

Enhancing gap model accuracy by modeling dynamic height growth and dynamic maximum tree height

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ABSTRACT

Gap models are flexible tools for the simulation of forest dynamics under different climatic conditions. An important area, however, has not yet received the attention it deserves: the formulation of height growth and maximum tree height. In most gap models, every tree approaches a fixed maximum height regardless of site conditions, and tree height as such is approximated via stem diameter. To address these issues, we converted maximum height from a parameter to a variable that depends on site-specific climatic conditions. We also established tree height as a separate state variable besides diameter, to allow for competition effects to influence the ratio between height and diameter growth. The new model formulations were tested against data from the Swiss National Forest Inventory (NFI) and from a forest growth and yield research plot. Lastly the new model version was applied to study productivity changes due to climate change along an environmental gradient.

The new model formulations increased the accuracy of simulations of stand characteristics without negatively influencing the general applicability of the model. The height/diameter relationship of a Douglas-fir stand in Switzerland simulated with the new model version resembled measurements closely, and biomass simulated along an environmental gradient agreed better with measurements (NFI) when using the new model version. Simulations with site-specific maximum height showed that the maximum heights of the dominant species on the gradient did not differ significantly from NFI data, whereas static maximum heights did.

The application of the old and new model versions to simulate productivity under climatic change along the same environmental gradient showed that the conversion of a static parameter such as maximum height to a site-specific variable is not only a desirable, but a crucial feature to incorporate, since climate-induced changes in productivity are simulated to be more pronounced with the new model formulation. We conclude that dynamic height growth and site-specific maximum tree height can significantly improve simulation results of forest succession models, especially with regard to forest management under climate change.

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1. Introduction

With rapidly changing environmental conditions and the associated loss in the applicability of traditional yield tables and growth models (Pretzsch, 1992) the interest of forest scientists and stakeholders in more reliable methods to estimate the future growth of forest is rising. Gap models have proven to be flexible tools with regard to estimating the impact of climatic change on natural forest dynamics (e.g. Didion et al., 2011; Huo et al., 2010), yet few have both the capacity to simulate forest management and the necessary

accuracy in simulating forest stand structure to serve as decision support tools.

Key aspects of locally accurate forest models are the simulation of height and diameter growth, as they result from allocation priorities under varying environmental conditions (Waring and Schlesinger, 1985). The allocation of total growth into diameter vs. height growth and the absolute height that is achievable under given conditions have not received much attention to date in forest gap models (for an exception, see Lindner et al., 1997). Assmann (1970) emphasized that height rather than diameter growth should be used as an indicator of growth patterns, as it is less influenced by management. Many individual-tree growth models simulate height and diameter increment separately (Vospernik et al., 2010), yet most gap models treat height as a derived variable that depends solely on the current diameter of a tree (e.g. Kellomäki et al., 2008;

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Kienast, 1987; Pacala et al., 1996; Pastor and Post, 1985), where all growing trees approach an asymptotic value of maximum height, regardless of site conditions. Such models are unable to account for thinning effects that may occur after thinnings of a specified intensity and are marked by an increase in diameter increment, yet not in height growth (e.g. Crecente-Campo et al., 2009; Pothier and Margolis, 1991). They cannot mimic the growth behavior of shaded trees in the understory either, which may invest dramatically varying amounts of resources in height vs. diameter growth with changing light conditions (e.g. Holbrook and Putz, 1989; Naidu et al., 1998).

There are several other factors that make a more reliable simulation of height and diameter growth an important feature: for instance, tree height to diameter (h/d) ratio influences vulnerability to wind and snow breakage (Kimmins, 2003), it may allow to infer the fraction of belowground biomass (Delagrange et al., 2004), and it is also important in terms of the fate of a tree in the stand, since in reality small initial differences in height tend to increase with age and allow for little change in rank in subsequent years (Ammer et al., 2008).

Besides a static h/d relationship, it is a strong simplification to assume that the maximum height that is being approached by the growth function is a site-independent constant (Albert and Schmidt, 2010). Foresters have long known that the “site” as a composite of climate, soil, topography, hydrology and other factors determines tree growth (Kimmins, 2003). In forest growth models, this is routinely taken into account, e.g. by choosing different potential height growth curves depending on site conditions (e.g. Pretzsch, 2001). It is therefore important to find a way to relate maximum potential tree height to site characteristics in gap models as well. An accurate estimation of maximum height influences not only stand structure and stand growth dynamics, but also derived properties such as productivity and carbon storage. Simulating these features accurately is particularly important in times of environmental change, as there is evidence that site index (e.g. Albert and Schmidt, 2010; Boisvenue and Running, 2006; Bravo-Oviedo et al., 2010) and maximum stand height (e.g. Bontemps et al., 2009; Kahle et al., 2008) is changing.

The goal of this paper is hence to (i) show how the traditional growth equation used in gap models can be altered to account for a changing ratio in diameter to height growth, (ii) propose a way to convert a usually static growth-constraining parameter such as maximum tree height to a dynamically calculated variable, and (iii) explore if these model changes improved the overall results and also determine how sensitive simulations under climate change are with regard to these changes. Our model development focuses on FORCLIM, which showed promise of becoming a decision support tool based on the implementation of a versatile management submodel (Rasche et al., 2011). We validate the new model version against long-term growth-and-yield plot and National Forest Inventory (NFI) data.

2. Methods

2.1. Model description

FORCLIM is a gap model that was developed with the premise to use as few parameters as possible and operate with the least amount of ecological assumptions (Fig. 1). It simulates forest dynamics on independent small patches of land and is currently parameterized for 31 species in Europe. Tree development is primarily determined by light availability and climatic parameters; besides these, only nitrogen availability, soil water holding capacity and slope/aspect are used to characterize site properties. The submodels WEATHER and WATER provide values for soil moisture,

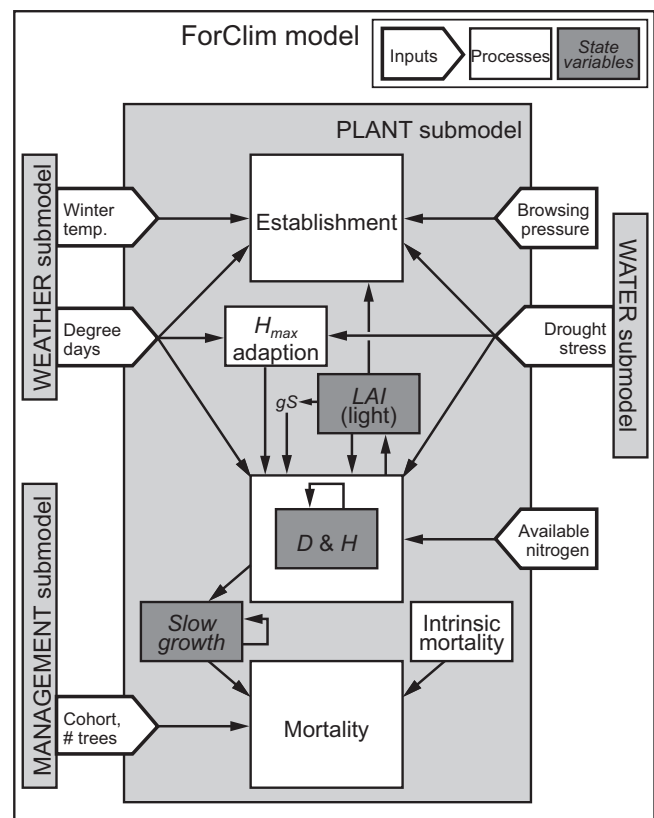


Fig. 1. Structure of the ForCLIM model with submodels PLANT, WEATHER, WATER and MANAGEMENT.

minimum winter temperature and growing season temperature, based on the long-term weather data and soil water holding capacity of the site. Values are drawn from a probability distribution around the climate parameters – derived from the standard deviation calculated from the time series – separately for each of the patches.

