ORIGINAL PAPER

Andrea D. Kupferschmid · Peter Brang
Walter Schönenberger · Harald Bugmann

Predicting tree regeneration in *Picea abies* snag stands

Abstract A bark beetle (*Ips typographus*) infestation caused the death of almost all Norway spruce (*Picea abies*) trees in a mountain forest in the Swiss Alps. We developed a tree regeneration model, 'RegSnag' (= REGeneration in a SNAG stand), to project the future amount and height of tree regeneration in these snag stands. The model combines a height-class structured tree module with a microsite-based module of snag decay and ground-vegetation succession. Microsite-specific rates of germination, mortality and height growth were modelled for four tree species (*Picea abies, Sorbus aucuparia*, *Acer pseudoplatanus* and *Betula pendula*) in eight height classes (from seedlings to saplings 5 m tall) and on 26 microsite types (e.g. moss, grass). Model tests with independent field data from 8 years after the *Picea* die-back demonstrated that microsites had a considerable effect on the development of tree regeneration on both the montane and the subalpine level. With microsite-specific parameters, the height and frequency of *Picea* in each microsite could be simulated more accurately than without considering microsite effects (e.g. bias of 8 vs. 119 saplings ha^{-1} on the montane level). Results of simulations 40 years into the future suggest that about 330–930 *Picea* saplings per ha out of those that germinated in 1994 and 1996 will reach a height of 5 m within 30–35 years after *Picea* die-back. This is due to differences in seed inflow and browsing intensities. *Picea* and not *Betula* or *Sorbus* trees will replace the current herbaceous vegetation in these snag stands.

A. D. Kupferschmid (✉) · H. Bugmann
Forest Ecology, Department of Environmental Sciences,
Swiss Federal Institute of Technology ETH,
Universitätstrasse 16, CH-8092 Zürich, Switzerland
E-mail: andrea.d.kupferschmid@alumni.ethz.ch

A. D. Kupferschmid · P. Brang · W. Schönenberger
Swiss Federal Research Institute WSL,
Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland

Introduction

Disturbances such as windthrow and beetle infestations drive forest ecosystem dynamics over a wide range of spatial scales. When large-scale disturbances strike stands that provide protection against natural hazards (i.e. protection forests, see Brang et al. 2001), a rapid restoration of the tree cover in the destroyed stands is needed if their protective effect against snow avalanches and rock fall is to be maintained (Chauvin et al. 1994; Mössmer 1998; Schönenberger 2000). In particular, regenerating trees should provide protection before the snags, stumps and logs of the destroyed stand lose their protective effect (cf. Kupferschmid Albisetti et al. 2003).

Although many studies have been performed on tree regeneration in closed forests and in windthrow areas (e.g. Veblen et al. 1989; Ishizuka et al. 1998; Ulanova 2000; Wohlgemuth and Kull 2002), little attention has been paid to the development of natural tree regeneration after disturbance agents that kill standing trees (i.e. beetles, fungi). In interior Alaska, a spruce bark beetle (*Dendroctonus rufipennis* Kirby) outbreak caused a forest conversion from *Picea glauca* into *Betula* stands because spruce regeneration was sparse (Baker and Kemperman 1974). The same happened in the Rocky Mountains where spruce-dominated snag stands with more than 10% fir in the overstory changed into fir forests, and only stands with less than 10% fir remained spruce forests (Schmid and Frye 1977). In snag stands in the Swiss Alps and in Bavaria, it was found that only small amounts of Norway spruce (*Picea abies* (L.) Karst.) and other tree species established during the first years after *Picea* die-back (e.g. Heurich 2001; Kupferschmid et al. 2002).

In closed *Picea* stands in mountainous regions of Switzerland, tree regeneration is often sparse as well

(Brang and Duc 2002), and *P. abies* regeneration grows slowly (e.g. Lüscher 1990; Frehner 2000). Furthermore, particularly in the subalpine zone, a crucial issue in the tree regeneration process is the availability of suitable microsites. In the case of *P. abies*, such sites comprise rotten wood, moss-covered rocks or other microtopographically elevated sites that provide sufficient direct sunlight, absence of competing ground vegetation and an early snowmelt (for a discussion, see Brang 1997). The availability of such microsites clearly varies during the decay of snag stands, mainly because of changes in ground vegetation and the increase in coarse woody debris. In addition, seed availability is limited more strongly in snag stands than in closed forest stands, as most conifer seeds do not travel far from their origin (Kuoch 1965; Lässig et al. 1995; Cameron 1996). However, more light and probably also more nutrients are available in snag stands (Beudert 1999), which results in a lusher ground vegetation and a better growth of tree regeneration. Thus, predicting the future dynamics of snag stands represents several challenges.

Mathematical modelling of snag stands can be used to analyse and predict tree regeneration processes. Many forest succession models have already been used to simulate stand development. In the specific context of the present study, tree regeneration is the core component for capturing forest succession. Therefore, model approaches that do not consider height increment of small tree saplings are not suitable for our purpose (e.g. traditional gap models with recruitment of trees of 1–2 cm diameter at breast height, cf. Urban et al. 1991; Lexer and Hönninger 2001). Several models, however, include fairly detailed descriptions of tree regeneration, e.g. SORTIE (Pacala et al. 1996), FORMIX (Bossel and Krieger 1991; Huth et al. 1998), SIMA (Kellomäki and Väisänen 1991), ForGra (Jorritsma et al. 1999), the regeneration submodels of the model FOREST (Monserud and Ek 1977) and MOSES (Golser and Hasenauer 1996, 1997) and the regeneration model by Sterba (1997). However, they all have one or several of the following shortcomings: (1) parameterisation is complex or has been done only for species groups, thus making it difficult to apply them in a species-specific manner, (2) light is assumed to be the major limiting factor for tree establishment, whereas in snag stands light availability is not a key factor, (3) functions are used that integrate all the processes from seed production, seed dispersal, germination and seedling establishment, which does not allow us to disentangle these processes, (4) competition effects by the ground vegetation are not taken into account, but they are quite important in snag stands, (5) browsing by ungulates is not considered, (6) data from yield tables or mature tree characteristics are extrapolated to seedlings, or (7) they consider forest succession only as averages over large patches (e.g. 400 m^2). Furthermore, we are not aware of a simulation model that takes into account both the strong dependency of tree establishment and growth on microsite types and the continuous change in microsite

availability. For a more detailed literature review of tree regeneration models, see Kupferschmid Albisetti (2003).

As we were mostly interested in the amount and height of trees and have already developed and tested a microsite-based model of decay and ground vegetation processes (Kupferschmid and Bugmann 2005), it was obvious to combine a new model of tree regeneration structured into height classes with our earlier microsite model. Germination, growth, mortality and browsing can thereby be modelled with different characteristics in each microsite type. For example, tree saplings on moss cushions can be modelled to grow faster than saplings on coarse woody debris, even though light availability would be the same.

The present paper is focusing on the development and testing of this new model 'RegSnag' (= REGeneration in a SNAG stand) and its application to a case study (Gandberg site). The tree regeneration submodel will be described in detail here, whereas only a brief summary of the microsite module will be given (Kupferschmid and Bugmann 2005). The ultimate objectives of this study were (1) to project the abundance and height distribution of tree regeneration in the snag stands on the Gandberg site into the future, and (2) to predict the future tree species composition on the Gandberg site.

Study site

As a case study, the snag stands of the Gandberg forest (northern Swiss Pre-Alps) were chosen because (1) this area was one of the largest steep slopes in Switzerland where almost all trees were killed in the early 1990s and it was decided to leave them unharvested (forest reserve), and (2) a considerable amount of data have been collected in the snags stands during the first 8 years of succession (cf. Kupferschmid 2002; Kupferschmid et al. 2002; Kupferschmid Albisetti et al. 2003). This wealth of data can be used for model parameterisation.

