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Improving the establishment submodel of a forest patch model to assess the long-term protective effect of mountain forests

Abstract Simulation models such as forest patch models can be used to forecast the development of forest structural attributes over time. However, predictions of such models with respect to the impact of forest dynamics on the long-term protective effect of mountain forests may be of limited accuracy where tree regeneration is simulated with little detail. For this reason, we improved the establishment submodel of the ForClim forest patch model by implementing a more detailed representation of tree regeneration. Our refined submodel included canopy shading and ungulate browsing, two important constraints to sapling growth in mountain forests. To compare the old and the new establishment submodel of ForClim, we simulated the successional dynamics of the Stotzigwald protection forest in the Swiss Alps over a 60-year period. This forest provides protection for an important traffic route, but currently contains an alarmingly low density of tree regeneration. The comparison yielded a significantly longer regeneration period for the new model version, bringing the simulations into closer agreement with the known slow stand dynamics of mountain forests. In addition, the new model version was applied to forecast the future ability of the Stotzigwald forest to buffer the valley below from rockfall disturbance. Two scenarios were simulated: (1) canopy shading but no browsing impact, and (2) canopy shading and high browsing impact. The simulated stand structures were then compared to stand structure targets for rockfall protection, in order to assess their long-term protective effects. Under both scenarios, the initial sparse level of tree regeneration affected the long-term protective effect of the forest, which considerably declined during the first 40 years. In the complete absence of browsing, the density of small trees increased slightly after 60 years, raising hope for an eventual recovery of the protective effect. In the scenario that included browsing, however, the density of small trees remained at very low levels. With our improved establishment submodel, we provide an enhanced tool for studying the impacts of structural dynamics on the long-term protective effect of mountain forests. For certain purposes, it is important that predictive models of forest dynamics adequately represent critical processes for tree regeneration, such as sapling responses to low light levels and high browsing pressure.

Keywords Mountain forest · Protection forest · Tree regeneration · Ungulate browsing · Forest patch model · ForClim · Stand density

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Introduction

Many mountain forests effectively protect people and their assets against natural hazards such as snow avalanches and rockfall (Brang et al. 2001). If the current protective effect of a forest is provided mainly by the adult trees, effective long-term protection is only possible if permanent tree cover is ensured by sufficient rates of renewal. A lack of regeneration is difficult to counter because trees grow slowly at high altitudes (Ott et al. 1997), and established tree seedlings require up to several decades before they contribute to the protective effect.

In many Swiss mountain forests, tree regeneration currently seems to be sparse. Based on inventory data, several authors concluded that the level of tree regeneration in mountain forests dominated by Norway spruce (*Picea abies* (L.) Karst.), which represent a large fraction of the protection forests in Switzerland, is quite low (Brändli and Herold 1999; Brang and Duc 2002; Zinggeler et al. 1999). The main reasons for the low level of tree regeneration are thought to be (1) recent silvicultural practices, which avoided regeneration harvests, resulting in dense and even-aged stands with low light availability for the understory (Bachofen and Zingg 2001, 2005), and (2) an increased browsing pressure due to high ungulate population densities (Duc and Brang 2003). Canopy shading and browsing pressure interact in a complex causal relationship (Reimoser and Gossow 1996; Bugmann and Weisberg 2003), often leading to reduced sapling growth and prolonging the regeneration phase of forest development (Eiberle 1975; Guler 2004). This may further result in the loss of ecologically valuable tree species, such as silver fir (*Abies alba* Mill.; Ammer 1996; Guler 2004; Wasem and Senn 2000). In this way, the protective effect of a forest might be reduced in the long term.

The importance of browsing and shading influences is difficult to determine due to the scarcity of long-term data sets for mountain forest regeneration under different conditions of browsing and shading (but see e.g., Mosandl and El Kateb 1988). Given this data gap, dynamic models could prove useful for exploring the structural dynamics of mountain forests and for forecasting long-term changes in their ability to provide protection from natural hazards. When coupled with models of natural hazards (Wehrli et al. 2003), accurate models of forest dynamics could even be of value for risk assessment in mountainous areas.

To be useful for this purpose, a model of forest dynamics should accurately project the development of structural forest patterns that characterize the protective effect of a forest, such as its diameter distribution. Additionally, the regeneration process needs to be included in sufficient detail to reflect the most important features of mountain forest tree regeneration.

Forest patch models have been relatively successful in reproducing structural forest patterns (cf. Huth and Ditzer 2000; Lindner et al. 1997; Shugart 1998; Risch et al. 2005; Wehrli et al. 2005). The regeneration process, however, is normally simulated without great detail (cf. Price et al. 2001). For example, sapling growth is seldom simulated explicitly, and the interactions between herbivores and tree regeneration, thought to be crucial in mountain forests (Mayer and Ott 1991, p. 483 ff.; Ott et al. 1997), are rarely considered (but see Jorritsma et al. 1999, or Seagle and Liang 2001). Predictions of how forest structure changes under browsing pressure may therefore be inaccurate. Such models, lacking a detailed representation of tree regeneration, might be unsuitable to judge the long-term protective effect of mountain forests.

The main objective of this study was to assess the efficacy of including a more detailed tree regeneration submodel into a forest patch model, with the goal of increasing the model accuracy in reproducing mountain forest dynamics over a multi-decadal period. We first disaggregated the original establishment submodel included in the ForClim patch model (Bugmann 1994, 1996) into a seedling establishment and a sapling growth module. After comparing the old and new model versions using data from a case study, we then applied the new model to give an example of its use for scenario modelling. Finally, the potential structural forest development and the long-term protective effect of a Swiss mountain forest were investigated under two alternative scenarios.

Methods

Stotzigwald case study

Study site

The Stotzigwald is a steep forest in the Swiss Alps (46°45′N and 08°39′E) with a mean slope of more than 40°, and some interspersed cliffs (Thali 1997). It protects one of the most heavily used traffic routes in Switzerland against rockfall. The elevation of the protection forest ranges from 650 to approximately 1,000 m above sea level, but its protective function is mainly restricted to a rockfall zone of approximately 7.5 ha in the lower part of the forest. Rockfall is frequent in this zone with the majority (79%) of canopy trees showing traces of recent damage. The forest within this zone consists mainly of Norway spruce and silver fir.

In the Stotzigwald, only minor timber harvesting took place from 1950 until 1998 (< 0.6 m³ ha⁻¹ a⁻¹; cf. Thali 1997). Its current ungulate population, which consists of chamois (*Rupicapra rupicapra*), roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*), is high since the site is partly located within a wildlife sanctuary (Odermatt 1997). A dense forest resulting from a lack of recent silvicultural treatments, combined with a high ungulate population density, has resulted in a low density of tree regeneration (Thali 1997).

Stand description and current protective effect

The current stand structure of the Stotzigwald was surveyed from June to August 2003, to provide initial conditions for the simulation experiments. Based on a stratified sampling design in the lower part of the Stotzigwald (approx. 34 ha), stand characteristics were sampled on 96 circular plots of 100 m². Thereby, a slope correction factor was applied (Köhl and Brassel 2001). For all trees ≥ 4 cm diameter at breast height (DBH) on the stand plots, DBH was measured and rockfall traces were counted. Tree height was measured

for approximately one third of all trees. Within each stand plot, regeneration characteristics were additionally sampled on concentric circular plots of 50 m², taking into account the slope correction factor mentioned above. On these plots, all seedlings and saplings < 4 cm DBH were tallied by species in six different height classes (< 0.10, 0.10–0.39, 0.40–0.69, 0.70–0.99, 1.00–1.3, > 1.3 m). For each individual seedling or sapling, browsing on lateral and terminal shoots was recorded. In addition, the light regime on each regeneration plot was recorded with five hemispherical photographs. Stand and regeneration characteristics were directly extrapolated from sampled plots within the rockfall zone to the entire rockfall zone.

