter describing the slope of the curve \(a\). This last was determined so that growth was equal to 75% of its optimum when uDD = kDDMin\(_s\) + 1000 for any species (Bugmann and Solomon, 2000). The asymptotic curve was then adjusted according to the rules described below in order to fit the dendrochronological data. The aim was to draw an envelope through the highest values (sites with the best conditions) in each window, so as to capture the temperature-related response. The first, general adjustment was to make the curve steeper by modifying the slope parameter \(a\) so that 75% of the maximum growth was reached when the degree-day sum was 250 degree-days (instead of 1000) above the minimum for species’s’ (kDDMin\(_s\)). Different values were tested visually and 250 degree-days gave good results for all the species in this study, but species-dependent values could be used for other species. The species parameters (kDDMin and maximum ring-width) were then adjusted individually for each species. The minimum degree-day sum was set to the lower limit of the coldest 25 degree-day sum window (in other words, the lowest degree-day sum value in the data set was rounded down to the nearest 25 degree-days). The maximum ring-width was set to the highest mean of 10% maximum ring-width value for that species, unless it was lower than the original model parameter, in which case the latter was retained. This was done on the assumption that if the highest value in the field data is lower than the model parameter, the field data sample might simply have missed the highest potential value, whereas if the field data yields a higher maximum than the model, then the real potential is at least as high as the field data. Maximum ring-width is not directly a parameter in the model, but is determined by the species’ growth factor (kGs) via the model’s growth equation (Eq. (4); Bugmann, 1994, 1996; Lischke et al., 2006), so it was in fact this last factor which was adjusted.

\[
\frac{\Delta D}{\Delta t} = \frac{k_G D (1 - (H/H_m))}{274 + (H_m - 137)((6D/D_m) - (4D^2/D_m^2))} \cdot f(e)
\]  

(4)

where \(D\) and \(H\) are the current diameter and height, respectively, \(D_m\) and \(H_m\) the maximum diameter and height for the species, \(f(e)\) a modifying function of environmental factors such as temperature, light, etc., the constant value of 137 represents “breast height” (in centimetres) and is also the minimum height for an “adult” tree in TreeMig.

2.3. Minimum winter temperature for seedling establishment

Next, we examined the temperature effect on seedling establishment. In the model, the latter is constrained by minimum winter temperature, in addition to degree-day sum. The tree chronologies used did not indicate birth years (or even pith age, as there was no guarantee it had been hit every time) and birth numbers were also not available for the same reason and because of selective sampling. To determine the minimum winter temperature allowing seedling establishment (kWIT\(_s\)), the minimum winter temperature (MinWIT) values for all years at each of the tree-ring data collection sites were used in
conjunction with the knowledge that regeneration had been possible at these sites, at least in some years. The coldest site for each species was selected and the kWiT was estimated as the 95th percentile of MinWiT for that site, rounded up to the next degree. This means that regeneration is assumed to occur on average once every 20 years at the most unfavourable site. Although 20 years is an arbitrary value, it meant that the new kWiTs value matched the existing parameters for Larch and Swiss Stone Pine. The sites used were Grindelwald S2 (P. abies) and Tschainas (L. decidua and P. cembra). The latter is an altitudinal transect and the highest plot (2410 m) was used.

2.4. Parameters for the boreal tree-line

The same methods were used to determine the model parameters for the three main boreal tree-line species in Finland and Sweden, namely Scots pine (P. sylvestris), Downy birch (B. pubescens) and Norway spruce (P. abies). Fewer chronologies were available, especially for birch and spruce (Table 1). The climate maps, also derived using the DAYMET simulation model (Thornton et al., 1997), cover a time-span of 30 years (1973–2002) and have a 600 m resolution (grid of square cells). The methods for calculating the degree-day sums and minimum winter temperatures were the same as for the Alps, as were the
criteria used to determine the species parameters (kWiT and kG) for *P. sylvestris* and *B. pubescens*. The sites used for calibrating kWiT were Muonio and Kevo, respectively. In the case of *P. abies*, for which we only had one site, the resulting potential curve was added to the subalpine sites’ plot, as a way of checking whether the subalpine calibration might be used.

Downy birch was a new species in the model and the other parameters were derived from various sources in the literature, according to the method described by Bugmann (1994) for the subalpine species (for details of the Downy birch parameters and literature used, see Supplementary data).