The Gandberg is located on the north face of the Gandstock, south of Schwanden (canton of Glarus, Switzerland) at an elevation of 1,100–1,600 m a.s.l. The Gandberg inclines towards the North at an angle of about 14–36° (30–80%), and the lower parts do not receive direct sunshine between October and April as a result of orographic shading. The soil is an acid brown soil with a tendency to podsol (Roth 1996). Its depth varies greatly due to the presence of Verrucano boulders deposited by rockfall, mainly at the montane level. The extrapolated mean annual temperature for the Gandberg forest is 2–3°C and the mean annual precipitation 1,600–2,000 mm. The Gandberg forest is normally covered by snow from about November to April.

Before the *Picea* die-back, the entire Gandberg forest was dominated by Norway spruce (*P. abies* (L.) Karst.). Only a few silver fir (*Abies alba* Mill., 1%) and sycamore maple (*Acer pseudoplatanus* L., 3%) trees were present. The stands belong to the *Galio-Abieti-Piceetum* association at the montane level (1,200–1,450 m a.s.l.) and to

the *Homogyno-Piceetum vaccinietosum myrtilli* at the subalpine level (1,450–1,600 m a.s.l.). In 1990, the forest had a growing stock of about 820 m^3 ha^{-1} at the montane level and 590 m^3 ha^{-1} at the subalpine level (Kupferschmid Albisetti et al. 2003).

Between 1992 and 1997, a large outbreak of the European spruce bark-beetle (*Ips typographus* L.) caused the death of almost all *P. abies* trees on an area of approximately 100 ha, with a peak in 1993 when about 20 ha of *P. abies*-dominated stands died in the Gandberg forest alone (Walcher and Kupferschmid 2001). Only about 2% of the *Picea*, but all *Abies alba* and *Acer pseudoplatanus* trees survived, scattered throughout the snag stands.

Description of the model RegSnag

Model structure

The model is composed of two modules: (1) a module that calculates the changes between microsite types (Kupferschmid and Bugmann 2005), and (2) a new module that simulates the development of tree regeneration.

Brief overview of the microsite type module

The model of decay processes and ground-vegetation succession developed by Kupferschmid and Bugmann (2005) was used to simulate the changes between microsite types. The model considers the frequencies of 7 woody, 15 non-woody (including 'Boulder', 'Bare Soil' and all types with plant cover) and 3 tree-dominated microsite types ('Betula', 'Sorbus' and 'Picea'). These microsite types were defined based on (1) the dominant plant species, (2) the associated soil surface characteristics (i.e. stones, raw humus, etc.), and (3) the decomposition stage of woody debris (for a detailed description, cf. the Appendix in Kupferschmid Albisetti 2003). The model does not track the location of the microsites (i.e., it is spatially non-explicit).

At the core of this module is a Markov process with a matrix that contains all possible transition probabilities between the non-woody microsite types. These transition probabilities were parameterised separately for the montane and the subalpine levels of the Gandberg site (cf. Fig. 1, Kupferschmid and Bugmann 2005). By contrast, the amount of logs, branches and coarse woody debris is calculated based on the decay rates of snags for the whole Gandberg site (cf. Fig. 1). Note that the self-replacement probabilities of all microsite types were not incorporated in the model equations, thus deviating from the standard formulation of a Markov model. This implementation enabled us to make the following two modifications compared to the model version used by Kupferschmid and Bugmann (2005) without re-estimating all the other transition probabilities: (1) we

added a new microsite type 'Acer' because of the focus on the explicit modelling of tree regeneration in the present study, and (2) we simulated the transition probabilities from all microsite types into the microsite types dominated by trees (i.e. 'Betula', 'Sorbus', 'Acer' and 'Picea') as a function of the number of trees that are 1.3 m tall on each microsite (see below).

Tree regeneration module

Tree regeneration was divided into height classes (class 1: 4–10 cm, 2: 10.1–20 cm, 3: 20.1–40 cm, 4: 40.1–70 cm, 5: 70.1–130 cm, 6: 130.1–250 cm, 7: 250.1–500 cm and 8: > 500 cm). A value of 500 cm was chosen as the uppermost class limit because we assumed that trees are part of the 'protective regeneration' (i.e. saplings tall and thick enough to provide protection against snow avalanches sensu Ott et al. 1997) when they are taller than twice the maximum snow depth, which is about 2.5 m at the Gandberg site. For the four main tree species in these snag stands (*Picea abies*, *Betula pendula*, *Sorbus aucuparia* and *Acer pseudoplatanus*), separate height-class matrices were modelled, and for each height class, the amount and average height of the tree regeneration were simulated over time.

Ingrowth into the first height class ($N1$) is assumed to be a function of the amount of viable seeds (nSeed), the species-specific germination rate (g) and the mortality rate until the first summer (m_0):

$$N1_{s,i} = g_{s,i}(1 - m_{o_{s,i}})(n\text{Seed}_i/s\text{freq} \times \text{freq}_s), \quad (1)$$

where i = species, s = microsite type, $s$freq = total frequency of microsite types that can be occupied by tree regeneration (i.e. all types except 'Boulder', 'Tree', 'Snag', 'Stump', 'Log' and 'Branch', cf. Table 2) and freq = frequency of the microsite type s. The minimum seedling height in the first height class was set to 4 cm.

Tree regeneration in each height class is characterised by constant, class-specific rates of growth, mortality and browsing. No individual trees are modelled, but the model keeps track of the number of trees in each height class and the average height of these trees. In each time step, the number of trees that change the height class is calculated. It is assumed that these trees enter the next height class with the minimal height of this class, thus reducing the average height of all trees in this class while increasing the number of trees in the class. The probability for changing height class was assumed to be class-dependent and to increase as the average tree size approaches the upper border of the size class (Eq. 2, cf. Bugmann et al. 1989).

$$p = \left(\frac{h_{\text{mean}} - h_{\text{min}}}{h_{\text{max}} - h_{\text{min}}}\right)^x, \quad (2)$$

where h_{mean} = average height of the trees in a given class, h_{min} = minimum height of the class, and h_{max} = maximum height of the class. The parameter x