The current structure of tree regeneration within the rockfall zone shows a rather low sapling density with approximately 2,230 saplings ha^{-1}. Silver fir (44%) and Norway spruce (20%) are most frequent, followed by European mountain ash (*Sorbus aucuparia* L.; 6%) and European white birch (*Betula pendula* Roth, 14%). As can be seen from the current height distribution (Fig. 1a), most of the saplings (85%) are smaller than 0.4 m. Silver fir saplings are particularly small, with 94% of the saplings < 0.1 m. A clear assessment of the browsing impact was not possible due to the lack of taller individuals of palatable tree species (particularly silver fir, but also European mountain ash). However, qualitative observations indicate a high impact by ungulate browsers (Odermatt 1997).

The current stand includes approximately 561 trees ha^{-1} > 4 cm DBH, and is dominated by Norway spruce (83%) and silver fir (13%). The diameter distribution shows a maximum of approximately 48 cm DBH with a low density of trees < 12 cm DBH (Fig. 1b).

The present forest in the rockfall zone of the Stotzigwald provides an almost optimal protective effect against rockfall when compared to target values as defined in the Swiss management guidelines for protection forests (Frehner et al. 2005). These guidelines define target stand structures (stem numbers, species composition) for different natural hazards and site conditions. As can be seen from Table 1, the recommended stem numbers for rockfall protection forests are reached in the current stand with the exception of the stem number for trees with DBH > 12 cm. However, the low levels of small tree density (< 12 cm DBH) are troublesome, particularly since rockfall events with smaller (i.e. < 40 cm rock diameter) and middle-sized rocks

(40–60 cm) are more frequent at the Stotzigwald (personal observation). Given the observed paucity of tree regeneration, the protective effect of the forest may decrease in the long term.

The ForClim model

The ForClim patch model was originally developed to assess the impacts of climatic changes on tree species composition and biomass of forests in the Swiss Alps (Bugmann 1994). During its construction, special emphasis was placed on developing a model with a minimum number of ecological assumptions (Bugmann 1996). The applicability of ForClim was successfully extended from the Swiss Alps to other climatic regions through several model refinements (Bugmann and Cramer 1998; Bugmann and Solomon 1995, 2000; Bugmann 2001; Shao et al. 2001). A detailed description of ForClim can be found in Bugmann (1996), and the latest version of ForClim, V.2.9.3, is documented in Risch et al. (2005). Even though ForClim was not originally designed to simulate structural forest patterns such as diameter distributions, it has since been shown to accurately reproduce such patterns in simulations over periods of several decades (Risch et al. 2005; Wehrli et al. 2005).

However, Wehrli et al. (2005) reported that the stress-induced mortality implemented in ForClim strongly overestimated mature tree mortality rates in dense stands, leading to an unrealistically drastic reduction of simulated tree numbers in short-term simulations. This artefactual effect arose from an underestimation of the calculated light availability on a patch, which in the current model is a function of the leaf area index (LAI) of idealized trees, i.e. trees with long crowns. However, many mountain forests such as the Stotzigwald are even-aged and dense, and trees with short crowns predominate (Ott et al. 1997). For such forests, the LAI calculated for long-crowned trees is too high, and fails to account for the self-pruning of crowns.

Improvement of the crown implementation in ForClim

For the present study, we implemented a simple dynamic crown structure to correct this problem. ForClim calculates LAI using a static, allometric relationship

Fig. 1 Current height distribution of tree regeneration (**a**) and diameter distribution of the stand (**b**) at the rockfall zone of the Stotzigwald
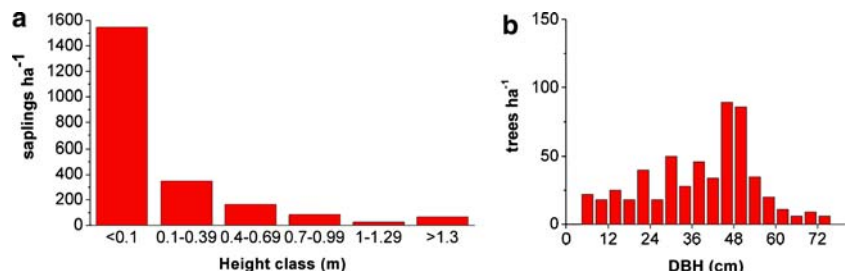
Table 1 Comparison of the current stem number in the Stotzig-wald study area with target values for the optimal stand structure against rockfall as defined in the Swiss management guidelines for protection forests (Frehner et al. 2005)

Rock diameter (cm)	Effective DBH (cm)	Target values (trees ha^{-1})	Stotzigwald (trees ha^{-1})
< 40	> 12	600	521
40–60	> 24	400	438
> 60	> 36	200	342

between foliage weight and DBH (Bugmann 1996). We instead use a light-dependent, dynamic relationship, where the foliar mass and LAI of a tree with a given DBH depend on the current light conditions on a patch, and can vary between a species-specific maximum and minimum. Our implementation of the new, dynamic crown structure was based on the original relationship between foliage fresh weight gFolW and DBH from Bugmann (1994):

$$gFolW = kA_1 DBH^{kA_2} \qquad (1)$$

where kA_1 and kA_2 are species-specific parameters estimated from empirical data (cf. Bugmann 1994, p. 202). To make the relationship dynamic, we replaced the original parameter kA_1 that describes a single, fixed rate of change by a LAI-dependent parameter gkA_1, which is calculated as follows:

$$gkA_1 = kA_{1,\max} - (kA_{1,\max} - kA_{1,\min})gkLAI \qquad (2)$$

where $kA_{1,\max}$ and $kA_{1,\min}$ are the maximum and minimum envelope of the relationship between foliage fresh weight and DBH, respectively. The factor $gkLAI$ ranges from 0 (no canopy shading) to 1 (full canopy shading), and is calculated as follows:

$$gkLAI = \min\left(\frac{curLAI_{patch}}{maxLAI_{patch}}, 1\right) \qquad (3)$$

where $curLAI_{patch}$ is the current LAI on the patch as calculated by ForClim and $maxLAI_{patch}$ is the maximal value for LAI on a patch. Thus, without canopy shading, i.e. without trees on a patch, gkA_1 is set to $kA_{1,\max}$. Consequently, new trees on such a patch are initialized with a very high DBH–leaf area relationship. With increasing canopy shading, gkA_1 and thus the DBH–leaf area relationship decreases until it finally reaches $kA_{1,\min}$, reflecting the maximum self-pruning of crowns. In contrast to the original, static crown structure, stress-induced mortality is assumed to initiate only if the DBH–leaf area relationship of a tree has already been reduced to the minimum. Following the death of one to several trees on a patch, the model does not allow gkA_1 of the remaining trees to increase in the following time steps, even though the available light on the patch increases.

While being simple and linear, we expected this approach to be promising, because it captures some salient features of the dynamics of tree crowns without undue

reliance on data for parameterization that are not readily available.