2.5. Model setup and evaluation—case study Alps

Comparing both the original and the new growth curves graphically against tree-ring data provides some insight into their ability to model tree growth realistically. To investigate the effect of the changes in the parameters on the model output further, we used a case study in the Alps. The test area was a 100 × 100 cell raster of 250 m resolution, situated in the Upper Engadine valley, Switzerland (Fig. 1). This was chosen because it was large enough to cover a range of different conditions (altitude, exposition), but at the same time offered a good compromise between resolution and computing time. Altitudes in the grid range from 1369 to 3723 m, but the lowest points in the Engadine valley itself are around 1630 m, while the lowest points in the grid are situated in a valley to the north-west, which belongs to a different catchment area. The bottom of the Engadine valley is only sparsely covered by forests, as most of it is either built-up, lakes or agricultural land. The forests are found mainly on the lower to middle mountain sides. Above the forest there is herbaceous vegetation and higher up bare rock, snow and ice.

The original version of TreeMig and the new one were run on that grid for 500 years under current climate conditions. The climate input data (degree-day sum, minimum winter temperature and drought stress) was generated, using the algorithms of ForClim-E (Bugmann, 1994, 1996; Lischke et al., 2006), from the DAYMET climate maps (monthly mean temperature and precipitation sum) and the bucket size found in the Swiss soil suitability map (SFSO, 1992). The bucket size is the difference between field capacity and the permanent wilting point, expressed as centimetres of water in the rooting zone. For the new version of TreeMig, additional maps of daily minimum and maximum temperatures were used and the ForClim-E algorithms modified to calculate the degree-day sum with Allen (1976) sine-wave method. The algorithms for minimum winter temperature and drought stress were unchanged.

In both cases (original and new TreeMig), trees were only allowed to grow on cells classified as “forest”, as defined by Gellrich et al. (in press). This rather broad definition includes scrubland, bushes/shrubs and groups of trees, as well as the various closed and open forest categories from the Swiss Area Statistics (SFSO, 2001). The tree-line ecotone, where trees are increasingly sparse and small, mostly falls into either open forest or one of these other categories, which are not strictly forests but contain woody vegetation. Seeds of all species were assumed to be present in the soil for the first 10 years (spin-up), after which normal forest dynamics, including seed production and dispersal, were allowed to run, i.e. forest composition was determined by growth, competition, regeneration of species within each simulated cell and migration between cells. The model output after 300 years, which showed no major differences with the 500-year output, was used to represent present-time forest, because most forests in Switzerland are managed and rarely exceed 300 years of age. The model output was expressed as biomass (total for all height classes) per species and grid cell. This was compared with the data from the first Swiss National Forest Inventory (NFI; Bachofen et al., 1988). As there are far fewer NFI plots than forest cells in the model test area, NFI plots from the entire Engadine valley were used, provided they were within the same altitudinal range as the study area (Table 2). This re-establishes the balance somewhat and is justified as the abiotic conditions (climate, soil, etc.) are similar throughout the valley. Only the model results from within the Engadine valley itself were used and the output from the small area situated in a different valley was excluded because of the possibility of different climatic influences.

The NFI data and the output from the two versions of TreeMig were plotted individually to show the respective proportions of larch, spruce, pine and other species (grouped) within 100 m altitudinal bands. This is necessary because model simulations give average responses to stochastic effects, whereas forest inventory data is subject to individual stochastic alterations. The results per species and altitudinal band from the two model runs were also plotted against the NFI data.

3. Results

3.1. Growth curves and parameter adjustment

The potential growth values calculated from the tree chronologies show considerable differences between the sites for all species (Fig. 3). The only exception is *B. pubescens*, for which all three sites show similar growth patterns (Fig. 3e). In the case of *P. abies* (Fig. 3b), there are large differences

Table 2
Number of National Forest Inventory plots and TreeMig forest cells per 100 m altitudinal band

<table>
<thead>
<tr>
<th>Altitude</th>
<th>1600</th>
<th>1700</th>
<th>1800</th>
<th>1900</th>
<th>2000</th>
<th>2100</th>
<th>2200</th>
<th>2300</th>
<th>2400</th>
<th>2500</th>
</tr>
</thead>
<tbody>
<tr>
<td>NFI plots</td>
<td>22</td>
<td>33</td>
<td>46</td>
<td>53</td>
<td>39</td>
<td>15</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>TM forest cells</td>
<td>12</td>
<td>133</td>
<td>302</td>
<td>277</td>
<td>253</td>
<td>203</td>
<td>113</td>
<td>32</td>
<td>7</td>
<td>2</td>
</tr>
</tbody>
</table>

The NFI plots are located in the whole of the Engadine valley, whereas the TreeMig cells come from the study area only.
between the subalpine sites; however, the single boreal site (represented by large black squares) does not stand out, although it must be noted that it contains only a few data points.