The submodel PLANT simulates establishment, growth and mortality of single tree cohorts. *Growth* is modeled based on the carbon budget approach by Moore (1989), in which an optimal growth rate is calculated and then decreased according to environmental factors, which also determine tree *establishment* rates. These factors include light and nitrogen availability, growing season temperature, soil moisture and crown length. Tree *mortality* consists of an age-related and a stress-induced component. For silvicultural treatments, an extensive MANAGEMENT submodel can be activated, which presently comprises the methods thinning, clear cutting, strip felling, target cutting, group selection (“Swiss femel”), shelterwood felling, continuous cover forestry (“plentering”) and planting. A more detailed description of the original model can be found in Bugmann (1996). Changes to the original model are described in Bugmann and Solomon (2000), Risch et al. (2005), Didion et al. (2009) and Rasche et al. (2011, ForCLIM v2.9.8).

Mathematical symbols in FORCLIM follow the notation suggested by Swartzman and Kaluzny (1987), with the first letter denoting the type of the symbol: *u* for input/output variables, *k* for model parameters and *g* for auxiliary variables; state variables do not possess a prefix. Below, this notation is used throughout to avoid confusion, even in equations from other sources.

2.2. Model improvement 1: implementing a dynamic h/d relationship

2.2.1. Description

In many gap models, diameter increment is calculated based on Moore's (1989) carbon budget approach:

$$\frac{dV}{dt} = \frac{\Delta(D^2 \cdot H)}{\Delta t} = kG \cdot D^2 \left(1 - \frac{H}{kH_{\max}}\right) \quad (1)$$

where V denotes volume, D diameter, H height, kG growth rate and kH_{\max} maximum tree height, with kG and kH_{\max} being species-specific parameters. In ForCLIM, this equation was adjusted to calculate diameter instead of volume increment, and to allow for the continuation of diameter growth as maximum height is approached:

$$\frac{dD}{dt} = kG \cdot D \frac{1 - (H/kH_{\max})}{2 \cdot kH_{\max} - kB \cdot \exp^{kC \cdot D}(kC \cdot D + 2)} \quad (2)$$

with $kB = kH_{\max} - 137$ cm (breast height), and $kC = -gS/kB$ where gS denotes initial height growth relative to diameter growth (Risch et al., 2005). Tree height is approximated as a function of diameter:

$$H = 1.3 + kB(1 - \exp^{kC \cdot D}) \quad (3)$$

This formulation may be appropriate for unmanaged forests, but Lindner et al. (1997) argued that this is not the case for managed ones, as thinnings promote diameter growth through the elimination of competition, whereas height growth may even subside. For this reason, Lindner et al. (1997) took into account the effect of competition on the parameter gS , and made it dependent upon the light available to the tree:

$$gS = kS_{\min} + kE_1 \left(\frac{1}{I_c} - 1\right) \quad (4)$$

where kS_{\min} and kE_1 are species-specific parameters, and I_c is the relative intensity of incoming solar radiation at the center of the tree crown. Making the ratio of diameter to height increment variable entails that height can no longer be calculated from diameter, but must be followed separately as a state variable. This was accomplished by rewriting Eq. (3) to a function f_h that distributes volume growth between diameter and height growth according to the competition-driven parameter gS :

$$f_h = gS \left(1 - \frac{H - 1.3}{kH_{\max} - 1.3}\right) \quad (5)$$

Lindner et al. (1997) assumed that ΔH and ΔD have the relationship $\Delta H = f_h \Delta D$, which yields, when substituted into the differential of Eq. (1), a measure for annual diameter increment:

$$\Delta D = \frac{\Delta(D^2 \cdot H)}{2 \cdot H \cdot D + f_h \cdot D^2} \quad (6)$$

2.2.2. Implementation

The variable gS has no upper limit in Eq. (4), which we felt was unrealistic and therefore constrained to $kS_{\min} + kE_1$:

$$gS = kS_{\min} + kE_1(1 - AL_H) \quad (7)$$

where AL_H denotes relative light availability at the top of the tree crown. AL_H is calculated for each cohort based on the cohort's height H . Above the tallest cohort, $AL_H = 1$, whereas further down light availability diminishes through shading of higher cohorts and self-shading until it may approach 0 near the forest floor. Due to this mechanism, it is necessary that in the initialization phase of the simulation (e.g. when starting from measured inventory data) the height of each cohort in the stand is determined. This can be accomplished either directly as input (measured heights) from the inventory data, or with the help of Eq. (3), in which gS is generically calculated as $kS_{\min} + 0.75kE_1$. During the simulation, gS is then

Table 1

Parameter values for kS_{\min} and kE_1 dependent on kLa , based on Eqs. (9) and (10) and resulting kS_{\max} value ($kS_{\min} + kE_1$). Depending on light conditions, the model parameter gS can take any value between kS_{\min} and kS_{\max} .

kLa	kS_{\min}	kE_1	kS_{\max}
1	41	27	68
2	42	41	83
3	43	55	98
4	45	69	114
5	46	83	129
6	47	97	144
7	49	111	160
8	50	125	175
9	51	139	190

determined as a function of AL_H (Eq. (7)), and this value is used in Eq. (5), which thus allows us to calculate the partitioning factor f_h . The latter is finally employed in a modified growth equation of ForCLIM, which results from combining Eqs. (1) and (6) and taking into account the environmentally induced reduction of growth ($gGRF$):

$$\frac{\Delta D}{\Delta t} = kG \cdot D \frac{(1 - (H/kH_{\max}))}{2 \cdot H + f_h \cdot D} \cdot gGRF \quad (8)$$

Then, ΔH can simply be calculated as $\Delta H = f_h \Delta D$.

Lindner (1998), Lindner et al. (1997) used data from several long-term observations of thinning trials in Germany to iteratively estimate the values of the parameters kS_{\min} and kE_1 (Eq. (4)) for *Fagus sylvatica*, *Picea abies*, *Pinus sylvestris* and *Quercus* sp. (cf. Table 2) through a series of simulations and subsequent visual comparisons of stand and simulation data. The authors then proceeded to estimate these parameters for 10 other species, based on the species' ecological characteristics in relation to those of the 4 fitted species.