The values for $kA_{1,\max}$ and $kA_{1,\min}$ were estimated from species-specific tree data (Burger 1947, 1948, 1950a, b, 1951, 1952, 1953) using quantile regression (Cade and Noon 2003, cf. Table 2 and Fig. 2 for an example). The accuracy of the new dynamic crown implementation was corroborated by comparing simulated values of available light at the forest floor with observed values of available light at forest floor derived from hemispherical pictures from the study site. Thereby, a linear regression analysis was performed and the modelling efficiency statistic EF (cf. Mayer and Butler 1993) was calculated. The latter is very similar to the commonly used R^2 statistic, but indicates the proportion of variation explained by the line of perfect fit instead of a fitted regression line. As can be seen in Fig. 3, the fit between observed and simulated values is only moderate. Moreover, there is a great deal of "noise" as evidenced by a low EF statistic (EF = 0.11). However, the fit is much higher compared to the one with the old crown implementation (EF = −3.28). Thus, considering the simplicity of the approach and the many factors influencing real light availability at the forest floor that are neglected in the model (e.g., microtopography), we consider our model refinement to be a substantial improvement.

To test the influence of the dynamic crown structure on the simulated tree mortality rates, model comparisons were conducted for the Stotzigwald and for another site from which empirical data were available from a preceding study (site Sigriswil, cf. Wehrli et al. 2005). The results of these test runs showed that the mortality rates obtained with the dynamic crown structure were significantly lower than the rates obtained with ForClim V2.9.3, and very similar to the empirical mortality rates at the Sigriswil site (Table 3). Therefore, subsequent simulation experiments utilize the modified, dynamic relationship between foliar mass and DBH.

Table 2 Parameter estimations for the relationship between foliage fresh weight (gFolW) and DBH for several species groups as derived from the data in Burger (1945–1953)

Species group	$kA_{1,\text{orig}}$	$kA_{1,\min}$	$kA_{1,\max}$	kA_2	n
a *Larix decidua*	0.1	0.048	0.221	1.4	99
b *Fagus silvatica, Quercus* spp.	0.06	0.025	0.105	1.7	144
c *Pinus silvestris*	0.17	0.071	0.346	1.4	210
d *Picea abies, Abies alba*	0.23	0.090	0.530	1.5	355

$kA_{1,\text{orig}}$ and kA_2 denote the original estimations of kA_1 and kA_2 as described by Bugmann (1994, p. 202); $kA_{1,\min}$ and $kA_{1,\max}$ represent the lower and upper boundary of the quantile regression; n denotes sample size
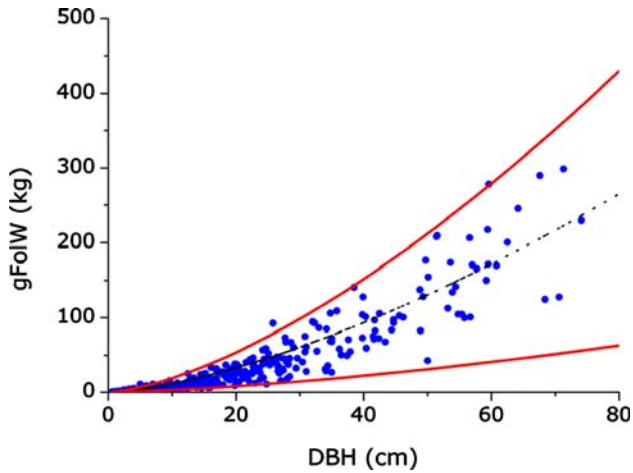
Fig. 2 Relationship between foliage fresh weight (gFolW) and DBH for the *Abies alba–Picea abies* species group as derived from the data in Burger (1945–1953). *Dashed lines* represent the original relationship included in ForClim, *solid lines* represent the minimum and maximum envelope based on a quantile regression (95%). Species grouping followed Bugmann (1994, p. 201 ff)

Improvement of the establishment submodel

In ForClim V2.9.3, tree establishment is determined by four limiting factors: light availability at the forest floor, browsing intensity, soil moisture and absolute winter minimum temperature. The response to these factors is species specific, and tree regeneration for a given patch is modelled by applying these limiting factors as environmental "filters" to determine the establishment rate of trees with an initial DBH of 1.27 cm (cf. Bugmann 1994, 1996; Price et al. 2001). This immediate establishment of trees with a DBH of 1.27 cm may be an over-simplification for mountain forests, where sapling growth is known to be very slow. In subalpine forests, for exam-

ple, it can take up to 50 years for Norway spruce to reach breast height (Brang and Duc 2002; Ott et al. 1997). Neglecting delayed regeneration periods in the models may lead to overestimation of the abundance of small trees. Therefore, we decided to more explicitly model the tree establishment process in our ForClim model refinement.

To maintain ForClim's simplicity, we decided to implement a simple sapling growth function that permits the explicit simulation of the regeneration time lag, rather than to develop a mechanistic regeneration model. Following Price et al. (2001), we first disaggregated the regeneration process into two stages, resulting in two new modules, one for seedling establishment and one for sapling growth. In the seedling establishment module, seedlings establish under optimal conditions with an initial height of 0.05 m. They are then transferred to the sapling growth module, in which they grow to a height of 2 m before recruiting as trees with an initial DBH of 1.27 cm. In the sapling growth module, individual saplings are modelled explicitly by taking into account suboptimal conditions due to canopy shading and ungulate browsing (see below). The structure of the new establishment submodel of ForClim V2.9.4 is shown in Fig. 4. The two new modules are described in detail below.

Seedling establishment module

Seedling establishment in ForClim V2.9.4 is based on the original tree establishment submodel in ForClim V2.9.3 (cf. Bugmann 1994, pp. 58–61). However, since data for a reliable parameterization and corroboration were not available, the recruitment module was not used for the present study. Thus, only the current tree regeneration at the Stotzigwald site but no additional
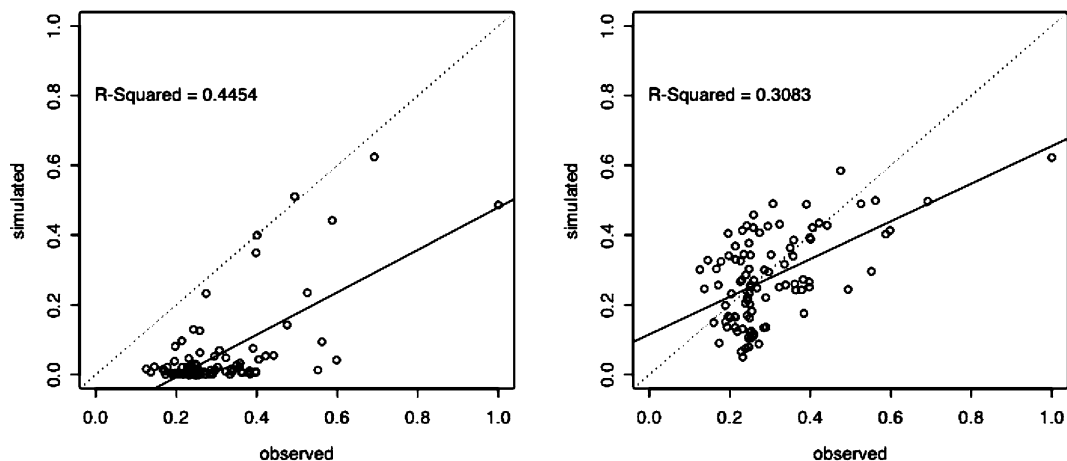

Fig. 3 Observed and simulated light availability relative to above crown values for the Stotzigwald site. Observed refers to the available light at forest floor derived from hemispherical pictures from 96 field plots. Simulated denotes the available light at forest floor as simulated by ForClim with the old (*left*) and the new (*right*) crown implementation. The *diagonal line* represents the line of perfect fit ($y = x$). Also shown is the regression line for observed versus simulated values of the proportion of available light at forest floor