Fig. 1 Schematic diagram of the microsite type module: the *boxes* represent the microsite types included in the simulation model. *Grey boxes* are woody microsite types, *white boxes* are types dominated by stones (i.e. boulder = 'B', boulders covered by mosses = 'MoB'), bare soil (= 'Soil') or ground vegetation ('Fe' = ferns like *Drypoteris*, 'Ru' = *Rubus idaeus*, 'Poly' = *Polytrichum formosum*', 'Hylo' = *Hylocomium splendens* 'Mo' = other mosses, 'Vege' = other vegetation, cf. detailed microsite type definition in Kupferschmid Albisetti 2003, appendix). The *arrows* show the transition probabilities on the montane and subalpine elevational level; *thick arrows* denote frequent transitions (annual probability > 5%), *dashed arrows* less frequent transitions (1–5%) and *dotted arrows* rare transitions (<1%). Note that for clarity *no arrows* are drawn from non-woody microsite types to 'Logs' or 'Branches' and the tree-dominated microsite types (cf. 'Betula', 'Sorbus', 'Acer' and 'Picea') and the transition probabilities into them are not included. Modified after Kupferschmid and Bugmann (2005)
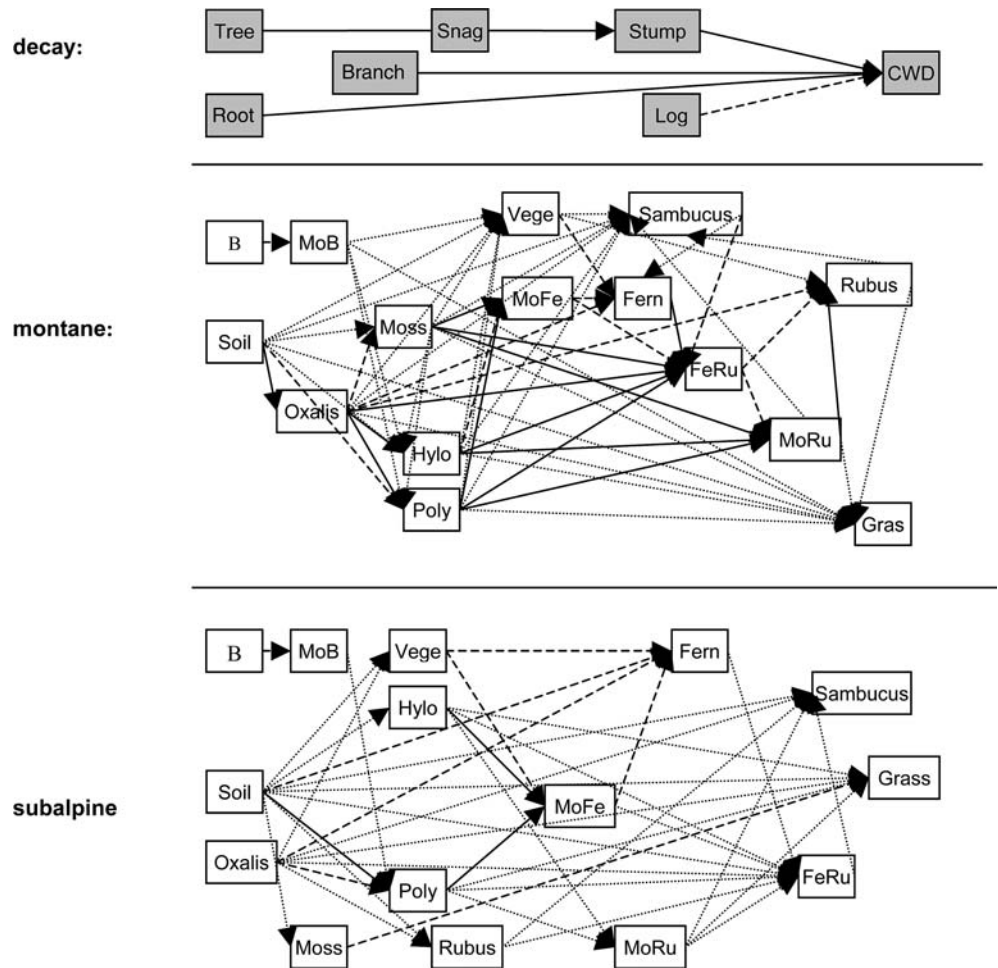
defines the shape of the curve. As some trees grow faster than an "average" tree, they would change size class earlier than average trees, thus increasing the transition probability with increasing average height. To take this into account, we used a value of $x = 20$.

Tree regeneration up to height class 5 (≤ 130 cm) was modelled separately for each microsite type. Consequently, saplings were stratified by microsite types within each height class. However, we assumed that boulders and all woody microsite types except 'Coarse Woody Debris' ('CWD') and 'Root' are unfavourable for tree regeneration, and therefore no trees establish there. For all other microsite types, microsite-specific rates of germination, growth and mortality were used (cf. Table 2). Tree regeneration in height classes 6–8 was assumed to be at least as tall as the ground vegetation, and thus to grow independently of the microsite types they inhabit. Therefore, height growth of the trees in height classes 6–8 is not microsite specific (Table 2).

Generally speaking, tree regeneration is modelled with a size class approach using continuous growth functions within each combination of species, microsite type, and height class.

Module coupling: tree regeneration in microsites

When a microsite type changes into another microsite type, the seedlings and saplings on this microsite type change their microsite type accordingly. When tree saplings reach the height of 1.3 m, the microsite type they currently inhabit is assumed to change into the tree microsite types 'Betula', 'Sorbus', 'Acer' or 'Picea'. To calculate the proportion of area that changes into a tree microsite type during such a transition, we assumed that a tree that is 1.3 m tall covers an area of 0.5 m² (calculated based on crown diameters from Hasenauer et al. 1994). However, when *Betula pendula* trees reach a height of 1.3 m in the microsite types 'Sorbus' or 'Acer', only half of this area was assumed to change into 'Betula', as we presumed a co-dominance of *Betula* with these other species. The same was assumed to happen in the opposite cases. When *Picea* trees reach the height of 1.3 m in the microsite types 'Betula', 'Sorbus' or 'Acer', it was assumed that 3/4 of this area change to 'Picea'. Conversely, we supposed that only 1/4 of the area changes from 'Picea' into 'Sorbus', 'Betula' or 'Acer', because *P. abies* is more competitive than the other three tree species. When a tree in one of these tree microsite

types died, the area it occupies was assumed to change into the microsite type 'Bare Soil'.

The number of saplings in a specific height class h on the microsite s at time $t+1$ (N_{t+1}) is therefore calculated based on the number of trees present in this height class at time t (N_t) minus the trees growing into the next height class (N_r), plus the trees 'translocating' into this microsite type ($N_{\text{trans\_into}}$), minus the trees translocating into another microsite type ($N_{\text{trans\_out}}$), minus the trees that died (N_m):

$$N_{t+1_{h,s,i}} = N_{t_{h,s,i}} - N_{r_{h,s,i}} + N_{\text{trans\_in}_{h,s,i}} - N_{\text{trans\_out}_{h,s,i}} - N_{m_{h,s,i}}. \tag{3}$$

Model implementation

The model was constructed for simulating annual changes; however, it was found to be fairly sensitive to the width of the height classes in combination with the annual height increments. For example, if the trees in height class 4 (40.1–70 cm tall) have an average height of 60 cm, they would grow on average 16 cm year^{-1} (Table 2). Thus, in the next year they would be transferred into height class 5, with an initial height of 70 cm, and therefore they would have "lost" 6 cm of height growth (discretisation problem). With a smaller time step, however, they would be allowed to change height class during the year, i.e. when they actually reach the upper height limit of class 4. Therefore, a weekly time step was chosen for the implementation of the model. Note that this choice was not biologically motivated, but resulted from the mathematical necessities of the size-class approach.

Thus, the decay rates, transition probabilities, height increments, mortality rates and browsing intensities were derived on an annual basis (p_{annual}), and were transformed into weekly parameters (p_{week}) for the simulation model according to Eq. 4.

$$p_{\text{week}} = 1 - (1 - p_{\text{annual}})^{1/52}. \tag{4}$$

Exceptions to this rule are the height increments and the reduction of terminal shoot length due to browsing, which were simply divided by 52.

The model was implemented with the STELLA® software (High Performance Systems 2001) using Euler's integration method with a time step of 1 week (discrete time model). Due to the random processes incorporated in the model (see below), we always performed 10 simulation runs. To be able to replicate the stream of random numbers in processes with a random component, we set the 'seed' in the STELLA® random number function between 1 and 10.

Model initialisation

The model was used to simulate an area of 100 m^2, and it was initialised with the conditions inferred for the Norway spruce stands in 1993. At that time, *Picea* trees had already been attacked by bark beetles, but they still carried their needles. Therefore it is reasonable to assume that the ground vegetation was still similar to that in a living stand (cf. Kupferschmid 2002).

The model was initialised separately for the montane and subalpine levels because the ground vegetation on these two levels differs considerably (cf. Kupferschmid and Bugmann 2005). The microsite module was used with the same initial values as in the original decay and vegetation development model (Kupferschmid and Bugmann 2005). The amount of tree regeneration at the beginning of the simulation (so-called "advance regeneration") was assumed to be zero for all species and height classes, as no tree regeneration was found at the Gandberg site in 1994 (Kupferschmid et al. 2002).