Lindner (1998) noted that the shade-intolerant pine trees in the under- and mid-storey behaved differently than trees of the three other species, as that they invested more into height than into diameter growth. A connection between shade intolerance and higher h/d ratios has been observed for other species as well (e.g. Beaudet and Messier, 1998; Delagrange et al., 2004; Messier et al., 1999; Williams et al., 1999), hence we assumed a correlation between the parameters kS_{\min} and kE_1 on the one hand and the species-specific shade tolerance (kLa) on the other hand. Instead of separately deriving parameter values for each of the species parameterized in ForCLIM, we plotted Lindner's (1998) kS_{\min} and kE_1 values against the ForCLIM kLa values (nine classes from 1 = shade-tolerant to 9 = shade-intolerant) and calculated a linear regression for each parameter. Both regressions showed a significant correlation ($p = 0.0028$ and 0.0071 , and $R^2 = 0.446$ and 0.373 for kS_{\min} and kE_1 , respectively), and therefore for each species these parameters were calculated according to the species' kLa value (for resulting values see Table 1):

$$kS_{\min} = 1.3kLa + 39.5 \quad (9)$$

$$kE_1 = 14kLa + 13 \quad (10)$$

2.2.3. Validation

In order to properly assess the benefit of the new dynamic h/d relationship, we obtained data of a colline forest growth and yield research plot from the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL). The plot has an area of 0.44 ha, is located near Küsnacht, Switzerland (630 m a.s.l.), and was planted in 1884 with *Pseudotsuga menziesii*. The stand was thinned from above in low to medium intensities at 3- to 10-year intervals starting in 1924, with inventories taking place just before treatments. In each inventory (15 in total), the species and diameter at breast height (DBH) of all trees were recorded, as well as the heights of a subset

Table 2

Maximum reductions ($kRedMax$, expressed in %) of the species parameter $kHMax$, determined by the maximum height of the lowest yield class ($MinH_{max}$) found for the species in the European Yield Table Database (Teobaldelli et al., 2010).

Species	$kHMax$ (m)	$MinH_{max}$ (m)	$kRedMax$ (%)
<i>Abies alba</i> Miller	60	26.4	44
<i>Acer campestre</i> L.	23	18.4	80
<i>Acer platanoides</i> L.	32	18.4	58
<i>Acer pseudoplatanus</i> L.	37	18.4	50
<i>Alnus glutinosa</i> (L.) Gaertn.	31	21.2	68
<i>Alnus incana</i> (L.) Moench	22	–	68
<i>Alnus viridis</i> (Chaix) DC.	4	–	68
<i>Betula pendula</i> Roth	29	18.4	63
<i>Carpinus betulus</i> L.	27	15.2	56
<i>Castanea sativa</i> Mill.	33	13.2	40
<i>Corylus avellana</i> L.	10	–	68
<i>Fagus sylvatica</i> L.	45	19.2	43
<i>Fraxinus excelsior</i> L.	42	16.9	40
<i>Larix decidua</i> Miller	52	19.6	38
<i>Picea abies</i> (L.) H.Karst.	58	19.6	34
<i>Pinus cembra</i> L.	26	–	38
<i>Pinus montana</i> Miller	23	–	38
<i>Pinus sylvestris</i> L.	45	17.1	38
<i>Populus nigra</i> L.	36	28.2	78
<i>Populus tremula</i> L.	30	21.5	72
<i>Pseudotsuga menziesii</i> (Mirbel) Franco	54	26.3	49
<i>Quercus petraea</i> (Mattuschka) Liebl.	45	19.2	43
<i>Quercus pubescens</i> Willd.	25	–	42
<i>Quercus robur</i> L.	52	21.7	42
<i>Salix alba</i> L.	27	–	68
<i>Sorbus aria</i> (L.) Crantz	22	–	68
<i>Sorbus aucuparia</i> L.	19	–	68
<i>Taxus baccata</i> L.	22	–	38
<i>Tilia cordata</i> Miller	30	–	40
<i>Tilia platyphyllos</i> Scop.	39	–	40
<i>Ulmus glabra</i> Huds.	43	–	40

of trees, serving as tariff trees to estimate the height of the others. The latest inventory took place in 2001, providing a period of 77 years for the simulations. Data from the first inventory were used to initialize the model's state variables (D , H), and a detailed management plan for the MANAGEMENT submodel was set up based on site records, in essence recreating the management interventions that had taken place (for more details on the method see Rasche et al., 2011).

For climate, we used the database of the Landscape Dynamics Research Group at WSL, which comprises climate data spatially interpolated across all of Switzerland to a 100 m grid using DayMet (Thornton et al., 1997). We chose data series from the grid cell covering the plot and additionally from the eight neighboring cells to derive long-term means of temperature and precipitation sums. The daily data from the nine grid cells were averaged, and from the resulting series we calculated means, standard deviations, and cross-correlations of monthly temperature and precipitation, thus reducing the potential bias associated with using data of a single grid cell (Daly et al., 2008; Didion et al., 2011). The other site-specific parameters in ForCLIM, i.e. soil water holding capacity ("bucket size") (cm) and available nitrogen ($\text{kg ha}^{-1} \text{ year}^{-1}$), were estimated from the site description as amounting to 12 and 80, respectively.

The stand was then simulated for 77 years, with a patch size of 880 m^2 and 250 patches overall (250 patches represent 50 repeat simulations of the plot, to reduce stochastic noise; cf. Wehrli et al., 2005). As we included all trees marked as "removed" into the management plan, we assumed that no further natural mortality had taken place. The measured vs. simulated h/d relationship of the Küssnacht stand at the end of the simulation were compared to assess whether the new growth formulation had improved model accuracy.

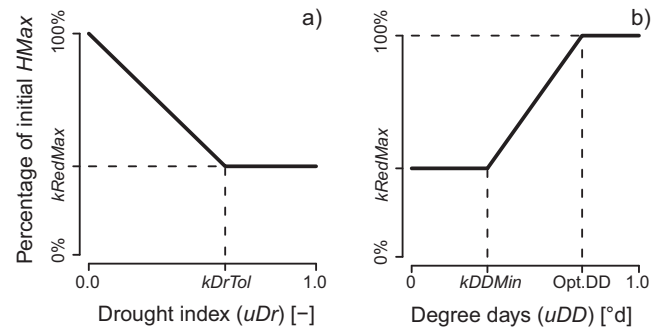


Fig. 2. Site-specific reduction of $kHMax$ based on (a) drought and (b) degree days. For the final reduction the lower value is used.

2.3. Model improvement 2: implementing a site-specific maximum height

2.3.1. Description

The maximum height a tree can reach depends on several factors, most notably available water (Friend, 1993; Koch et al., 2004; Ryan and Yoder, 1997), length of the growing season (Ott, 1978) and nutrients (Tilman, 1988; Wilcke et al., 2008). Soil-bound nutrients are represented in ForCLIM by available nitrogen, a site-specific constant that does not change with climate or vegetation cover. Therefore we decided to forego the effect of nutrients on maximum tree height and to make it solely dependent on the two climatic variables. It has to be stressed at this point that this only concerns the adjustment of the maximum height variable to site conditions. The calculation of annual tree height increment is of course subject to nutrient availability.

The ForCLIM drought index (uDr) is appropriate for representing available water (Bugmann and Cramer, 1998), since it comprises not only water holding capacity of the soil, but also precipitation. Growing season length and warmth are well represented by the number of degree-days (uDD).