Table 3 Mortality rates simulated with ForClim V2.9.3 (FC 2.9.3) and ForClim V2.9.4 (FC 2.9.4) for the sites Stotzigwald and Sigriswil (cf. Wehrli et al. 2005 for a detailed description of the Sigriswil site)

	Stotzigwald			Sigriswil		
	2005 (trees ha^{-1})	2015 (trees ha^{-1})	Mortality rate	1930 (trees ha^{-1})	1943 (trees ha^{-1})	Mortality rate
FC 2.9.3	561	231	0.59	425	220	0.48
FC 2.9.4	561	511	0.09	425	405	0.05
Empirical data	NA	NA	NA	425	397	0.07

For Sigriswil, additional empirical data were available allowing a comparison with real mortality rates. Since for simulations of real stands, the overestimation by the stress-induced mortality is highest in the first years (cf. Wehrli et al. 2005, p. 157), the test runs were only performed over short periods
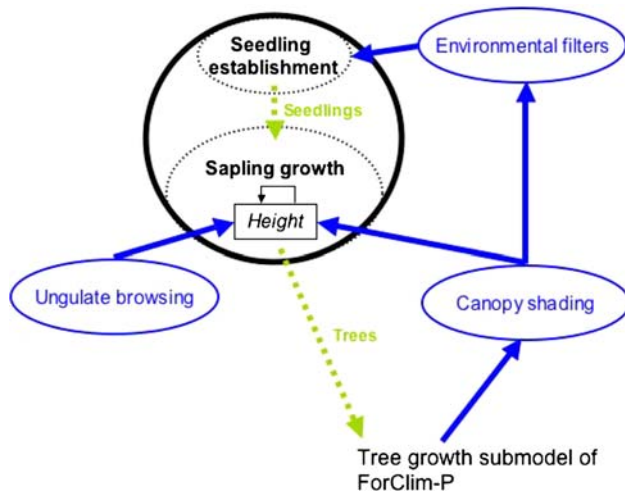*NA* no data available

Fig. 4 Structure of the new establishment submodel in ForClim V2.9.4. The *square box* denotes the state variable (height increment); *ellipsoid boxes* represent the different factors that influence the regeneration process

regeneration was considered in the simulations. As was evident from a comparison of preliminary simulation runs conducted without and with additional seedling recruitment, the omission of additional recruitment did not have a significant influence on the stand structure after 60 years. This is not surprising since tree growth is slow in high-altitude environments, and seedlings require several decades before they markedly influence stand structure.

Sapling growth module

Similar to the tree growth module of ForClim, individual sapling growth is calculated using an optimal growth potential derived from empirical data, which is then reduced by limiting environmental constraints. Sapling height growth is modelled instead of diameter growth, since sapling height is ecologically more relevant and more sensitive to environmental constraints. Therefore, we introduced a new height growth function based on the growth equation of Bertalanffy (Bertalanffy 1957; Rammig et al. 2006). The appeal of this equation lies in its simplicity and biological plausibility (Zeide 1993; Pretzsch 2001). The equation includes only two parameters, one for the asymptote (i.e. maximum tree height) and one for the slope (i.e. growth rate). Thus, the function is less flexible than equations with more parameters, but at the same time, it is more robust in parameter estimation procedures (Pretzsch 2001). The optimum species-specific height increase $h_{\text{inc,opt}}$ of a sapling is calculated as:

$$h_{\text{inc,opt}} = 3H_{\text{max}}kG_{\text{sap}}e^{(-kG_{\text{sap}}\text{age}_{\text{sap}})}\left(1 - e^{(-kG_{\text{sap}}\text{age}_{\text{sap}})}\right)^2 \quad (4)$$

where H_{max} is maximum tree height in cm, and kG_{sap} is the species-specific growth rate. These two parameters are estimated from empirical data. The *sapling age parameter* is calculated as

$$\text{age}_{\text{sap}} = \text{Ln}\left(1 - (h_{\text{curr}}/H_{\text{max}})^{(1/3)}\right)/(-kG_{\text{sap}}) \quad (5)$$

where h_{curr} is the current sapling height.

Parameterization of the growth function and corroboration of the parameter estimations

The two species-specific parameters needed for the Bertalanffy equation were estimated for the four main tree species at the study site, i.e. Norway spruce, silver fir, European white birch and European mountain ash. Maximum tree height H_{max} was parameterized using data collected at the Stotzigwald site. While keeping H_{max} constant, the growth rate kG_{sap} was estimated using data from the literature (Commarmot 1995; Schönenberger 2002). The Bertalanffy equation was fit to data from similar sites where saplings had grown under optimal conditions, i.e. no canopy shading and no browsing, using nonlinear curve fitting (cf. Rammig et al. 2006). In this way, the estimated growth factors were intended to reflect a site-specific optimum height growth, but not the absolute maximum height growth. Estimates of the species-specific parameters are shown in Table 4.

By comparing calculated sapling height to field data from our study site, the estimated values of kG_{sap} were corroborated. For that purpose, only those saplings were used that had grown under near-optimal conditions

at the study site (i.e. neither canopy shading nor browsing). Unfortunately, data for corroboration were rather sparse due to the low level of tree regeneration at the study site. Therefore, additional data from a nearby site were used for European mountain ash (Truninger and Bucher 1994). For the other species, no additional data were available. The data sets were compared graphically and by means of the EF statistic and a linear regression (Mayer and Butler 1993; cf. above). As can be seen from Fig. 5, the fit between observed and simulated sapling height is reasonably good. This is confirmed by the EF statistics: While being only moderate for Norway spruce (EF = 0.14), it is high for the other species (silver fir 0.86, European mountain ash 0.87, European white birch 0.89).

Growth reduction by environmental constraints

In the model, maximum height growth is reduced by a species-specific response to canopy shading and ungulate browsing. Sapling growth thus responds dynamically to the prevailing environmental conditions. Canopy shading is calculated as available light on the forest floor using Beer's extinction law as a function of LAI (Bugmann 1994, p. 63).

Simulated ungulate browsing affects saplings throughout their growth period, from 0.05 to 2.0 m in height, taking into account the different ungulate species that occur in the Stotzigwald. Since more palatable species are subject to a higher browsing impact, a species-specific factor kBrS was introduced. The values for kBrS for the four main tree species at the Stotzigwald were derived from the literature (Ammer 1996; Brändli 1996; Brassel and Brändli 1999; Kindermann and Hasenauer 2003; Motta 1996, 2003; Rüegg and Schwitter 2002; Table 5).

We also introduced a site-specific browsing intensity factor (kBrI), scaled from 0 (no browsing) to 4 (very high browsing for the least sensitive species, i.e. Norway spruce). The species-specific browsing impact is calculated by multiplying kBrS with kBrI.