Neither the traditionally used parabola nor the ForClim V2.9 asymptotic curve captured the observed growth very well. In fact, although conceptually an improvement, the latter was systematically too flat, whereas the slope of the parabola was adequate in some cases, for example, *P. cembra* (Fig. 3c). The kDDMin value (lowest annual degree-day sum allowing growth) had to be reduced for all three species (i.e. trees grow at colder temperatures than the original parameters suggest). The difference was slightly larger for *Larix* and *P. cembra* than for *P. abies*, but the biggest change occurred for *P. sylvestris* (boreal tree-line). The maximum ring-width (asymptote of the new function) was set to the largest value across all sites for larch, Scots pine and birch by modifying the growth parameter (kG). The original model maximum was kept for spruce and Swiss stone pine, as in both cases it was higher than the largest measured value in our data.

The new minimum degree-day sum and growth parameters for all five species are given alongside the original values in Table 3 (kDDMin and kG). For *B. pubescens*, only the new values are given as it was not part of the original set of species in the model. The growth rates are linked to the maximum ring-widths (Fig. 3) by means of Eq. (4), so the relation between the two depends on the species’ maximum height and diameter.

### 3.2. Minimum winter temperature for seedling establishment

The summary statistics and 95th percentile of the minimum winter temperature at the coldest site for each species are shown in Table 4, along with the parameter value derived from the 95th percentile (see also Table 3; kWiT). In the two cases where there was a winter temperature limit to regeneration in the original model (*L. decidua* and *P. cembra*), the new parameters are equal to the old ones. *P. abies* and *P. sylvestris* have been given minimum winter temperature limits, instead of the “no limit” value (−999).

#### 3.3. Model evaluation—case study Alps

Comparing the tree biomass in the TreeMig simulations with that in the NFI data shows that both model versions tend to err on the high side (Fig. 4a). This is mostly due to the over-optimistic representation of spruce (Fig. 4c), although this is marginally better in the new version. At altitudes up to 2000 m, the new calibration improves the results for larch (Fig. 4b). At higher altitudes however, the new TreeMig version clearly over-estimates *Larix’s* biomass, although the lack of NFI plots above 2300 m makes comparison difficult. The third species shown is *P. cembra* (Fig. 4d), for which both models underestimate the biomass at lower altitudes. In the highest band where NFI data exists (2200 m), the new model gives good results and above that it continues the trend (increasing biomass with altitude) before evening out and decreasing sharply at 2500 m. The original TreeMig version results in a similar pattern but with larger biomass values around 2200–2400 m, which are possibly a bit too high.

Finally, several other species are present in smaller quantities in the NFI data and the TreeMig simulation results. In the forest inventory plots, we find mainly *P. sylvestris* (up to 2000 m) and *Pinus mugo* ssp. *uncinata* (above 1600 m). The original model results in very small quantities of these two species, along with other species (e.g. *Alnus incana, Populus tremula, Sorbus aucuparia*) also found as traces (<1 t/ha on average) in the NFI data. The new version of the model gives better results for *P. sylvestris*, although it is still under-represented on average. The results of the two models differ only marginally for *P. cembra* and the other species.