Model parameterisation

The model was parameterised separately for the two elevational levels, as tree regeneration grows more slowly on the subalpine than on the montane level. In this study, we assume that height increment decreases by about 10% from the montane to the subalpine level (cf. Lüscher 1990; Frehner 2000), but that germination and mortality rates are identical on these two levels.

Seed rain, germination and seedling mortality

No detailed information on seed input or seed germination rates was available for the snag stands at the Gandberg. However, vegetation succession and tree regeneration have been investigated in a pilot study on 24 permanent plots on the lower-montane level since 1994. Germinants of six tree species were found during the first 8 years after *Picea* die-back in these permanent plots (Fig. 2).

In the model context, the measured numbers of germinants are the result of seed rain, germination rates and survival rates of seedlings until July/August. Therefore, we derived the annual numbers of seeds by dividing the number of germinants in the permanent plots (cf. Fig. 2) by an average germination (g) and seedling survival rate ($= 1 - $ average seedling mortality rate $= 1 - m_o$; Eq. 5):

$$\text{seed amount} = \frac{\text{germinants}}{g(1 - m_0)} \quad (\text{N/m}^2). \tag{5}$$

For example, we assumed for *Picea* an average germination rate (g) of 30% (Brang 1996b; Holeksa 1998) and an average annual seedling mortality rate of 25% (Kupferschmid et al. 2002). Given the observed number of germinants in the permanent plots (Fig. 2), this resulted in 0 to ca. 14 seeds m^{-2} year^{-1} ($= 140,000$ seeds ha^{-1} year^{-1}) during the first 8 years after *Picea* die-back (cf. Table 1).

In addition, information about the magnitude of seed years (cf. Burkart 2001) was taken into account. In

winter 1993/1994, when the first *Picea* trees died in the Gandberg forest, many *Picea* seeds were produced on the montane level (about 3 seedlings m^{-2} in 1994, Fig. 2), even though this was not a mast year in the region (Burkart 2001). Therefore, in our model we assumed an exceptional fructification (some authors would call this a 'fear fructification') at the end of 1993 for the montane level (Table 1). Afterwards, seed availability of *Picea* probably decreased dramatically due to the almost complete die-back of *Picea* (cf. Table 1). Note that we assumed the same number of *Picea* seeds for the entire montane Gandberg forest, regardless of the distance to the adjacent green forest (minimum 50 m), because a counting of seeds on the snow surface in winter 2001 showed a uniform seed distribution with distance to the living forest (A.D. Kupferschmid, unpublished).

We assumed that seed production on the two elevational levels was not identical (cf. Table 1). Firstly, there were more living trees in the neighbourhood of the snag stands at the montane level in winter 1993 than at the subalpine level (which borders to alpine meadows, a large avalanche track and the montane snag stands); therefore, the montane stands probably received more seeds during the exceptional seed year 1993. Secondly, a larger number of *Picea* trees survived at the subalpine level until the good seed years 1995, 1997 and 1999. Thirdly, the extent of mast years is known to decrease with elevation (Mencuccini et al. 1995).

Details about the amounts of seeds for *Betula pendula*, *Sorbus aucuparia* and *Acer pseudoplatanus* are given in Kupferschmid Albisetti (2003), together with the germination and mortality rates for each of these tree species and microsite type. The results of the estimation procedure are shown in Tables 1 and 2.

Height increment

Height increments were estimated based on the data from *Picea* saplings on all microsite types of the Gandberg forest. To this end, we measured 113 *Picea* saplings that were selected randomly in 2001 on the subalpine level. The height increment in the year 2000 was related linearly to the height of these unbrowsed *Picea* saplings (height without terminal shoot of the year 2000, cf. Eq. 6, Fig. 3):

average height increment $r_{subalp} = 0.438 \times$ height (cm),

$$R^2 = 0.44, \; P < 0.001. \tag{6}$$

In addition, the height and height increment of 69 unbrowsed *Picea* saplings that were taller than about 1 m were measured in a *Picea* thicket (i.e. microsite type 'Picea') on the lower montane level beneath the snag stands of the Gandberg forest (same site conditions and also a north-facing slope). Again, terminal shoot length exhibited a linear relationship to the height measured without the terminal shoot (cf. Eq. 7, Fig. 3).

Average height increment r_{mont}
$$= 11.2 + 0.078 \times \text{height (cm)}, \tag{7}$$
$$R^2 = 0.27, \; P < 0.001.$$

Using Eq. 6, we calculated the average height increment of *Picea* saplings in the height classes 1–3 on the subalpine level (Table 2). However, there was no information about the height increment of taller *Picea* saplings on the subalpine level, because no tree taller than ca. 35 cm was found in 2001 (cf. Fig. 3). For the taller saplings in classes 5–7, we therefore used Eq. 7 as derived from the randomly sampled *Picea* saplings on the montane level, and reduced the parameters of this

Fig. 2 Number of germinants that survived until July/August when the annual field surveys were carried out in the 24 permanent plots on the montane level of the Gandberg forest. Modified after Kupferschmid et al. (2002)
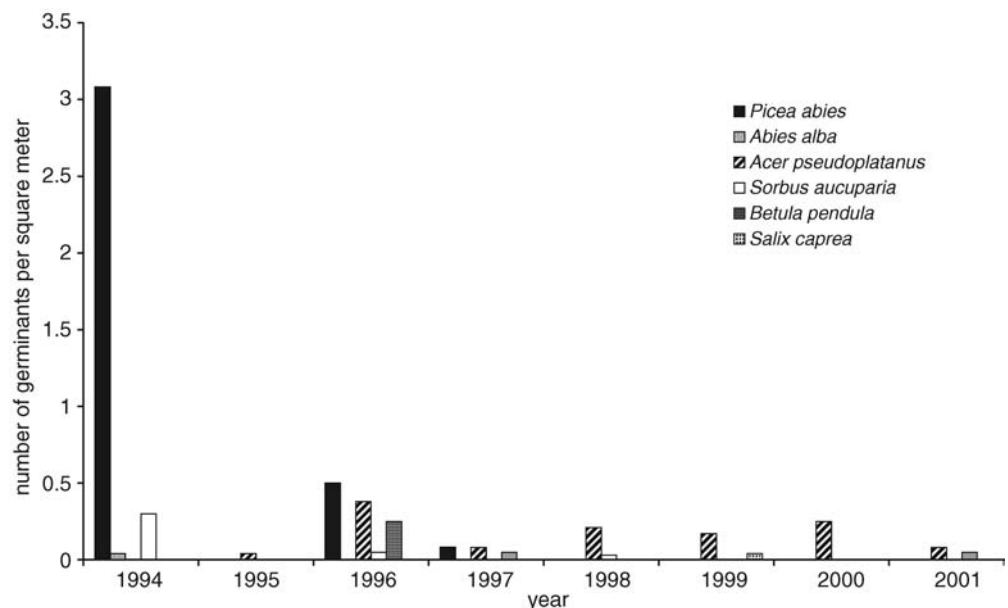
Table 1 Amount of seed inflow (ha^{-1}) assumed in the model for *Picea abies*, *Betula pendula*, *Acer pseudoplatanus* and *Sorbus aucuparia* on both elevational levels

Year	Montane (seeds/ha)	Subalpine (seeds/ha)	Mast years
Picea			
1993	140,000	46,000	Exceptional fructification
1995	22,000	66,000	Mast
1997 and 1999	3,000	9,000	Partial mast
After 2001	At random on average every 5 year 10,000–22,000	At random on average every 7 year 33,000–66,000	Full or partial mast
Other years	At random 1–1,000	At random 1–3,000	–
Sorbus	At random 1–500	At random 0–2,000	
Acer	At random 1–4,000	At random 0–500	
Betula	At random 1–350	At random 0	