Data on the long-term development of tree regeneration in mountain forests under different shading and browsing regimes are rare. Therefore, we calculated the integrated response of sapling growth to these factors using simulation experiments with the mechanistic tree regeneration model HUNGER of Weisberg et al. (2005). HUNGER simulates sapling growth and the response to light availability and ungulate browsing based on a well-established formulation for plant nutrient transport and conversion processes (Weisberg et al. 2005). It was calibrated with empirical data from mountain forests of eastern Switzerland. In a test with independent data, HUNGER was applied to Norway spruce, and it accurately represented sapling response to browsing intensity and relative light availability. It slightly over-predicted sapling height, while no significant differences were found between simulated and observed basal diameter, total biomass or leaf biomass (Weisberg et al. 2005). We used HUNGER to derive a response surface for Norway spruce saplings with respect to the browsing-light interaction. From this surface, a simplified response matrix was derived by approximating the values obtained by HUNGER (cf. Fig. 6). This response function was used in the sapling growth module as a multiplier to reduce optimum species-specific height increase $h_{inc,opt}$ to yield current height increase h_{inc} as follows:

$$h_{inc} = h_{inc,opt} f(\mathrm{br}, l) \tag{6}$$

where $f(\mathrm{br}, l)$ denotes the response function (Fig. 6). Due to the lack of data, HUNGER could not be applied for the other species. Therefore, the response matrix for growth rate reduction due to browsing and shading was assumed to be equal for all species.

Sapling mortality due to environmental constraints such as ungulate browsing (cf. Ammer 1996; Eiberle and Nigg 1983; Eiberle 1989) was omitted in the present study since data for a reliable parameterization and corroboration of a sapling mortality routine were not available. This simplification had, however, no significant influence on the simulated stand structure after 60 years as evidenced from a comparison of preliminary simulation runs conducted without and with a simplistic sapling mortality routine based on the widely used approach of growth-dependent mortality (cf. Keane et al. 2001). This is probably due to the relatively short simulation period during which saplings with strongly reduced growth are not able to recruit as trees anyway, no

Table 4 Model parameters for the sapling growth function

	H_{max} (cm)	kG_{sap}	Std. error	n	t_{200} (years)	Data source
Silver fir	3,500	0.017	0.0002	3,354	24	Commarmot (1995)
Norway spruce	3,500	0.020	0.002	53	21	Schönenberger (2002)
European white birch	2,500	0.090	0.023	13	7	Schönenberger (2002)
European mountain ash	1,500	0.055	0.004	320	13	Schönenberger (2002)

The parameter estimation for European white birch shows a relatively large standard error. However, since a variation of $kG_{sap} \pm$ std. error has only a marginal influence on the t_{200} ($\pm$ 1 year), the value of kG_{sap} was set to 0.090
H_{max} denotes the maximum tree height and was derived from field data from the Stotzigwald. kG_{sap} stands for the sapling growth parameter, which was estimated for each species from empirical data with a nonlinear curvefit based on data from Schönenberger (2002, site Schwanden) and from Commarmot (1995, site Bourrignon). t_{200} indicates the time a sapling needs to pass the threshold of the sapling growth submodel of 200 cm
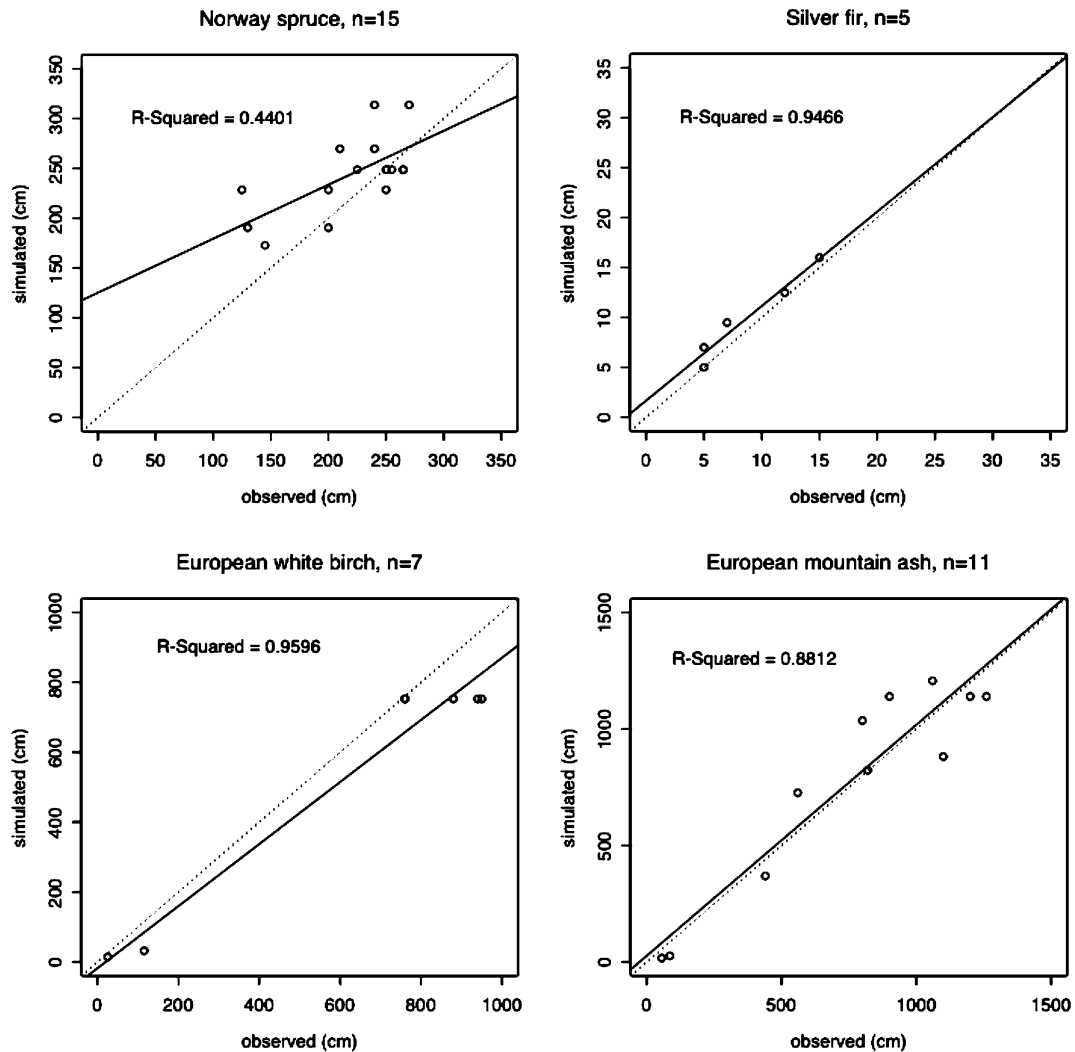
Fig. 5 Observed and simulated sapling height. Observed refers to sapling heights from field data from the Stotzigwald (Norway spruce, silver fir, European white birch) and to data from a nearby site (European mountain ash; cf. Truninger and Bucher 1994). Simulated denotes the sapling height calculated by ForClim V2.9.4 under optimum height growth (cf. Table 4 for parameter values). *n* denotes sample size of field data

Table 5 Species-specific susceptibility to browsing according to various authors

Species	Ammer (1996a)[d]	Brändli (1996)[a]	Brassel and Brändli (1999)[d]	Kindermann and Hasenauer (2003)[d]	Motta (1996)[b]	Motta (2003)[c]	Rüegg and Schwitter (2002)[a]	Mean susceptibility	kBrS
Norway spruce	0.35	0.11	0.12	0.27	0.60	0.34	0.15	0.23	0.25
Silver fir	1	0.6	1	0.55	1	NA	1	0.76	0.75
European white birch	NA	0.38	NA	0.64	NA	NA	NA	0.51	0.50
European mountain ash	NA	1	NA	1	NA	1	0.88	1	1

For standardization, all values are scaled to the range [0...1], where 0 = least susceptible to browsers and 1 = most susceptible to browsers. Mean susceptibility relates to the averaged susceptibility as derived from the different sources

*k*BrS denotes the parameter included in ForClim V 2.9.4; *NA* no data available

Dimension for measuring species-specific susceptibility:

[a]Browsing intensity

[b]Species-specific damage

[c]Browsing incident in terminal shoot

[d]Percentage browsed (Verbissprozent)

matter if they just grow slowly or if they die after a certain period of slow growth. Therefore, the inclusion of a mortality module for saplings does not seem to be mandatory for relatively short simulation periods such as those upon which we are focusing in this study.