Under poor site conditions, stand-specific maximum height is thus reduced by unfavorable temperature (uDD) or drought (uDr) conditions. Hence, the task at hand was to introduce a dependency of the species-specific maximum height parameter ($kHMax$, parameterization see Bugmann, 1994) on uDr and uDD . In the case of uDr we assumed that there would be no reduction of $kHMax$ when $uDr=0$ and a maximum reduction ($kRedMax$) when $uDr \geq kDrTol$ (the drought tolerance of the respective species, i.e. its dry distribution limit). We assumed a linear decline to $kRedMax$ for intermediate uDr values (Fig. 2a). We made a distinction between evergreen and deciduous species in using the seasonal drought index for the latter and the annual drought index for the former group (Bugmann and Solomon, 2000).

In the case of uDD we assumed that the reduction of $kHMax$ is maximum ($kRedMax$) when $uDD \leq kDDMin$ (species' minimum degree day sum required for growth), using the annual sum of degree-days for evergreen and the seasonal sum for deciduous species. Next, the question arose at which degree-day sum the upper boundary should be placed. This could not be answered readily for all species, but Ott (1978) reported that in the Lötschental (Switzerland) the height growth of *P. abies* declines sharply at altitudes above 1900 m a.s.l., and Tschermak (1930) indicated a corresponding altitude of 1000 m a.s.l. for *F. sylvatica* in Vorarlberg (Austria). Based on this information, we employed long-term weather data from the climate stations Visp (640 m a.s.l.) and Montana (1508 m a.s.l.) for the Lötschental (time period 1931–1960) and the stations Feldkirch (440 m a.s.l.) and Galtür (1587 m a.s.l.) for Vorarlberg (time period 1900–1940) to calculate the average degree-day sums at these locations and altitudes and used the

Table 3

Sites along a broad drought and elevation gradient used in the present study, the long-term annual mean temperature (Temp.) and precipitation sums (Prec.), their observation period, bucket size (BS) and available nitrogen (AvN) as used as input parameters in ForCLIM, and dominating tree species of the potential natural vegetation (PNV) according to Ellenberg and Klötzli (1972), Krausch (1992) and Ellenberg and Leuschner (2010). All sites are located in Switzerland.

Site	Latitude (°N)	Longitude (°E)	Elevation (m a.s.l.)	Temp. (°C)	Prec. (mm)	Observation period	BS (cm)	AvN (kg/ha year)	PNV
Bever	46.6	9.9	1712	1.5	841	January 1901–December 1982	10	60	<i>Pinus cembra</i> , <i>P. montana</i> , <i>Larix decidua</i>
Grande Dixence	46.1	7.4	2166	1.2	1016	January 1965–December 1984	10	60	<i>Pinus cembra</i> , <i>Picea abies</i> , <i>Larix decidua</i>
Davos	46.8	9.8	1590	3.0	1007	January 1867–December 2003	10	60	<i>Picea abies</i> , <i>Larix decidua</i>
Adelboden	46.5	7.6	1325	5.5	1351	January 1959–December 2005	15	80	<i>Picea abies</i> , <i>Fagus sylvatica</i> , <i>Abies alba</i>
Huttwil	47.1	7.8	638	8.1	1290	January 1972–December 1995	20	100	<i>Picea abies</i> , <i>Fagus sylvatica</i> , (<i>Abies alba</i>)
Bern	46.9	7.4	570	8.4	1006	January 1864–December 2003	20	100	<i>Fagus sylvatica</i> , (<i>Picea abies</i>)
Schaffhausen	47.7	8.6	400	8.6	882	January 1880–December 2003	15	80	<i>Fagus sylvatica</i> , (<i>Quercus</i> ssp.)
Basel	47.5	7.6	317	9.2	784	January 1864–December 2003	15	80	<i>Fagus sylvatica</i> , (<i>Quercus</i> ssp.)
Sion	46.2	7.4	542	9.7	597	January 1864–December 2003	15	60	<i>Pinus sylvestris</i> , <i>Quercus</i> ssp.

resulting values as the upper boundary of height reduction (Fig. 2b). For the other species, we calculated the difference between the $kDDMin$ values of spruce and beech and the degree-day sums from the Lötschental and Vorarlberg, and added the differences to the species-specific $kDDMin$ values to obtain the value at which the reduction of $kHMax$ becomes nil; this amounted to a difference of 353 °C d from the Lötschental for evergreen and 471 °C d from Vorarlberg for deciduous species.

For the estimation of the maximum reduction ($kRedMax$) of $kHMax$, we used data from 52 yield tables downloaded from the European Yield Table Database (Teobaldelli et al., 2010), which were selected according to species, number of yield classes (more than two), and presence of data on dominant height (H_{dom}). We then plotted the columns age and H_{dom} of each table against each other and proceeded to fit an asymptotic Chapman-Richards function to the lowest yield classes present, with H_{max} as the asymptotic value (Richards, 1959). Estimates of the model parameters were obtained by using the *stats* package of the open source statistics software R (R Development Core Team, 2010), enabling us to determine minimum H_{max} values ($MinH_{max}$) for 18 of the species considered in ForCLIM and thus via the difference between $kHMax$ and $MinH_{max}$ a value for $kRedMax$. Values for the other species were estimated according to the similarity of their ecological characteristics to those of the species for which yield table data were available (Table 2).

2.3.2. Implementation

During the initialization process for a simulation and subsequently every year the submodels WATER and WEATHER calculate uDr and uDD separately for every patch based on a probability distribution of the monthly weather data. Averaging those values over all patches thus assures a balanced estimation of site conditions without the danger of distortion due to climatically extreme years. uDr and uDD are then separately used to determine the reduction of $kHMax$ for each species, and subsequently the lower value of both is employed (minimum approach). Other, more complicated approaches for deriving the final percentage of reduction, such as the multiplication, the geometric mean or the cubic root used to combine several growth factors in JABOWA and ForCLIM (cf. Botkin et al., 1972; Bugmann, 1996), were deemed unnecessary, as tree growth is usually either limited by degree-days or drought, but rarely by both.

It is reasonable to assume that the growth potential at a site – here represented by $kHMax$ – stays constant as long as environmental conditions stay roughly the same. We therefore implemented that $kHMax$ of every species is calculated once based on site conditions during the initialization stage of the model (i.e., under current climate), and thus stays constant. Only during the simulation of climate change scenarios is the value adjusted again; once every 10 years as long as the change continues (usually 100 years, as climate change scenarios beyond the year 2100 are not available, but simulations do not necessarily stop there). For the adjustment we use the mean uDr and uDD values in the current year, just like in the beginning of the simulation. The decadal time step is arbitrary, but it allows for a smoother transition of $kHMax$ values instead of changing the value abruptly at the end of the simulation of climate change, which might cause relicts in the simulation results.