### Table 3

Minimum degree-day sum (kDDMin), growth factor (kG, with corresponding maximum ring-width, maxRW, in mm) and minimum winter temperature (kWiT, in °C) parameters for three Alpine and two boreal tree-line species in the original and new versions of TreeMig

<table>
<thead>
<tr>
<th>Species</th>
<th>Original kDDMin</th>
<th>kG (maxRW)</th>
<th>kWiT</th>
<th>New kDDMin</th>
<th>kG (maxRW)</th>
<th>kWiT</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Larix decidua</em></td>
<td>323</td>
<td>170 (4.029)</td>
<td>−11</td>
<td>225</td>
<td>219 (5.190)</td>
<td>−11</td>
</tr>
<tr>
<td><em>Picea abies</em></td>
<td>385</td>
<td>171 (4.178)</td>
<td>−999</td>
<td>300</td>
<td>171 (4.178)</td>
<td>−7</td>
</tr>
<tr>
<td><em>Pinus cembra</em></td>
<td>323</td>
<td>115 (4.803)</td>
<td>−11</td>
<td>225</td>
<td>115 (4.803)</td>
<td>−11</td>
</tr>
<tr>
<td><em>Pinus sylvestris</em></td>
<td>610</td>
<td>119 (2.683)</td>
<td>−999</td>
<td>400</td>
<td>131 (2.943)</td>
<td>−11</td>
</tr>
<tr>
<td><em>Betula pubescens</em></td>
<td>−</td>
<td>−</td>
<td>−</td>
<td>325</td>
<td>180 (2.510)</td>
<td>−13</td>
</tr>
</tbody>
</table>

### Table 4

Minimum winter temperature (minimum of December, January and February monthly means) at the coldest site for each species

<table>
<thead>
<tr>
<th>Species</th>
<th>Site</th>
<th>Minimum</th>
<th>Mean</th>
<th>Median</th>
<th>95th percentile</th>
<th>kWiT</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Larix decidua</em></td>
<td>Tschainas</td>
<td>−19.2</td>
<td>−15.0</td>
<td>−15.0</td>
<td>−11.4</td>
<td>−11</td>
</tr>
<tr>
<td><em>Picea abies</em></td>
<td>Grindelwald S2</td>
<td>−15.0</td>
<td>−10.8</td>
<td>−10.9</td>
<td>−7.5</td>
<td>−7</td>
</tr>
<tr>
<td><em>Pinus cembra</em></td>
<td>Tschainas</td>
<td>−19.2</td>
<td>−15.0</td>
<td>−15.0</td>
<td>−11.4</td>
<td>−11</td>
</tr>
<tr>
<td><em>Pinus sylvestris</em></td>
<td>Muonio</td>
<td>−24.9</td>
<td>−17.3</td>
<td>−17.5</td>
<td>−11.1</td>
<td>−11</td>
</tr>
<tr>
<td><em>Betula pubescens</em></td>
<td>Kevo</td>
<td>−24.6</td>
<td>−19.4</td>
<td>−19.5</td>
<td>−13.7</td>
<td>−13</td>
</tr>
</tbody>
</table>
4. Discussion

4.1. Growth curves and parameter adjustment

The difference in the maximum growth observed at the various tree-ring sampling sites indicates that in some cases local conditions, such as drought frequency or soil type, may affect growth more than air temperature does. The increase in CO₂ levels over the last few decades may also affect growth and therefore mask the temperature response signal (Nicolussi et al., 1995; Rathgeber et al., 2003), though this response may be temporary, depend on the tree type (evergreen or deciduous) or interact with defoliation events (Handa et al., 2005). The direct effect of CO₂ on growth may also be counteracted by the associated indirect effect of drought stress due to increased temperature (Martinelli, 2004). This shows the importance of using many sites, as well as a large number of trees, when attempting to establish growth potential from tree rings. We were only able to use that part of the tree-ring data which fell within the time-span of the climate maps, but our sample included trees of different ages, so the age-related variability was also taken into account.

For all the species in this study, the first adaptation necessary to fit the new growth curve to the tree-ring data was a sharp increase of its slope. This concurs with the findings by Paulsen et al. (2000), that radial tree growth declines rapidly within the tree-line ecotone. The asymptotic curve shape, with a sharp increase in growth at the lower end of the temperature range, would also explain why these authors found a decrease in correlation between ring-width and altitude throughout the 20th century, particularly during the warmest phases (1920–1950 and 1980 onwards): during warmer periods, the whole range of degree-day sum values within the altitudinal gradient is situated in the “flat” part of the growth response curve, so there is little...
correlation between growth and altitude; in colder periods on the other hand, the same sites have heat sums which correspond to the steeper part of the curve.