Comparison of the model versions and preliminary application of the improved model

In order to compare the old and the new establishment submodel of ForClim, we first simulated the potential development of the stand for 60 years under current climatic conditions with both model versions. The simulation experiment with the new model version was performed using maximum sapling growth, considering neither canopy shading, nor browsing constraints. Although this scenario is rather hypothetical for the present stand at the Stotzigwald, it allows evaluating the differences in behaviour between the two model versions.

As a first application of the new model, we then investigated the effect of sparse tree regeneration on the long-term protective effect of the Stotzigwald. This was done by simulating the potential development of the stand for 60 years under current climate conditions, given two scenarios. The first scenario "canopy shading and no browsing impact" (S-scenario) only considered canopy shading, by setting browsing intensity to zero. The second scenario "canopy shading and high browsing impact" (SB-scenario) considered both factors, using

Fig. 6 Contour plot of the browsing–light interaction. Browsing intensity ranges from 0.0 to 1.0 and refers to the annual probability of a sapling to be browsed. The light availability similarly ranges from 0.0 to 1.0 and refers to the proportion of light that is available to the sapling layer. The labelled contour lines represent the reduction factors included in the sapling growth module (see text). Example: For a light availability of 0.4 and a browsing intensity of 0.4, the reduction factor equals 0.45

empirical data for browsing intensity at the Stotzigwald provided by Odermatt (1997). Relative browsing intensity (kBrI) was set to 1, resulting in a species-specific browsing impact of 1 for European mountain ash, 0.75 for silver fir, 0.5 for European white birch and 0.25 for Norway spruce.

Initialization of ForClim with stand and weather data

In ForClim, simulations are performed for small patches that are mutually independent (i.e. no horizontal spatial effects). Therefore, model initialization with our field data (see Stotzigwald case study) was necessary at the scale of individual patches. ForClim patch size was thereby set to 225 m^2 (15 m × 15 m), and stand and regeneration data were extrapolated from the sample plots (see above) to this patch size, assuming a homogenous spatial distribution of trees and regeneration. To reduce stochastic "noise" in the results, simulation experiments were performed with numerous repetitions (n = 250 patches, cf. Bugmann 1996; Pretzsch and Dursky 2001).

The input for the weather generator in the abiotic environment submodel of ForClim was derived from monthly precipitation sums and mean temperatures from the weather station at Gurtnellen (739 m asl), located approximately 2.5 km from the Stotzigwald.

Results

Comparison of model versions

Simulating the structural development of the Stotzigwald with ForClim V2.9.3, i.e. without the improved establishment submodel, yielded a high rate of recruitment of all four species after 20 years (Fig. 7a), resulting in an overall tree density of 1,874 trees ha^{-1} (Table 6). Since no species-specific time lag is considered in ForClim V2.9.3, the species composition after 20 years was strongly influenced by the current species composition of tree regeneration at the Stotzigwald (see The ForClim model). This resulted in a large increase in the relative proportion of silver fir, European white birch and European mountain ash (Table 6), leading to co-domination by silver fir and Norway spruce. After 40 years, the overall tree density decreased to 1,435 trees ha^{-1} (Table 6), which was due to the ongoing competition between small trees, resulting in a high stress-induced mortality. The density of shade-intolerant species decreased faster than that of the shade-tolerant silver fir (Table 6). Still, the frequency histogram for tree diameter showed a strong peak at 4–16 cm DBH (Fig. 7b). Twenty years later, the overall tree density had decreased again, and the peak of young trees was found at a higher DBH (8–20 cm DBH, Fig. 7c). Thus, after 60 years most of the regeneration had already reached pole stage. Compared to the situation after 20 years, the
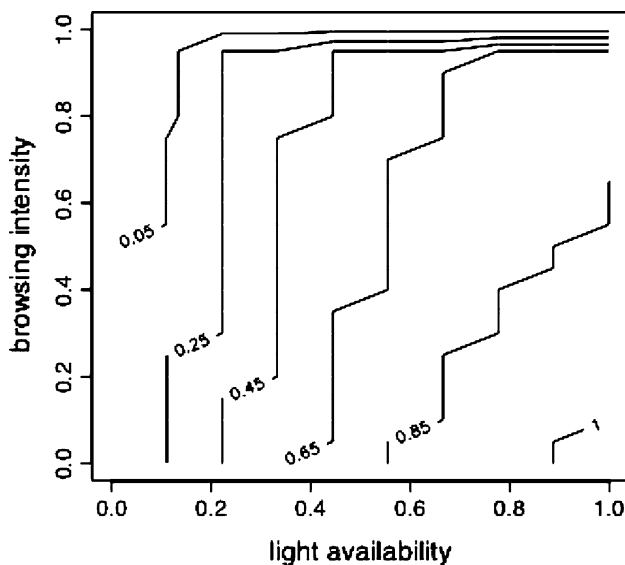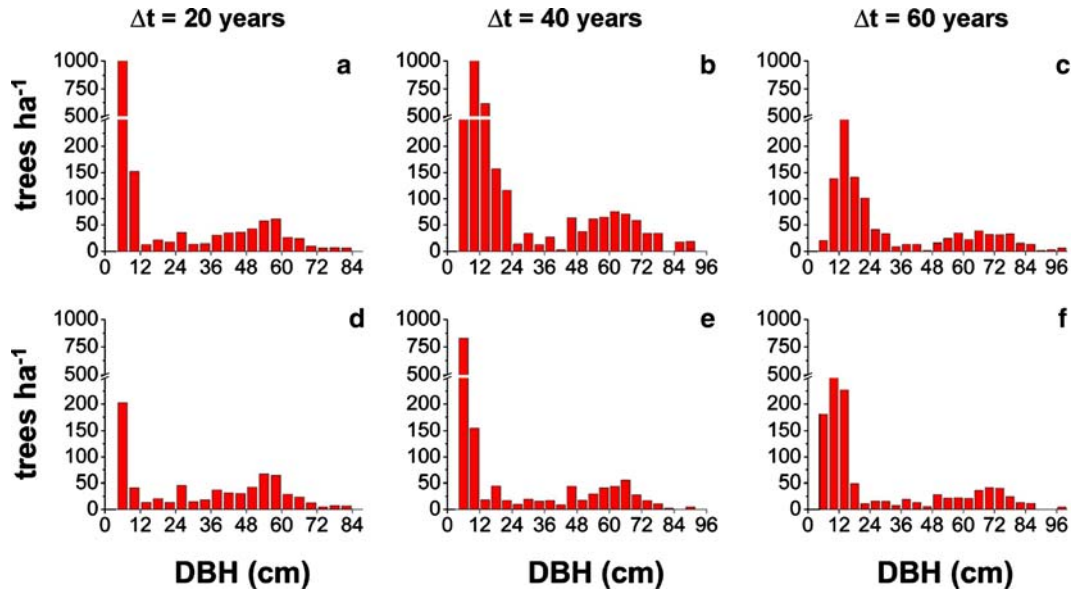
Fig. 7 Simulated diameter distribution of trees > 4 cm DBH at the Stotzigwald site after Δt = 20 (**a**, **d**), 40 (**b**, **e**) and 60 (**c**, **f**) years. Simulations were conducted with ForClim V2.9.3 (**a–c**) and with ForClim V2.9.4 (**d–f**), respectively

species composition remained relatively constant, dominated jointly by Norway spruce and silver fir (Table 6).