2.3.3. Validation

Maximum tree height depends on climatic factors in the new model version, and thus these changes need to be tested against data from a range of environmentally different locations. For this we chose 9 sites from a previously utilized environmental gradient (e.g., Bugmann and Solomon, 2000; Didion et al., 2009), which comprises a variety of elevations (i.e., temperature regimes) and drought conditions in Europe (Table 3). We obtained data from the first Swiss National Forest Inventory (NFI1, Bachofen et al., 1988) for the 16 NFI plots that were nearest to each site. The NFI1 plots are located at every forested intersection of a 1 km grid mapped over Switzerland, from which a 200 m² and a 500 m² circle are drawn. In the smaller circle, every tree with a DBH larger than 12 cm is measured, in the bigger one every tree larger than 36 cm. Additionally, the height of every tree with an azimuth smaller than 151° is recorded. Using these data, we estimated maximum heights for the most abundant species at each of the 9 sites by again fitting an asymptotic Chapman-Richards function to the measurements.

For climate, we used the same data that had been employed in previous studies, i.e. long-term daily temperature and precipitation data from climate stations at the 9 locations converted to monthly means of temperatures and precipitation sums. Values for available nitrogen and bucket size for each stand were also adopted from previous studies (e.g. Bugmann, 1994) and set as stated in Table 3. With these data we calculated the temperature- and drought-related reduction factors of $kHMax$ as described above, took the minimum

and adjusted species-specific maximum height separately at each of the 9 locations. We then compared for each location the adjusted *khMax* values of the species to the potential maximum heights of the same species that we had calculated from the NFI data to assess the performance of our approach.

2.4. General validation of new model version

After assessing the performance of the two model improvements, we also wanted to test whether the general applicability of the new model version, FORCLIM v3.0, was still maintained. To this end, we applied both the new and the old model versions at the 9 sites of the environmental gradient mentioned in Section 2.3.3 to analyze the impact of the two changes (separate height growth and flexible maximum tree height) on simulated total biomass, species composition and forest productivity.

Climate data were taken from the respective weather stations at the locations (for other site-specific parameters see Table 3), and the duration of the simulations was set to 3000 years, with 1500 years under current climate, then 100 years of climatic change, and a further 1400 years under a scenario of future climate, for which we used data from the ENSEMBLES project (Hewitt and Griggs, 2004) of the Institute for Atmospheric and Climate Science, ETH Zürich, which focuses on the A1B scenario of the IPCC AR4 (IPCC, 2007) that was regionalized to a 10 km grid. For each of the 9 locations, data from the grid cell covering the location and its eight neighbors were employed, with the periods 1961–90 as baseline and 2075–99 as representative years for a hypothetical “future climate”. Seasonal temperature and precipitation anomalies as well as anomalies of the monthly cross-correlations were derived based on the mean monthly temperatures and precipitation sums of the two periods and applied to modify the current climate. For the simulations we assumed that the climate changed linearly between the baseline and the future climate scenario (for more details on the process see Didion et al., 2011).

The first evaluation focused on the results from the simulation year 1500. When starting simulations from bare ground with FORCLIM, this time span ensures that the stand is in equilibrium with the current climate. We compared the simulated total biomass in this year with biomass estimates from the NFI for these locations. We further compared the simulated species composition in this year with the potential natural vegetation of these locations (Table 3). These analyses were made to ensure that the improvement of local accuracy had no detrimental effect on the general applicability of the model.

The second evaluation compared the two model versions in terms of simulated changes in forest productivity from the simulation years 1500–3000. The results from this last year represent unmanaged stands in equilibrium with the future climate. This was done to assess what effects the model improvements had on simulations under climate change.

3. Results

3.1. Model improvement 1: stand structure on a forest growth and yield research plot

A visual comparison of simulated vs. measured *h/d* data (Fig. 3) showed that the new formulation of the diameter growth equation with height being a new, independent state variable is a clear improvement: instead of simulating a static relationship between height and diameter that is independent of stand structure or age (FORCLIM v2.9.8), in v3.0 it was possible to generate a more differentiated picture with trees of the same species that had the same diameter but different heights, or vice versa. Uncoupling tree

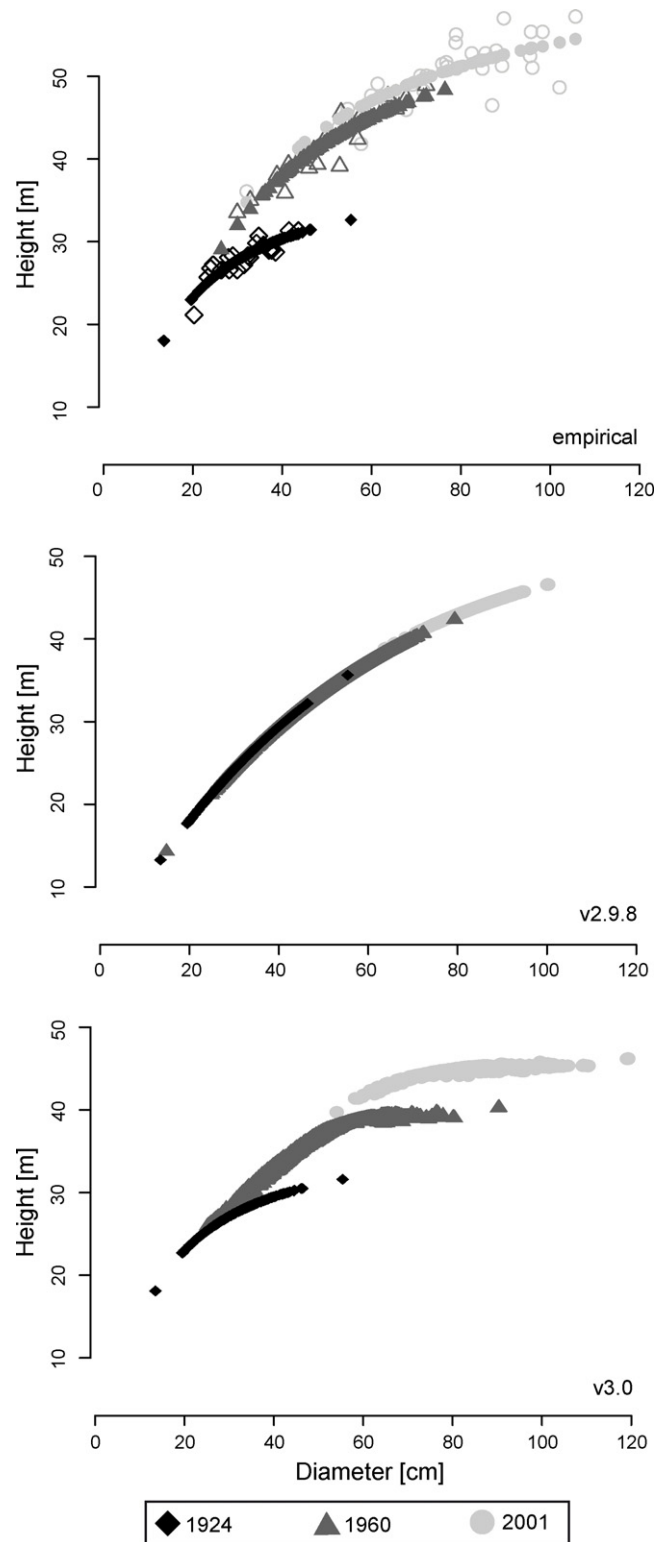


Fig. 3. Tree height vs. diameter for three points in time in a *Pseudotsuga menziesii* stand in Küssnacht (CH). Measured (top) and simulated data (middle: v2.9.8, bottom: v3.0). In the first panel blank symbols represent the tariff trees, solid ones the estimated heights of the remaining trees.

height from diameter has the additional advantage that the model can be initialized with tree height measurements, improving the starting conditions of simulations and thus of the stand structure depiction in the early years (Fig. 3, year 1924 in first and last panel). In later years, simulations with v3.0 overestimated diameter

Table 4

Maximum tree heights (H_{max}) on an environmental gradient; comparison between National Forest Inventory (NFI) and simulation data (ForCLIM versions 3.0 and 2.9.8) for the dominant species (dom. sp.) present the NFI sample plots at the specific sites, with N as the number of height-measured trees.