The minimum degree-day sum parameters had to be lowered for all species. The largest adjustment of kDDDMin occurred for *P. sylvestris*, which was expected as the model was originally developed for Central Europe whereas the tree-ring data came from Fennoscandia, so it may be put down to different ecotypes. It is also possible that the original calibration reflects the realised niche because Scots pine is out-competed by other pine species and larch towards the tree-line in Central Europe. *P. sylvestris* is not excluded from the subalpine tree-line by temperature, but by the lower resistance to desiccation and higher light requirements of its seedlings, in comparison with those of *P. cembra* (Hättenschwiler and Körner, 1995). On the other hand, the spruce measurements from the boreal tree-line fell within the range of those from the subalpine sites. Although we cannot draw firm conclusions from a single site, it does indicate that the spruce parameters from the Alpine calibration may be adequate for simulations in northern Europe. Finally, the birch chronologies allowed us to get a reasonable estimate of the growth parameters for that species and add it to the model. However, those parameters should still be used with caution because of the small amount of data from which they were derived.

The growth rate (kG) of *L. decidua*, which was originally similar to that of *P. abies*, was increased in the new version to match the larger values found in the tree-ring data. This supports the findings of Dullinger et al. (2005), that larch grows faster than spruce on average. For *P. abies* and *P. cembra*, the growth rates remained the same, as the tree-ring data did not yield higher values than the original maximum; for the latter species, the measured values were actually considerably lower, indicating that the data used may not have captured the full growth potential. For *P. sylvestris*, the measured growth was only slightly larger than expected and kG was adjusted accordingly.

Although the tree-ring-based parameter estimates could still be improved, particularly in species for which little data was available, the new growth curves are a step in the right direction. They not only match the field data (tree-ring widths) better but are based on a more solid theoretical background: drought is no longer accounted for twice, as was the case when a parabolic growth response curve was used in a model which accounted for drought effects per se.

### 4.2. Minimum winter temperature for seedling establishment

Values for the minimum winter temperature allowing establishment were derived for all the species in this study, including those which previously had no limit to establishment (*P. abies* and *P. sylvestris*). For Spruce, the new value matches the minimum January temperature (often equivalent to kWiT) given by Kienast (1987). The kWiT value for *B. pubescens* is the lowest of all the species in this study, which is unsurprising as it has the most northerly distribution of the boreal tree-line species. The kWiT values were derived indirectly from the species’ presence and an empirical frequency of regeneration events, so they may need refining through further studies. However, they at least ensure that these species are ranked correctly in the model with respect to this variable.

One of our key findings was that regeneration seems to be the principal factor limiting tree species’ distributions at the cold forest limits, as changing the growth curve alone did not improve the model results when compared to the NFI data, even when the uncertainties contained in the latter, such as stand age or management, were taken into account. On the contrary, changing the growth response to degree-day sum but not the minimum winter temperature (which limits regeneration) would have resulted in an even greater over-estimation of spruce’s biomass, well above the altitude at which it is currently observed (not shown). Further evidence is the fact that there are practically no missing rings in our tree-line data, which implies that once trees are established, they manage to grow most years, even if only very little. This corroborates findings by several authors that a large part of the regeneration pool should survive, at least as stunted growth forms (Kullman and Engelmark, 1997; Gamache and Payette, 2005). Although degree-day sum also plays a role in seedling establishment (if growth is not possible for adult trees, seedlings cannot grow either), the main factor limiting recruitment in TreeMig is minimum winter temperature. For perennial plants like trees, establishment from seed occurs less frequently and winter survival is therefore more important, so temperature during the nil or low growth period (i.e. winter in temperate regions) is crucial in controlling species’ distributions; annual plants on the other hand are mostly affected by growing season temperature (Woodward, 1988).