Values for *Betula, Sorbus* and *Acer* were calculated every year, using the function random (min, max) in the STELLA® software which produces a uniformly distributed random number between the minimum and maximum value listed

equation by 10% to account for lower growth rates on the subalpine level (Eq. 8, Table 1, cf. Lüscher 1990; Frehner 2000):

$$\text{average height increment } r_{\text{subalp5}-7} = 10 + 0.070 \times \text{height (cm)}. \tag{8}$$

By contrast, for the small *Picea* saplings at the montane level we increased the slope of Eq. 7 by 10%, thus resulting in Eq. 9:

$$\text{average height increment } r_{\text{mont1}-3} = 0.481 \times \text{height (cm)}. \tag{9}$$

Table 2 Germination rates (g), mortality rates of seedlings (m_0), annual mortality rates of saplings (m_{1-7}) and annual height increments [r_{1-7} (cm)] of *Picea abies*, *Betula pendula*, *Acer pseudoplatanus* and *Sorbus aucuparia* in each height class (0: seeds, 1: 4–10 cm, 2: 10.1–20 cm, 3: 20.1–40 cm, 4: 40.1–70 cm, 5: 70.1–130 cm, 6: 130.1–250 cm, 7: 250.1–500 cm) on the montane (mont) and subalpine (sub) elevational level

Species	Microsite type/elevational level	g	m_0	m_1	m_2	m_3	m_4	m_5	m_6	m_7	r_1	r_2	r_3	r_4	r_5	r_6	r_7
Picea	Mont	0.3	0.25	0.3	0.2	0.1	0.05	0.03	0.02	0.01	3.4	7.2	14.4	16.0	18.9	26.0	40.4
	Sub	0.3	0.25	0.3	0.2	0.1	0.05	0.03	0.02	0.01	3.1	6.6	13.1	14.5	17.0	23.3	36.3
	Bare Soil	=	=	=	=	=	=	=			=	=	=	=	=		
	Oxalis	−	+	+	=	=	=	=			−	−	=	=	=		
	Root: Mont	+ +	−	=	=	=	=	=			− −	− −	−	−	−		
	Sub	+ +	− −	− −	−	−	−	−			− −	− −	−	−	−		
	MossBoulder	+	+	+	=	=	=	=			=	=	=	=	=		
	Polytrichum	=	+	=	=	=	=	=			=	=	=	=	=		
	Hylocomium	−	+	=	=	=	=	=			=	=	=	=	=		
	Other Moss	+	+	=	=	=	=	=			+	+	=	=	=		
	Fern	=	+ +	+ +	+ +	+ +	+ +	=			−	−	−	−	=		
	Rubus	− −	+ +	+ +	+ +	+ +	+ +	+			− −	− −	− −	− −	− −		
	MossRubes	=	+	+	+	+	+	+			=	=	=	=	=		
	MossFern	=	+	+	+	+	+	=			=	=	=	=	=		
	CWD: Mont	+ +	−	=	=	=	=	=			− −	− −	−	−	−		
	Sub	+ +	− −	−	−	−	−	−			− −	− −	−	−	−		
	FernRubus	− −	+ +	+ +	+ +	+ +	+ +	+ +			− −	− −	− −	− −	− −		
	Grass	− −	+ +	+ +	+ +	+ +	+	=			=	=	=	=	=		
	Other Vege: Mont	=	=	+	+	+	+	+			−	−	−	−	−		
	Sub	=	+	+	+	+	=	=			=	=	=	=	=		
	Sambucus	=	=	=	−	−	−	−			+	+	+	+	+		
	Betula	+	=	=	−	−	−	−			+	+	+	+	=		
	Sorbus	+	=	=	−	−	−	−			+	+	+	+	+		
	Picea	−	+	+ +	+ +	+ +	+ +	+ +			=	=	=	=	=		
	Acer	+	=	=	−	−	−	−			+	+	+	+	+		
Betula	Mont	0.4	0.1	0.2	0.1	0.08	0.03	0.02	0.01	0.005	13.0	15.0	18.0	23.0	33.0	53.0	95.0
Sorbus	Mont	0.4	0.1	0.2	0.1	0.08	0.03	0.02	0.01	0.005	5.0	9.0	16.0	18.0	20.0	26.0	32.0
	Sub	0.4	0.1	0.2	0.1	0.08	0.03	0.02	0.01	0.005	4.5	8.1	14.4	16.2	18.0	23.4	28.8
Acer	Mont	0.5	0.05	0.05	0.04	0.03	0.02	0.01	0.005	0.001	3.4	7.2	14.4	18.0	22.0	30.0	45.0
	Sub	0.5	0.05	0.05	0.04	0.03	0.02	0.01	0.005	0.001	3.1	6.6	13.1	16.2	19.8	27.0	40.5

Germination and mortality are probabilities, whereas height increment is given in cm year^{-1}. For *Betula* only average values are listed, while for *Picea* average values and microsite specific variations are inclued, i.e. for germination rates (g) and height increments (r_{1-5}), the signs stand for; − −, 50% of mean rate; −, 75%; =, 100%; +, 125%; and + +, 150%. In contrast, for mortality rates (m_{0-5}) the signs stand for; + +, 50% of mean rate; +, 75%; =, 100%; −, 125%; and − −, 150%. Note that m_{6-7} and r_{6-7} are not microsite dependent. The microsite type 'Other Vege' was mostly composed of *Senecio ovatus* on the montane, and of *Vaccinium myrtillus* on the subalpine level

The average height increment of class 4 saplings (r_4) was interpolated between r_3 and r_5 for both elevational levels (Table 2).

We would have preferred to use one single regression equation for the height increment of *Picea* on each level based on measurements of *Picea* seedlings and saplings of 0 up to 5 m height. However, this was not possible with the available data. Yet, using the procedure described above, we obtained plausible height increments for each height class (cf. Table 2).

Based on a literature survey, the microsite-specific height increments were estimated as deviations from the mean values (described above) for each height class. Thereby we took into account the range between the maximum and minimum values in the data set (Fig. 3). We assumed that saplings in a 'very unfavourable' habitat ("−−" in Table 2) had only 50% of the average height increment, whereas saplings in a 'very favourable' habitat ("+ +" in Table 2) had 150% (see Kupferschmid Albisetti (2003) for the derivation of the microsite-specific rates as well as for the details of the derivation of the parameter values for *Betula pendula*).

Sorbus aucuparia and *Acer pseudoplatanus* seedlings and saplings were found to be browsed very heavily by chamois at the Gandberg site (cf. Kupferschmid et al. 2002). Hence, we modelled *Sorbus* and *Acer* regeneration in a simpler manner than *Picea* and *Betula* regeneration, i.e. by abandoning microsite-specific rates and only using mean germination, mortality and growth rates. Again, the parameterisation details were described by Kupferschmid Albisetti (2003).

Browsing intensity

Browsing was assumed to be distributed uniformly within a height class, i.e. all saplings were browsed with the same probability. Therefore, it was assumed that individual losses of the terminal shoot that result from ungulate browsing can be summed up to derive the total annual height increment loss within a height class. The total height increment of the trees in each height class was therefore reduced each year by the browsing intensity as estimated in Table 3. This procedure was chosen because no individual trees were modelled with our height-class approach. The parameter values were estimated as described below.