Site	Dom. sp. (N)	H_{max} NFI (m)	H_{max} v3.0 (m)	H_{max} v2.9.8 (m)
Bever	<i>Pinus cembra</i> (32)	28 ± 13.3	20	26
Grande Dixence	<i>Picea abies</i> (22)	36 ± 5.9	37	58
Davos	<i>Picea abies</i> (50)	48 ± 5.6	58	58
Adelboden	<i>Picea abies</i> (83)	45 ± 6.8	58	58
Huttwil	<i>Abies alba</i> (17)	50 ± 6.4	59	60
Bern	<i>Fagus sylvatica</i> (22)	43 ± 5.1	44	45
Schaffhausen	<i>Fagus sylvatica</i> (15)	35 ± 3.4	38	45
Basel	<i>Fagus sylvatica</i> (20)	42 ± 4.9	36	45
Sion	<i>Picea abies</i> (16)	28 ± 5.1	20	58

increments slightly but underestimated height increments, whereas v2.9.8 underestimated both. The trend of the h/d ratios in the simulated (v3.0) results was slightly different from the measured ones, though, with the measured values steadily increasing and the simulated ones apparently approaching an asymptotic value, indicating that kH_{max} is somewhat larger in reality than estimated for this stand by the new model formulation.

3.2. Model improvement 2: potential maximum height along an environmental gradient

Table 4 shows the results of the simulations regarding maximum height of the dominant species on the NFI sample plots at the 9 locations of the environmental gradient. The maximum heights calculated by ForCLIM v3.0 did not differ significantly from the NFI estimations ($p=0.72$, asymptotic Wilcoxon Mann–Whitney rank sum test), whereas those of v2.9.8 differed significantly from the NFI data ($p=0.03$). However, it is obvious that the reduction still does not mimic reality perfectly, as shown by the values for spruce and fir in the lower subalpine and montane sites Davos, Adelboden and Huttwil. At these sites, ForCLIM v3.0 did not compute any or only a slight reduction of kH_{max} , whereas NFI estimations yielded maximum heights that are about 10 m lower. Overall, however, the distribution of maximum heights of the NFI and ForCLIM v3.0 along the gradient is what one would expect both qualitatively as well as quantitatively, with the highest values in the warm-moist center of the gradient, and the lowest at the extreme (i.e., cold and dry) ends.

3.3. General validation of ForCLIM v3.0

In terms of total biomass, results from ForCLIM v3.0 agreed closely with NFI estimates along the whole gradient, whereas the earlier model version showed differences particularly at the sites Bever and Grande Dixence (Fig. 4). The lower simulated biomasses of v3.0 at both the sub-montane and dry colline end of the gradient were most likely due to the substantial reductions in maximum height, which gave rise not only to lower simulated tree volumes but also to diminished growth rates, capturing growth conditions at least at sub-montane sites more accurately. In Sion, simulated biomass was even lower with v3.0 than with v2.9.8 and far lower than the NFI data. This probably results from the fact that the weather station (which was used to drive the model) is located in the very dry bottom of the Rhône valley, whereas forested NFI sample plots are only found higher up on the adjacent slopes, where climatic conditions are more favorable for tree growth.

As several authors have analyzed in great detail the simulated potential natural vegetation (PNV) along the gradient (Bugmann and Cramer, 1998; Bugmann and Solomon, 2000; Didion et al., 2009), we will not do so again but focus on the differences between the model versions 2.9.8 and 3.0 (Fig. 5). The most notable difference was found in the amount of biomass each species contributed

to the simulated equilibrium forests. In Bever and Grande Dixence, *Pinus cembra* experienced the greatest reduction in v3.0, and *Larix decidua* disappeared almost completely. In Adelboden, *Populus nigra* appeared, which had also been the case in older model versions, but not in v2.9.8. In Huttwil and Bern, changes were not substantial, although the biomass of *Castanea sativa* and *Acer pseudoplatanus* declined slightly, and *Abies alba* biomass increased in Bern. In Schaffhausen and Basel, *C. sativa* was still simulated as a co-dominant species, but had lost a considerable portion of its biomass in v3.0, whereas *Ulmus glabra* and *Tilia platyphyllos* increased theirs and joined *C. sativa* as co-dominant species. In case of *T. platyphyllos* (lime), this appears realistic, as analyses of the NFIs show a substantial fraction of lime stem numbers; however, *U. glabra* tree numbers keep decreasing in Switzerland due to the Dutch elm disease, a factor that is not considered in ForCLIM. The simulation for Sion, lastly, showed little change except for the disappearance of *Pinus montana*.

3.4. Model behavior under a changed climate

Productivity changed noticeably from current climate to a scenario of future climatic conditions (Fig. 6). It rose at the subalpine and montane sites, gently declined in the warm-moist center of the environmental gradient, and sharply declined at the colline sites to a degree where conditions became unsuitable for forest growth in Sion – at least for the species currently parameterized in ForCLIM. Both model versions agreed on this general pattern,

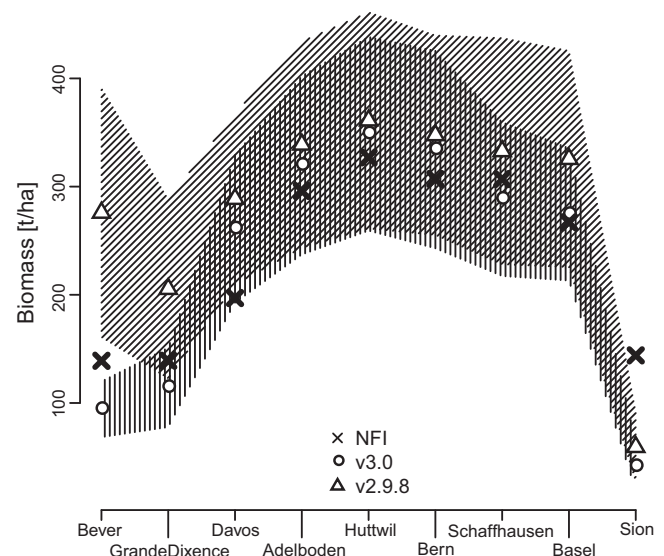


Fig. 4. Total biomass along an environmental gradient in Europe, measured (crosses), and simulated values. Shaded areas: standard deviation of simulation results (vertical stripes: v3.0, diagonal stripes: v2.9.8).