Winter temperature appears as a key factor for regeneration success in several tree-line species: *Picea obovata* (Siberian spruce) at the altitudinal tree-line (Moiseev et al., 2004), *P. sylvestris* and *P. abies* at the boreal tree-line (Kullman, 1986; Kullman and Engelmark, 1997; Kullman, 2005), although for the latter precipitation (protective snow cover in winter and absence of drought in the growing season) is at least as important. Calibrating Norway spruce’s response to drought more accurately and adding drought-dependence to the factors controlling germination would probably help reduce that species’ presence in the model results to more realistic proportions, as it is still over-represented despite the improvement brought by the present work. Some studies at the boreal tree-line have shown that regeneration is also strongly influenced by wind and that correlations between regeneration and temperature match lower-frequency (decadal) trends better (Esper and Schweingruber, 2004; Gamache and Payette, 2005). For *P. sylvestris*, mortality remains high and climatically controlled up to 20–30 years after germination (Kullman, 1986), whereas for *P. abies* mortality declines after the second growing season (Kullman and Engelmark, 1997). As it is not possible to include all the likely factors, particularly those which affect only few species, in a model, we decided to concentrate on improving the existing parameters. Furthermore, some factors may have several effects which counteract...
each other: snow cover, for example, protects seedlings against frost and browsing, but increases the risk of fungus infections (Hättenschwiler and Körner, 1995; Cunningham et al., 2006).

These findings seem to oppose the idea that tree-line position is controlled mainly by growing season temperature (Körner, 1998; Jobbágy and Jackson, 2000; Hoch and Körner, 2003; Körner and Paulsen, 2004). However, as winter temperature seems to affect the survival of saplings over several growing seasons, at least for some species (Kullman, 1986; Kullman and Engelmark, 1997), it is possible that establishment success depends on both summer and winter temperatures. If winter temperature affects the survival of young trees up to a certain height, then growing season temperatures allowing faster growth will increase their chances of reaching that critical height before the next time winter temperatures fall below the survival threshold. Nevertheless, winter temperature appears to be the key factor in view of our results.

4.3. Model evaluation—case study Alps

The mean biomass values are systematically too high for the sum of all species and in some cases also for individual species. The variation in biomass per altitudinal band is greater in the NFI data than in the model output, because the inventory plots are much smaller than the simulated grid cells. In the latter, the biomass is averaged over the entire cell surface, so extreme values are less likely. However, the model results are generally within range of the National Forest Inventory data. At those altitudes for which National Forest Inventory data is available, for comparison, the results per species in the newly calibrated model generally show a slight improvement, although some strong differences remain, such as the ratio of larch to Swiss stone pine (especially around 2000–2300 m) or the absence of the latter at lower altitudes. As *L. decidua* is mostly present in early succession stages and *P. cembra* in later ones (Delarze et al., 1998; Motta and Nola, 2001; Timmer and Kaltenrieder, 2005), one could imagine that the model was not allowed to run long enough for pine to establish itself. However, running TreeMig for 500 years did not really change this competitive balance, as the biomass of *P. cembra* remained constant, but *L. decidua* had all but disappeared at lower altitudes while remaining very present higher up. The discrepancy between model results and NFI data may be due to the mixture of early- and late-successional stages in the field data, which is subject to disturbances such as wind-throw (stand ages vary from 1 to 359 years), whereas the model cells are more homogeneous, since they represent the average of differently aged “patches”. Including disturbance in the model would probably improve this and lead to a better ratio of *L. decidua* to *P. cembra*. However, we were not able to use this option (which exists in TreeMig) in the present study, due to the absence of data from which to parameterise the frequency and severity of disturbance episodes in our study area. Two other factors which affect larch in particular are larch bud moth (*Zeiraphera diniana*) attacks (Motta and Nola, 2001) and pasturing, as *Larix* roots seem especially sensitive to trampling by cattle (R. Niederer, personal communication). The latter is most likely to occur in the higher altitudinal bands, where cattle might wander in from the summer pastures above and could partly explain the depressed biomass of *L. decidua* in the NFI data for the 2200 m band. However, the difference may also simply be due to chance, as there are only three NFI plots in that band. For *P. abies*, although the new temperature parameters reduce its biomass slightly, the model is still far too optimistic. This is most probably linked to the drought response. In fact, it may be necessary to review this aspect for other species in the model too, as it may have been affected by the removal of the hidden drought effect in the temperature response.