The Gandberg forest lies within the wildlife sanctuary 'Freiberg Kärpf', and chamois (*Rupicapra rupicapra*) is by far the most frequent ungulate species (Schmidt 1983). The only browsing data available indicate that the terminal shoots of 9 out of 13 living *Picea* saplings were browsed in the year 2001 in the 24 permanent plots in the Gandberg forest (Kupferschmid et al. 2002). This is equal to a browsing intensity of about 70% for *Picea* in height classes 2 and 3 (Table 3). Generally, browsing by chamois affects saplings that are shorter than about 1.3 m (Eiberle and Nigg 1986), in particular those in the height range 10–40 cm, i.e. saplings in the height classes 2–3 of the model. Saplings in height class 1 are browsed less often than taller ones (Eiberle and Nigg 1986; Wunder 2002). Hence we assumed a lower browsing intensity in class 1 than in classes 2 and 3 (Table 3). Seedlings and small saplings may die due to browsing. For example, Rüegg

Fig. 3 Height increment of 113 unbrowsed randomly sampled *Picea abies* saplings on the subalpine level of the Gandberg forest and 69 in a thicket of *Picea* saplings on the montane elevational level beneath the Gandberg forest. The *solid lines* represent the result of linear regression (Eqs. 6, 7), while *dotted lines* indicate a height increment of 50 and 150% of the average, respectively
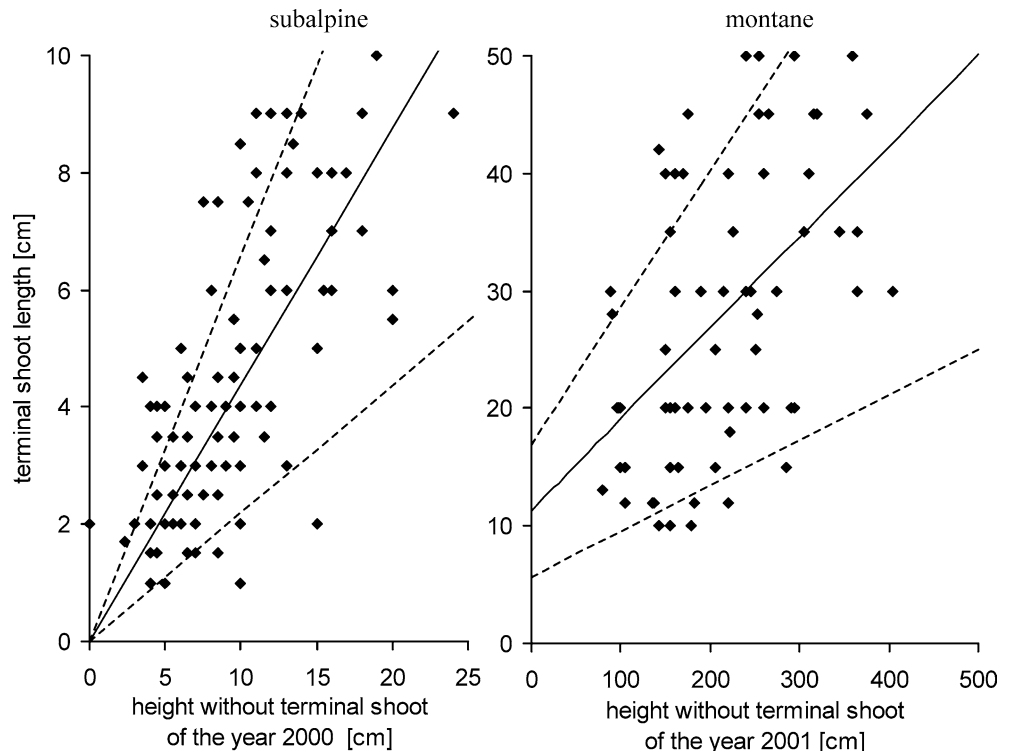
Table 3 Estimated browsing intensity (*br*, i.e. annual probability that terminal shoot is browsed) and mortality induced by ungulates (*bm*, i.e. annual probability of death due to browsing by ungulates in height class 1) on *Picea abies*, *Sorbus aucuparia*, *Acer pseudoplatanus* and *Betula pendula*

Species		Height classes				
		1 (4–10 cm)		2–3 (10.1–40 cm)	4 (40.1–70 cm)	5 (70.1–130 cm)
		bm (%)	br (%)	br (%)	br (%)	br (%)
Picea	Montane	15	10	70	40	20
	Subalpine	15	30	35	20	10
Sorbus and Acer	Montane	30	50	80	70	60
	Subalpine	30	50	75	65	55
Betula	Montane	0	0	0	0	0

and Schwitter (2002) observed in windthrow areas an annual mortality rate due to browsing of about 5% for *Picea*. Due to the exceptionally high browsing pressure on the Gandberg forest, we assumed that the browsing-induced mortality was about three times as high, i.e. 15% per year (Table 3). In the model, this browsing-induced mortality rate acts in addition to the normal mortality rate of seedlings and saplings in the first height class (m_1, Table 2).

Browsing intensities were assumed to be equal on all microsite types due to a lack of microsite-specific data. According to personal observations in the Gandberg forest, browsing pressure was higher in winter on the montane than on the subalpine level, presumably because of lower snow depth. Therefore, browsing intensities on the subalpine level were assumed to be about half of those on the montane level (cf. Table 3), except for *Picea* seedlings in the first height class, because ground vegetation was generally shorter on the subalpine level, which probably resulted in a better detectability of seedlings by the ungulates.

Furthermore, we assumed a higher browsing intensity on *Sorbus aucuparia* and *Acer pseudoplatanus* than on *Picea*, as we found no unbrowsed *Acer* sapling in the permanent plots (cf. also Ott et al. 1991; Nüsslein and Faisst 1998; Wunder 2002). As ungulates preferentially browse these two species and seedlings and saplings are easier to detect on the subalpine level, we assumed a reduction in browsing intensity on saplings by just 5% relative to the montane level (Table 3). By contrast, *Betula* seedlings and saplings were assumed to be unattractive for chamois and therefore not to be browsed (Table 3).

Although there were some large *Abies alba* trees on the Gandberg forest, we ignored *Abies* and *Salix* in our tree regeneration model because only very few seedlings were found in the permanent plots (cf. Fig. 2), and *Abies* was browsed even more than *Acer* (i.e. 100% regeneration failure of *Abies* in the Gandberg, Kupferschmid et al. 2002).

Data for model validation

In June 2001, tree regeneration was investigated on the Gandberg forest in those *Picea* stands in which *Picea* trees had died in 1993. Sampling took place at three elevational levels (lower montane: 1,220–1,280 m a.s.l., upper montane: 1,310–1,370 m, and upper subalpine: 1,540–1,600 m). At each level, eight blocks were selected randomly. Each block contained four strip transects that were arranged (1) parallel to, (2) perpendicular to, and (3,4) at an angle of 45° to the contour lines, i.e. the four strip transects spanned a tetrahedron. Each strip transect was 10 m long and 2 m wide. Along these 96 strip transects (3 levels × 8 blocks × 4 transects per block), the following characteristics were measured/determined for each tree seedling and sapling: height (the terminal shoot of 2001 was not included), terminal shoot increment in 2000, browsing and other damages, and the microsite type.

In total, 251 *Picea abies*, 248 *Acer pseudoplatanus*, 60 *Sorbus aucuparia* and 15 *Betula pendula* saplings were sampled on the montane level, whereas on the subalpine level, 195 *Picea*, 10 *Acer*, 64 *Sorbus* and no *Betula* saplings were found. These data, which were not used for parameter estimation, served to evaluate the accuracy of the model after eight simulation years, as described below.

Model evaluation

Parameter sensitivity analyses were conducted to answer the following main question: Is it important to differentiate microsite-specific rates of germination, mortality and growth, or would it be sufficient to use average rates? In other words, do predictions from model runs with microsite-specific rates match validation data better than those with average rates only? Eight different simulation experiments (i.e. scenarios) were carried out over 8 years for *Picea* (Table 4), so that the model output could be compared against independent field data (validation data set).