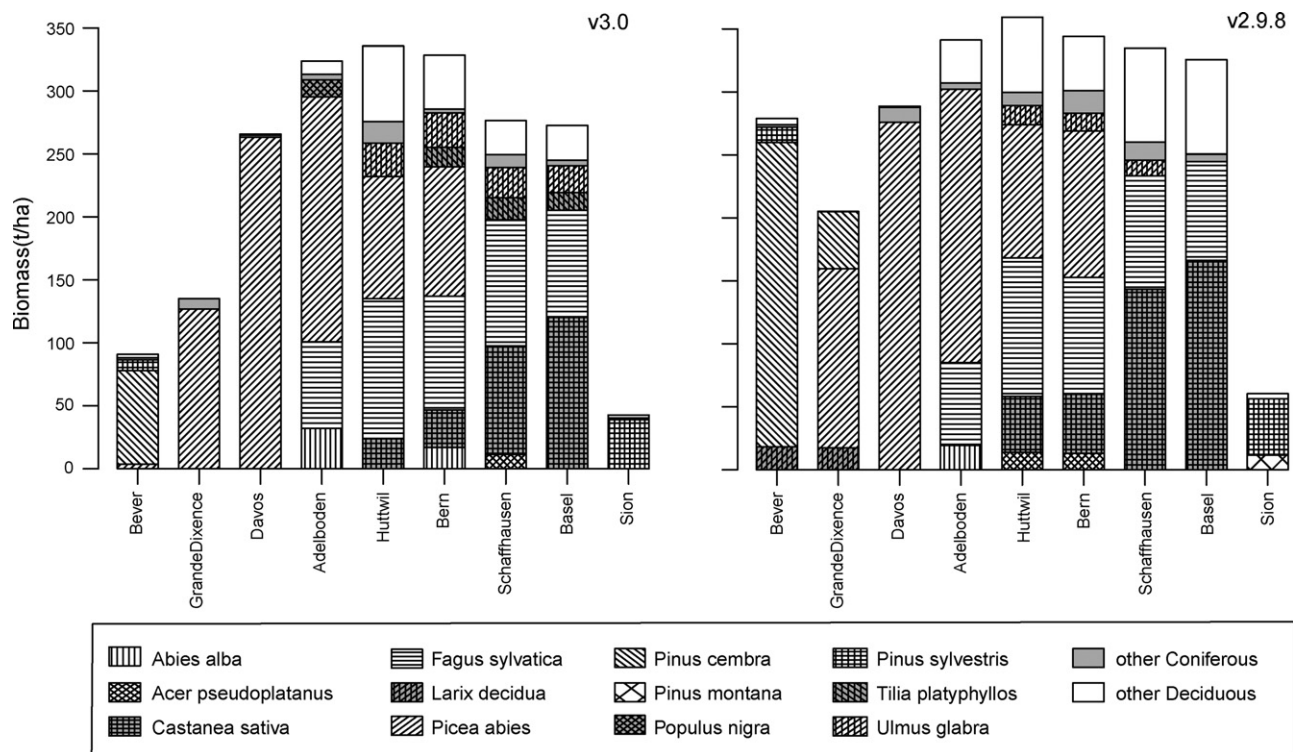


Fig. 5. Simulations of species composition along an environmental gradient in Europe using FORCLIM versions 3.0 (left) and 2.9.8 (right). Species grouped into the “other” categories failed to contribute at least 5% to total biomass, respectively.

but the magnitude of change was portrayed differently, especially at either end of the gradient.

In Bever, the earlier model version showed nearly no change in productivity, whereas v3.0 indicated a clear increase, yet not to the overall level of the old model version. Analyses of the diameter distributions (data not shown here) indicated that this was due to the numbers of trees with large diameters, which slightly declined in v2.9.8 but rose in v3.0. By comparison, at Grande Dixence (and to some extent also at Davos), where temperatures are comparable

to Bever but precipitation is more abundant, the pattern was closer to what one would expect: productivity in v3.0 started at a lower level due to temperature-constrained maximum heights, but rose to approximately the same values as simulated with v2.9.8 when this reduction was gradually diminished with a warmer, yet not overly dry climate.

In the warm-moist center of the gradient (Adelboden, Huttwil, Bern), the two model versions produced nearly identical growth rates, as neither temperature nor drought warranted an adjustment of kH_{max} . At Schaffhausen, both model versions agreed on the productivity level for the current climate, but the new model version estimated noticeably larger losses in productivity under future climatic conditions. In Basel and Sion, due to the new mechanism of reduced maximum height caused by dry conditions, v3.0 simulated a lower productivity under current climate conditions than v2.9.8. Both model versions, however, agreed on the magnitude of change in Basel, and that conditions become unsuitable for tree growth in Sion under climate change.

4. Discussion

In this study we developed, validated and applied a new version of the forest succession model FORCLIM that features a dynamic relationship of height to diameter increment and a climatically sensitive modification of maximum tree height. These changes clearly increased the local accuracy of the model, as the h/d relationship over time was simulated much more realistically, in quality comparable to the results achieved with individual-tree growth models (Vospertnik et al., 2010), while not negatively influencing the model's general applicability. On the contrary, the new model version depicted biomass and maximum tree heights along an environmental gradient very close to NFI estimations, and certainly better than the old one.

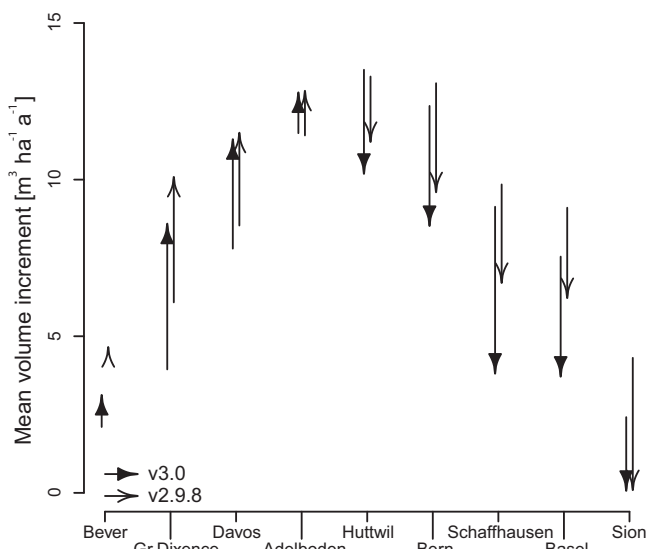


Fig. 6. Simulations of productivity change along an environmental gradient in Europe. Start of arrow: productivity at equilibrium under current climate; arrow-head: productivity at equilibrium under future climate.

4.1. Model improvements

In their growth equations, gap models – and many other types of forest models – require one or several parameters constraining growth. By definition, parameters are constants and thus cannot be affected by environmental influences. Using the example of maximum height, we showed that converting such a parameter to a variable had a non-negligible influence and highly positive effect on the simulation results, especially when considering scenarios of climatic change.