The simulation experiment with the new model version and maximum sapling growth yielded a strong recruitment of European mountain ash and European white birch after 20 years, which altered forest composition and resulted in an overall tree density of 725 trees ha^{-1} (Table 6, Fig. 7d). After 40 years, the density of small trees increased to a higher level (Fig. 7e), leading to an overall tree density of 1,429 ha^{-1} (Table 6). Thus, tree density almost doubled between years 20 and 40, primarily due to abundant silver fir recruitment, whereas European mountain ash and European white birch densities had decreased (Table 6). Overall tree density finally decreased to 1,241 ha^{-1} after 60 years (Table 6), with many young trees of 4–16 cm DBH (Fig. 7f). Again, as for the experiment with ForClim V2.9.3, the decrease after 60 years was due to stress-induced, density-dependent self-thinning.

Preliminary application of the improved model

Stand dynamics

The simulation runs conducted with ForClim V2.9.4 under the S-scenario ("canopy shading and no browsing impact") yielded a slow recruitment of small trees. As is evident from Fig. 8a–c, the density of small trees reached a high level only after 60 years. Overall tree density increased moderately from a density of 619 trees > 4 cm DBH ha^{-1} after 20 years to 755 after 40 and 944 and 60 years (Table 7). The increase after 20 years was mainly due to the recruitment of broad-leaved trees (European mountain ash and European white birch), whereas after 40 years it can be attributed to European mountain ash and particularly silver fir (Table 7). The final increase after 60 years was due to a massive recruitment of silver fir, which considerably changed species composition (Table 7).

Table 6 Overall tree density (> 4 cm DBH) and species composition of the potential stand after Δt = 20, 40 and 60 years. Simulations were conducted with ForClim V2.9.3 and ForClim V2.9.4, respectively

	Stotzigwald	ForClim V 2.9.3			ForClim V 2.9.4 (maximum sapling growth)		
	Current stand	Δt = 20 years	Δt = 40 years	Δt = 60 years	Δt = 20 years	Δt = 40 years	Δt = 60 years
Overall tree density (trees > 4 cm DBH ha^{-1})	561	1,874	1,435	1,033	725	1,429	1,241
Norway spruce	466 (83%)	753 (40%)	589 (41%)	478 (46%)	405 (56%)	655 (46%)	541 (44%)
Silver fir	73 (13%)	766 (41%)	679 (47%)	470 (46%)	68 (9%)	605 (42%)	632 (51%)
European white birch	7 (1%)	104 (6%)	60 (4%)	35 (3%)	98 (14%)	60 (4%)	28 (2%)
European mountain ash	0 (0%)	242 (13%)	100 (7%)	45 (4%)	142 (20%)	101 (7%)	35 (3%)
Others	15 (3%)	7 (0%)	5 (0%)	4 (0%)	12 (1%)	8 (1%)	5 (0%)
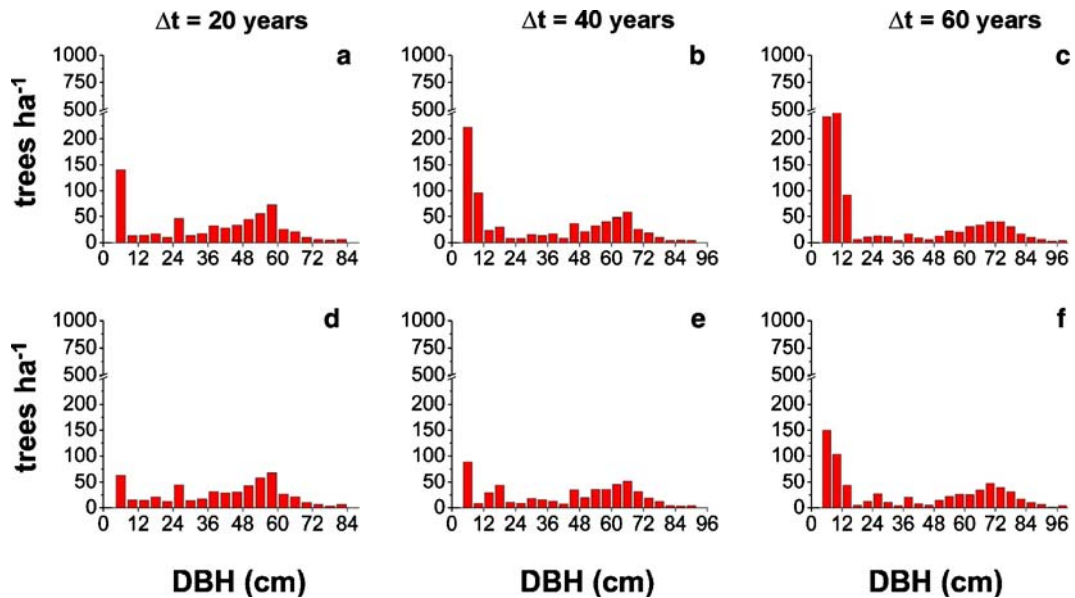
Fig. 8 Simulated diameter distribution of trees > 4 cm DBH at the Stotzigwald site after Δt = 20 (**a**, **d**), 40 (**b**, **e**) and 60 (**c**, **f**) years. Simulations were conducted with ForClim V2.9.4 under the scenarios S (canopy shading and no browsing; **a–c**) and CS (canopy shading and high browsing; **d–f**), respectively

Table 7 Overall tree density (> 4 cm DBH) and species composition of the potential stand under the two scenarios after Δt = 20, 40 and 60 years, respectively. Simulations were conducted with ForClim V2.9.4

	Stotzigwald	Canopy shading and no browsing			Canopy shading and high browsing		
	Current stand	Δt = 20 years	Δt = 40 years	Δt = 60 years	Δt = 20 years	Δt = 40 years	Δt = 60 years
Overall tree density (trees > 4 cm DBH ha^{-1})	561	619	755	944	538	542	672
Norway spruce	466 (83%)	388 (62%)	431 (57%)	485 (51%)	383 (71%)	398 (73%)	436 (65%)
Silver fir	73 (13%)	65 (11%)	142 (19%)	373 (39%)	61 (11%)	64 (12%)	187 (28%)
European white birch	7 (1%)	84 (14%)	53 (7%)	33 (4%)	81 (15%)	69 (13%)	43 (6%)
European mountain ash	0 (0%)	70 (11%)	120 (16%)	44 (5%)	0 (0%)	0 (0%)	0 (0%)
Others	15 (3%)	13 (2%)	9 (1%)	8 (1%)	13 (3%)	11 (2%)	6 (1%)

The introduction of browsing impacts ("canopy shading and high browsing impact", SB-scenario) yielded even slower recruitment of small trees (< 12 cm DBH; Fig. 8d–f). Overall tree density dropped below the initial density of 561 trees ha^{-1}, and exceeded the initial density only after 60 years, due to a substantial recruitment of silver fir (Table 7). Compared to the S-scenario, silver fir recruitment was considerably lower and delayed by 20 years, as can be expected under conditions of high browsing pressure. The highly palatable European mountain ash was prevented from reaching the canopy layer.