The comparison was performed by calculating three indices: (1) bias, describing the mean difference between simulated and observed tree numbers (Eq. 10), (2) precision, expressed as the standard deviation of the difference between simulated and observed numbers (Eq. 11), and (3) accuracy, describing the degree of convergence of simulation to observation (Eq. 12). The bias can be positive or negative. If there is no difference between observed and simulated numbers, the value of all three indices becomes zero:

$$\text{bias} = \overline{e} = \frac{\sum\limits_{i=1}^{n}(e_i)}{n} = \frac{\sum\limits_{i=1}^{n}(\text{simulated}_i - \text{observed}_i)}{n} \quad (10)$$
$$(\text{N/ha}),$$

$$\text{precision} = s_e = \sqrt{\frac{\sum\limits_{i=1}^{n}(e_i - \overline{e})^2}{n-1}} \quad (\text{N/ha}), \quad (11)$$

$$\text{model accuracy} = m_e = \sqrt{s_e^2 + \overline{e}^2} \quad (\text{N/ha}), \quad (12)$$

where simulated and observed stands for the simulated and observed numbers of trees ha^{-1}, respectively, and i for the 26 microsite types ('Tree', 'Snag' and 'Stump' were pooled, and so were 'Acer', 'Betula' and 'Sorbus') or the seven height classes, respectively. The model was evaluated separately for the frequency of *Picea* in each microsite type (cf. Evaluation of the frequency of *Picea* in each microsite type) and in each height class (cf. Evaluation of the frequency of tree regeneration in each height class). These analyses focused on *Picea*, as a comparison between observed and simulated data for *Acer pseudoplatanus*, *Betula pendula* and *Sorbus aucuparia* would have made little sense due to the small numbers of observed saplings (cf. Data for model validation), whereas in the case of *Acer* on the montane level, the saplings were browsed too heavily.

We also carried out a sensitivity analysis for the effect of browsing intensity on the number and height of *P. abies* trees. The results are presented elsewhere (Kupferschmid Albisetti 2003).

Evaluation of the frequency of *Picea* in each microsite type

Montane level

The largest differences between simulated and observed frequencies of *P. abies* seedlings and saplings in 2001 were found for the microsite types dominated by *Rubus idaeus* (Fig. 4). The numbers of *Picea* on 'Fern-Rubus' and 'Rubus' were overestimated considerably ($e_{\text{FernRubus}} = 280.19$ saplings ha^{-1} and $e_{\text{Rubus}} = 137.31$), while the numbers on 'MossRubus' were underestimated ($e_{\text{MossRubus}} = -96.25$, cf. Table 5). Besides these differences, the numbers of *Picea* on all moss microsite types,

Table 4 Possible combinations between microsite-specific (*s*) and average (*a*) rates of germination (*g*), mortality (*m*) and growth (*r*)

	ga	gs
ma	ga ma ra	gs ma ra
	ga ma rs	gs ma rs
ms	ga ms ra	gs ms ra
	ga ms rs	gs ms rs

on 'Other Vegetation', 'Root', 'CWD' and 'Boulder' were underestimated just slightly (e_i values < -10 saplings ha^{-1}), whereas on the microsite types 'Fern', 'MossFern', 'MossBoulder' and 'Sambucus', they were overestimated slightly (e_i values > 10 saplings ha^{-1}, cf. Table 5).

The scenario with only average process rates, i.e. 'gama-ra', always resulted in the poorest agreement between observed and simulated data (bias = 119 saplings ha^{-1}, model efficiency = 338, cf. Table 6). Hence, *Picea* was not distributed uniformly across the microsite types. Compared to the 'all average' scenario, microsite-specific rates of germination ('gs-ma-ra') or microsite-specific rates of mortality ('ga-ms-ra') improved the agreement with the observed frequencies considerably (Table 6). However, the simulated frequencies were closest to the observed data when all rates were assumed to be microsite-specific ('gs-ms-rs': bias = 8 saplings ha^{-1}, cf. Table 6).

Subalpine level

The agreement between simulated and observed frequencies of *Picea* seedlings and saplings in each microsite type was generally lower on the subalpine than on the montane level (Fig. 3, Table 6). In particular, the numbers of *Picea* on the microsite types 'Bare Soil', 'Polytrichum', 'MossFern' and 'Fern' were overestimated strongly with the model for the subalpine level ($e_i > 100$ saplings ha^{-1}, cf. Table 5). In contrast, the frequencies of trees on the microsite types 'Root', 'Coarse Woody Debris' ('CWD') and 'Other Vegetation'

Table 5 Difference between simulated and observed numbers of *Picea abies* seedlings and saplings on each microsite type ($= e_i$ (N/ha), i.e. Eq. 10). The model with microsite-specific parameters 'gs-ms-rs' was used

Microsite type	Montane	Subalpine
Tree/Snag/Stump	0.00	0.00
Log	0.00	0.00
Branch	−7.81	−31.25
Root	−35.00	−908.63
CWD	−13.63	−727.25
Bare Soil	5.00	293.38
Oxalis	0.56	−16.25
Polytrichum	−91.69	912.38
Hylocomium	−133.06	−71.13
Other Moss	−18.06	−38.75
MossBoulder	82.44	50.75
Boulder	−15.63	0.00
MossFern	48.13	324.75
Fern	39.38	225.38
FernRurbus	280.19	8.00
Rurbus	137.31	−12.63
MossRubus	−96.25	−36.88
Sambucus	20.19	16.75
Other Vege	−23.38	−198.25
Grass	−7.63	76.13
Acer/Betula/Sorbus	0.00	0.00
Picea	0.00	0.00

Fig. 4 The number of *Picea abies* seedlings and saplings on the microsite types in percent of all saplings in 2001. A comparison of simulated and observed (average ± standard deviation) frequencies is shown. Simulations were carried out with average values (*a*) or microsite-specific values (*s*) of the rates of germination (*g*), mortality (*m*) and height increment (*r*). For the subalpine level, simulation results with microsite-specific height increments (*r_s*) are not shown because they were found to be almost indistinguishable to results with average growth rates (*r_a*). Where only *filled symbols* are visible, the simulation with average and microsite-specific germination rates gave identical results
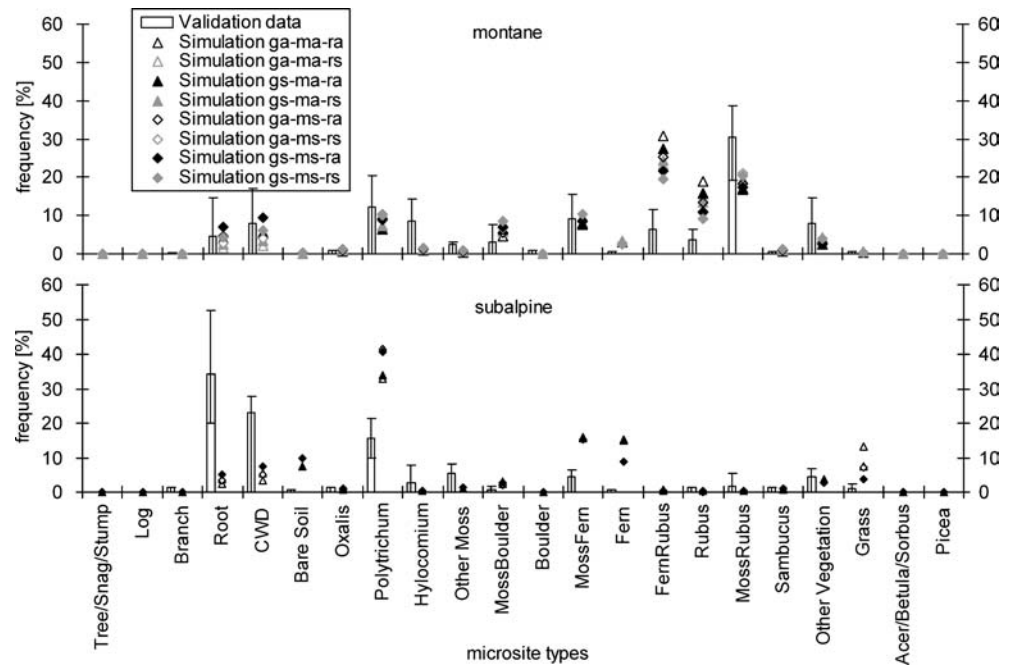
were underestimated considerably ($e_i < -100$ saplings ha^{-1}, cf. Table 5).