For the three uppermost altitudinal bands (2300 m and above), there is no data in the first National Forest Inventory, which we used for comparison. However, this does not mean that there are no trees, but that no plots matched the NFI’s definition of “forest” (area width ≥50 m and tree coverage ≥20%; tree height ≥3 m). TreeMig results extend right up to the tree species line, whereas the NFI plots are only found below the timber-line (both definitions according to Körner and Paulsen, 2004). In the third National Forest Inventory, which is currently being conducted, the presence of trees in plots which do not match the above definition is also recorded through aerial photograph analysis. Preliminary results show that trees are present up to 2400 m in the sampled points (C. Ginzler, personal communication), but without any indication about species. Field observations at tree-line also show the presence of *P. cembra* at 2355 m (trees ≥5 m high) and *L. decidua* at 2452 m (shrub form) in the Engadine (J. Gehrig-Fasel, personal communication). Nevertheless, the overall biomass simulated by the model in the uppermost altitudinal bands is too high for the scattered trees observed at tree-line. This can in part be explained by the fact that the model simulates the potential forest, whereas subalpine forests are to a large extent shaped by human activities, with centuries of pasturing leading to a depressed tree-line (Ellenberg, 1986; Timmer and Theurillat, 2003). For Swiss stone pine, the high altitude biomass levels in the model are consistent with these observations and with the trend shown by the NFI data at lower altitudes. However, larch constitutes the bulk of the biomass above 2200 m in the model, which is much less plausible as observations in the field indicate mostly scattered, small (shrub-like) trees of that species. The over-estimation of *L. decidua’s* biomass in the model may result from that species’ age-related sensitivity to climate. Carrer and Urbinati (2004) showed that growth in older larches (over 200 years old) was more highly correlated to variations in climatic conditions, such as summer temperature. As the larches in our dendrochronological data were mostly quite young (a few decades to 150 years), it is possible that the parameters and temperature growth response curve are too optimistic for older trees and that an age-related response curve may need to be developed, or at least two different curves, for trees younger or older than 200 years.

Finally, a few other species appear, albeit in small quantities, in the model results and the NFI plots. The latter are smaller and less numerous than the cells in the TreeMig grid, so less frequent tree species could have been missed. On the other hand, the model might include species which could potentially
grow in that area, but are not actually present for some reason (e.g. geographical barriers). The two main non-dominant species in the NFI data are *P. sylvestris* and *P. mugo* ssp. *uncinata*. In the new model, the former is better represented, but both models underestimate the presence of the latter. Generally speaking, however, the main secondary species which appear in the model results are also present in the National Forest Inventory data, although their relative importance may differ. Their representation in the model could perhaps be improved by a similar calibration exercise. Human influences, such as forest management practices (which are not included in the model at present), could also account for the differences between the model results and the field data for these other species.

5. Conclusions

Both the old and new versions of TreeMig give a reasonable estimate of present forest composition, as it gives the right species in approximately correct proportions, though like all models it cannot be expected to match field data exactly. However, the new version has the advantage of a better theoretical basis for its growth response curve. We have also developed a methodology for deriving the species-related parameters of this curve from dendrochronological data (tree-ring width). In some cases this has led to a slight improvement in the model results, in comparison with the National Forest Inventory data, but more importantly we now have a method which can be used to add other species to the model. This could be useful for portability to other regions, such as the boreal tree-line mentioned in this paper, or in the context of climate change and the immigration of new species.

This calibration work also brought to light the importance of regeneration as a factor controlling species' distributions. Further improvement of the model would require calibrating the temperature controlling establishment for some of the other species, in particular those with no lower limit. Seedling and sapling dynamics is modelled in the same manner as that of adult trees in TreeMig, except for light requirements; once established, the influence of temperature on growth and mortality is the same for all trees. It should therefore be possible to improve the simulation of the species' distributions further by taking into account the winter temperature of several years following germination, instead of just the birth year. Although temperature is the main limiting factor for growth and establishment at tree-line, other factors, such as precipitation, wind or human activities, no doubt play a role, though their influence may be limited to certain species or regions and may be more difficult to calibrate and include in a model. They should however always be taken into consideration, at least when discussing model results.

Although the newly calibrated version of TreeMig does not differ greatly from the original model in terms of simulation results, the theoretical framework on which it is built has been improved. We have also produced a method to derive species parameters for the model from tree-ring data. Furthermore, the newly established functions and parameters can also be used, with some adaptations, in other forest growth models. Finally, this work has also increased our knowledge of the various factors controlling tree species' distributions and opened up perspectives for further research.

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Appendix A. Supplementary data


References


Gellrich, M., Baur, P., Zimmermann, N.E. Natural forest regrowth as a proxy variable for agricultural land abandonment in the Swiss mountains: a spatial