Protective effect

As indicated by the simulated stem densities across size classes, the protective effect in the S-scenario was equal to the initial protective effect of the Stotzigwald during the first 20 years (Table 8). After 40 years, the density of trees > 24 cm DBH fell below the target value

(Table 8). Even though the target value for trees > 12 cm DBH was not reached after 60 years, the density of 478 trees > 12 cm DBH ha^{-1} at that time could indicate buoyancy, in that the target value might be reached in the coming decades.

The protective effect in the SB-scenario was equal to that of the first scenario after the first 40 years. After 60 years, however, the density of trees > 12 cm DBH did not show an upward tendency, whereas the density of trees > 24 cm DBH stayed at a low level (Table 8).

Discussion

Comparison of model versions

The simulation with both model versions suggests a rather optimistic stand development with a large recruitment of young trees during the first 40 years (Fig. 7). This is particularly true for the simulations conducted

Table 8 Comparison of target values for effective protection against rockfall with the potential stand structure under the two scenarios after $\Delta t = 20$, 40 and 60 years, respectively. Simulations were conducted with ForClim V2.9.4

Effective DBH	Target values	Stotzigwald Current stand	Canopy shading and no browsing			Canopy shading and high browsing		
			$\Delta t = 20$ years	$\Delta t = 40$ years	$\Delta t = 60$ years	$\Delta t = 20$ years	$\Delta t = 40$ years	$\Delta t = 60$ years
Trees ha^{-1} > 12 cm	600	521	467	441	478	460	446	443
Trees ha^{-1} > 24 cm	400	438	424	373	341	415	361	357
Trees ha^{-1} > 36 cm	200	342	345	335	310	335	319	316

with ForClim V2.9.3, which yielded a very high tree density > 4 cm DBH after 20 years (Table 6). This extreme increase is due to fact that the initially present saplings of all species directly establish as young trees with an initial DBH of 1.27 cm after the first year in ForClim V2.9.3.

In Forclim V2.9.4, however, saplings first grow to a height of 2 m before establishing as trees. This is the reason why even under unrealistic maximum sapling growth, as used in this comparison, the recruitment of young trees was significantly lower and delayed compared to the simulations with ForClim V2.9.3.

The integration of the new establishment submodel had two additional effects on the simulated stand development. First, the species composition, and in particular the proportion of the two dominant species (Norway spruce and silver fir) changed more slowly than in the simulations with the old model version (cf. Table 6). Second, the onset of density-dependent self-thinning was significantly delayed (Table 6).

The most important aspect for the assessment of a forest's long-term protective function is, however, the prolonged regeneration period. Whereas after 60 years in the simulations with ForClim V2.9.3 most of the regeneration had already reached the pole stage, a large proportion of the young trees was still < 12 cm DBH at this time when simulated with ForClim V2.9.4 and maximum sapling growth. Thus, by simulating the stand without the new establishment submodel, the impact of a sparse level of tree regeneration on a forest's long-term protective function is likely to remain undetected.

Preliminary application of the improved model

Evaluation of stand dynamics

Stand development was quite slow under both scenarios, as evidenced by the moderate increase of overall tree density (Table 7). This is due to the combination of a high mortality rate and a modest recruitment rate.

During the first 20 years in both scenarios, the number of trees decreased drastically (Table 7). This was especially true for Norway spruce, which decreased by 17–18% for the > 4 cm and 13–15% and > 8 cm DBH classes, respectively. However, given the current size distribution at the Stotzigwald site (Fig. 1b) with its maximum around 44–52 cm DBH, the simulated mortality rates are comparable with values observed in other mountain forests of the region. For the three sites reported in Wehrli et al. (2005), the empirical natural mortality rates for trees > 8 cm DBH during a period of 20 years were between 10 and 12%, with peaks up to 21%.

In contrast to the mortality rates, the recruitment rates of young trees differed greatly between scenarios. The high browsing level included in the SB-scenario led to a considerable delay of the regeneration period. European mountain ash was prevented from growing into the canopy layer, and the establishment of other species was prolonged. These findings are in agreement with the literature, which reports a delayed regeneration period (Eiberle 1975; Guler 2004) and eventual loss of overstory species (Ammer 1996; Guler 2004; Wasem and Senn 2000) as a consequence of severe ungulate browsing. Such delayed regeneration periods can be expected to have a severe impact on the long-term protective effect of a mountain forest.

Evaluation of the protective effect

The results of both scenarios projected a similar decrease of the protective effect during the first 40 years, with densities of trees > 12 cm DBH and > 24 cm DBH falling below the target values (cf. Table 8). After 60 years, the density of trees > 12 cm DBH increased only slightly (S-scenario) or even decreased (SB-scenario; Table 8). Thus, in the absence of browsing, the projected decline in the protective effect of the forest may be only temporary, and the high density of trees < 12 cm DBH after 60 years (Fig. 8c) raises hope for a recovery.

Given the simulated stand development under the current high browsing pressure (SB-scenario), however, the long-term prospects for an effective protection forest are rather limited, due to the moderate density of trees < 12 cm DBH (Fig. 8f). The high browsing pressure influences both species composition and stand structure, by preventing European mountain ash from growing into the canopy layer, and prolonging the regeneration period.

The two scenarios are not intended to forecast the future, but represent two points along a complex gradient of environmental constraints in the context of which stand development is likely to occur. For exam-

ple, browsing pressure fluctuates over time, rather than being constant at a high level. Windows of relatively low browsing intensity, even if infrequent, may prove to be vital for allowing tree saplings to grow beyond the reach of ungulate browsing. Nevertheless, our simulation results of the two scenarios indicate that the protective effect of the stand is likely to decrease in the coming decades, confirming the expectations of Thali (1997).

Additionally, the site-specific requirements as postulated in the Swiss management guidelines for protection forests (Frehner et al. 2005) can hardly be achieved during the coming decades (Table 7). Even if the proportion of fir increases to 39% (S-scenario) and 28% (SB-scenario) after 60 years, a higher proportion of fir would be desirable for this site. For protection effects, silver fir has several advantages. Silver fir is highly shade tolerant and thus able to regenerate on smaller patches, minimizing the opening of the canopy and in this way maintaining the protective effect. It is also less susceptible to competing ground vegetation, and much less susceptible to biotic disturbances (Ott et al. 1997).

Simulation approach

The new model version of ForClim contains a number of simplifications that could be improved in future studies.

First, we only included canopy shading and ungulate browsing as limiting factors for sapling growth. There are, however, several other highly relevant factors. In particular, microsite types and competition with understory vegetation are known to be important for the establishment of tree regeneration in mountain forests (Brang 1998; Diaci et al. 2000; Frehner 2001; Kupferschmid 2005). However, in the current dense stands of the Stotzigwald, understory vegetation is sparse due to low light availability at the forest floor. Therefore, we assumed its impact on sapling growth to be small and did not include it in the present study. Yet, with increasing light availability in the future, the impact of competing understory vegetation is likely to increase (Ammer and Weber 1999).

A second simplification, the exclusion of sapling mortality due to environmental constraints, has already been mentioned (see Improvement of the establishment submodel). While being insignificant for short simulation periods, an explicit consideration of sapling mortality could be essential for longer simulations than used in this study. However, before including a sapling mortality routine, additional long-term data on the survival of saplings under different growing conditions are necessary. The impact of browsing on sapling mortality, still a subject to debate (Ammer 1996; Eiberle 1989; Kindermann and Hasenauer 2003; Motta 1996; Parks et al. 1998; Rüegg and Schwitter 2002; Senn and Suter 2003; Wasem and Senn 2000), requires further investigation.

In spite of these simplifying assumptions, we think that the improved model version is useful for investi-gating the structural dynamics of mountain forests over periods of multiple decades.

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