One could, of course, argue that instead of further refining a simple growth equation, a more sophisticated approach should have been taken that would entirely abolish the need for parameters like maximum height. In the model 4C, for example, maximum tree height and other tree state variables are determined by the allocation of NPP, which itself is influenced by environmental conditions (Bugmann et al., 1998). An even more “realistic” approach would be to incorporate, e.g. the findings of Koch et al. (2004) and explicitly model maximum height as limited by leaf water stress due to gravity and path length resistance. For a variety of reasons, we do not believe that taking such a route would be more promising and more successful than the approach we adopted here: besides the fact that a more detailed, highly mechanistic approach would by far exceed the frame of a gap model, we feel that our work is congruent with the principle of parsimony (“Ockham’s razor”). The new parameters that we introduced are either derived from existing ones, eliminating the need for elaborate parameterization, or are easily calculated from readily available data such as yield tables, and as such make it straightforward to add new species should the need arise. Another possibility would have been to follow the example of Kellomäki et al. (2008) and not adjust the growth-constraining factor to site conditions, but the height/diameter relationship based on the temperature sum at the location. This would have been a valid approach if we had stayed within the concept of a fixed relationship between d and h , but not with our new, light-dependent allocation of volume growth to diameter and height growth.

Concerning the parameterization of the maximum reduction of kH_{Max} with the help of yield tables, the approach may be debatable since yield tables are usually only available for commercially interesting species and sites where a commercially rewarding yield is to be expected. We also acknowledge that there are many different types of yield tables, usually constructed for one location, one species and one silvicultural regime, which ordinarily should not be mixed. But we feel that we can safely disregard these limitations, as we only wanted to get an idea of the average height growth of the least productive classes of one species. The large number of yield tables we considered made sure that we actually captured a wide range of yield classes in Europe, most likely including very poor conditions (irrespective of the exact stand conditions and silvicultural regimes), as they were derived for climatically very different parts of Europe ranging, for example, from Hungary to Great Britain.

Another matter is the parameterization of the value of the optimal degree days (Fig. 2b, Section 2.3.1), marking the point below which kH_{Max} is becoming lower. We assumed that all deciduous and all evergreen species followed the patterns set by the available data for *F. sylvatica* and *P. abies*, respectively, mostly because, as mentioned above, this parameter could not readily be derived for other species. Ott (1978), however, in his study not only measured *P. abies*, but also *L. decidua* and noticed that they indeed followed the same pattern and started to have lower asymptotic heights at roughly the same altitude. We therefore feel comfortable with having the species follow these two height-reduction patterns, even though it would of course be desirable to discriminate further. At least we can distinguish deciduous (via *F. sylvatica*) from evergreen (via *P. abies*) species in our approach.

Another aspect that could further improve the simulation results is the inclusion of soil nutrients into the estimation of maximum height. For example, Albert and Schmidt (2010) and Bravo-Oviedo et al. (2010) identified this factor as being significant for the explanation of site productivity. However, as mentioned in Section 2.3.1, this would only be warranted if soil nutrient availability varied over time, which is not the case in the current version of FORCLIM.

4.2. Model validation

The h/d ratios simulated with FORCLIM version 3.0 show a slightly different trend than the measured ones (Fig. 3). Additionally, height growth is slightly underestimated in Küssnacht and diameter growth slightly overestimated as compared to the measured data. It should be kept in mind, however, that this result, which we view as being highly promising, was achieved without any calibration of species parameters. By doing so, we ensure the general applicability of the model, while simultaneously yielding less-than-perfect, but quite satisfactory results in terms of local accuracy. The goal of implementing the variable height to diameter growth function was to enable FORCLIM to render realistic patterns of h/d relationships, which clearly was achieved, even down to a slight scattering of values with the new model version.

Concerning the validation study for the reduction of maximum height (Section 3.2, Table 4), one should keep in mind that comparisons of simulated data with NFI data are not always straightforward. For example, it is uncertain how accurate our estimation of these (asymptotic) values of tree height from the NFI dataset is. Spruce stands, for instance, are on average a little younger than beech stands in Switzerland, and even though there are many old stands on unproductive locations, there are also quite a number of young ones (Brändli, 2010), which makes it possible that some estimations of their maximum height could be too low. Therefore, the differences between “observed” and simulated maximum heights at the sites Davos, Adelboden and Huttwil, for example, could be smaller than currently shown.

Furthermore, the estimation of biomass from the NFI raises some questions as well (Fig. 4). It is not clear if it would be more desirable to have a systematic overestimation of biomass by the model, as the model results show an unmanaged forest in an equilibrium state, whereas most of the NFI plots represent managed stands that are typically 80–120 years old. This may apply to Grande Dixence, for example, but we believe that the total biomass simulated at Bever with v2.9.8, which reached nearly the same level as the one at the submontane site Adelboden, is strongly overestimated and approximated more accurately with v3.0.

4.3. Simulation of productivity under climate change

This simulation was undertaken to assess the impact of the model improvements on simulated forest properties under scenarios of climate change. The results clearly showed that it is important to implement a site-specific growth constraint (kH_{Max} in our case) into the model, since it has a strong and beneficial influence on the results. Not only is simulated productivity under current climate markedly different, especially at the two ends of the gradient, but also the changes of forest productivity under climate change are simulated to be much more severe in the new model version.

The overall results, a simulated rise in productivity levels in the subalpine and upper montane zone, and a fall in the lower montane and colline zone, are consistent with earlier studies by Prentice et al. (1993), Lasch et al. (2002b) and Albert and Schmidt (2010), who found that future productivity is likely to decrease at sites that are currently subject to drought, and also with estimations by Lindner et al. (2010), who suggested that productivity on

sites currently limited by low temperature may rise with climatic change. The latter authors also stress that temperature and precipitation trends for mountain regions are highly uncertain, and that dry valleys may show a different trend, which may explain the surprisingly minor changes in productivity simulated in Bever.

The simulation results provided here should be considered with caution, however, as there are some variables that may influence forest productivity in the future that FORCLIM does not consider, such as rising CO₂ values, pests, insect damage and a higher frequency of disturbances. It should also be considered that choosing a different climate change scenario may result in different findings (Lasch et al., 2002a), although a test with a scenario that was not as harsh as the one we selected at the sites Grande Dixence, Huttwil and Basel showed that while changes in productivity were not as severe, the overall trends stayed the same. Hence we are confident that the patterns we found are robust.

5. Conclusions

In this paper we showed (i) that the traditional growth equation used in many forest gap models can be altered to account for a dynamic h/d ratio, thereby improving the simulation of stand structure in FORCLIM, and (ii) that it is possible to convert a growth-constraining parameter (maximum tree height) to a site-dependent and temporally flexible variable without strongly complicating model structure, thus enhancing model reliability under changing climatic conditions. We further showed that (iii) these changes to the model improved overall model performance in terms of biomass, basal area and species composition of strongly different forest types.

Moreover, the study on productivity under climatic change suggests that a flexible height–diameter relationship and a climatically sensitive growth constraint are not only desirable, but crucial features to incorporate, since climate-induced changes in productivity are simulated to be more severe with the new model formulations.

Taking these changes into account, we propose that our work is an important step on the way towards using gap models in decision support for adaptive forest management.

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