Nevertheless, particularly the microsite-specific mortality rates were important in explaining the differences between a uniform distribution of *Picea* on all microsite types (scenario 'ga-ma-ra', bias$_{gamara}$ = 46 saplings ha^{-1}) and the observed distribution (bias$_{gamsra}$ = −2 saplings ha^{-1}, cf. Table 6).

Evaluation of the frequency of tree regeneration in each height class

Montane level

The numbers of *Picea* trees in each height class varied strongly between the eight simulation scenarios (cf. Fig. 5), and so did the values of bias, precision and model accuracy (Table 6). Particularly the microsite-

specific rates of growth and mortality had a large effect on tree numbers in each height class (Fig. 5, Table 6), whereas microsite-specific germination rates had only a small influence on the number of *Picea* in each height class.
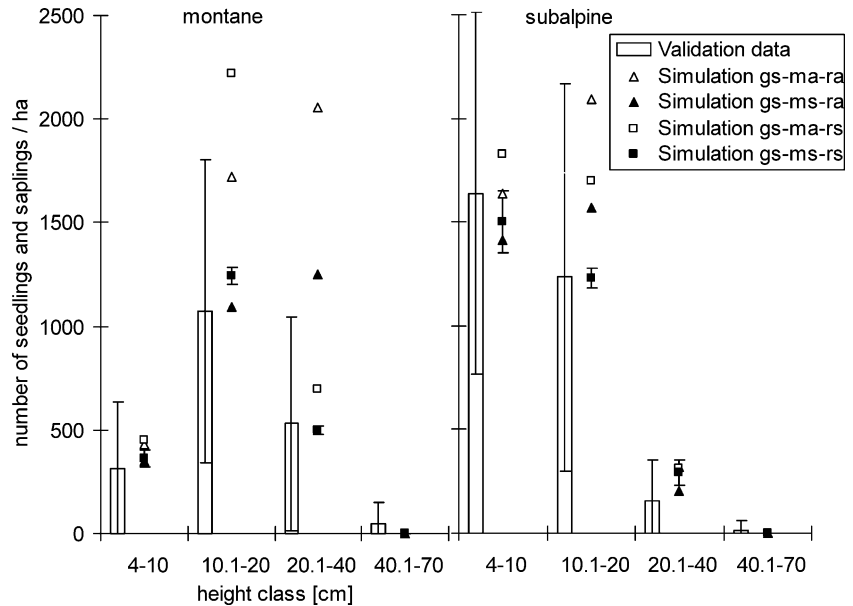
Overall, 1961 *Picea* seedlings and saplings per ha were observed on the montane level of the Gandberg forest in 2001, while 2091 ha^{-1} resulted for the simulation where all rates were assumed to be microsite-specific (i.e. 'gs-ms-rs'). It is noteworthy that no *Picea* regeneration taller than 70 cm was found 8 years after *Picea* die-back on the Gandberg forest, a feature reproduced by the simulations over 8 years (i.e., trees only in classes 1–4, Fig. 5). In addition, most *Picea* saplings were found in height class 2 (10.1–20 cm) on the Gandberg forest (54.6%), and this was reproduced nicely in the 'gs-ms-rs' scenario (59.4%, Fig. 5).

Similarly encouraging results were obtained for the other three tree species (cf. Kupferschmid Albisetti

Table 6 Bias (ē), precision (se) and model accuracy (me) for each microsite type and height class according to Eqs. 10, 11, 12 for *Picea abies* seedlings and saplings on both elevational levels (N/ha)

Model	Microsite types						Height classes					
	Montane			Sulbalpine			Montane			Subalpine		
	ē	se	me	ē	se	me	ē	se	me	ē	se	me
ga-ma-ra	119	317	338	46	399	402	670	743	1001	283	628	688
gs-ma-ra	99	247	266	40	377	379	562	707	903	251	548	603
ga-ma-rs	78	219	233	38	399	401	427	599	735	237	337	412
gs-ma-rs	64	175	186	31	380	381	351	539	643	198	266	332
ga-ms-ra	36	141	145	−2	349	349	207	343	400	26	295	296
gs-ms-ra	31	116	120	0	333	333	182	359	403	36	287	289
ga-ms-rs	12	99	99	6	356	356	64	121	137	0	116	116
gs-ms-rs	*8*	*83*	*84*	*−6*	*344*	*344*	*42*	*119*	*127*	*2*	*94*	*94*

174

Fig. 5 Number of *Picea abies* seedlings and saplings in each height class in 2001. A comparison of simulated (mean, respectively mean ± standard deviation for "gs-ms-rs") and observed (mean ± standard deviation) tree numbers is shown. Simulations were carried out with average values (*a*) or microsite-specific values (*s*) of the rates of mortality (*m*) and height increment (*r*). Simulation results with average germination rates (*ga*) are not shown because they were found to be almost indistinguishable to the results with microsite-specific germination rates (*gs*)

2003). In total, 117 *Betula pendula* seedlings and saplings ha^{-1}, 496 *Sorbus aucuparia* and 1938 *Acer pseudoplatanus* were found in 2001 at the Gandberg site, and 194, 485 and 2,123 seedlings and saplings ha^{-1} were simulated, respectively.

Subalpine level

Again, the numbers of *Picea* per height class varied strongly between the eight simulation scenarios, and microsite-specific rates of mortality had the largest effect on the numbers of trees (Fig. 5, Table 6). Overall, 3,047 *Picea* seedlings and saplings per ha were observed on the subalpine level of the Gandberg forest in 2001, while 3,023 ha^{-1} resulted for the scenario where all rates were assumed to be microsite specific (i.e. 'gs-ms-rs').

Similar to the montane level, no *Picea* regeneration taller than 70 cm was found on the subalpine level of the Gandberg forest 8 years after *Picea* die-back. However, in contrast to the montane level, *Picea* seedlings and saplings were mostly found in height class 1, followed by class 2. Both features were reproduced well by the 'gs-ms-rs' scenario (Fig. 5).

The results obtained for the other three tree species were satisfactory as well (cf. Kupferschmid Albisetti 2003). In total, 156 *Acer* and 1,000 *Sorbus* seedlings and saplings ha^{-1} were found in the subalpine Gandberg forest, and 264 *Acer* and 1,014 *Sorbus* were simulated by the model.

Results of long-term simulations

Long-term simulations were carried out over 40 years with the following aims: (1) to project the density and height distribution of *Picea* regeneration into the future,

and (2) to predict the future species composition of the snag stands, separately for each elevational level of the Gandberg forest.

Future amount and height of *Picea* regeneration

Montane level

The total number of *Picea* saplings declined strongly in the first years (Fig. 6) due to mortality and the much larger amounts of seeds at the end of 1993 and 1995 than in the other years. When only the sapling cohorts of 1994 and 1996 were simulated over time, their amount decreased to about 330 trees ha^{-1} after about 35 years (cf. Fig. 6), while their average height increased strongly (note that class 8 in the model with trees taller than 5 m had no height increment and mortality, thus explaining the constant values in the top right part of Fig. 6).

Subalpine level

Almost three times as many *Picea* saplings of the cohorts that germinated in 1994 and 1996 were simulated to survive at the subalpine level (930 ha^{-1}) compared to the montane level (330 ha^{-1}, cf. Fig. 6). Two reasons are responsible for this result: first, we assumed for the subalpine level a seed inflow that was three times larger than at the montane level during mast and partial mast years, as there were considerably more surviving *Picea* seed trees at the subalpine level (cf. section Model parameterisation); and second, browsing intensities in height classes 2–5 were only half as high in the subalpine compared to the montane level (Table 3). For the same reason, it took less time for trees at the subalpine level to grow up to 5 m height (cf. Fig. 6).
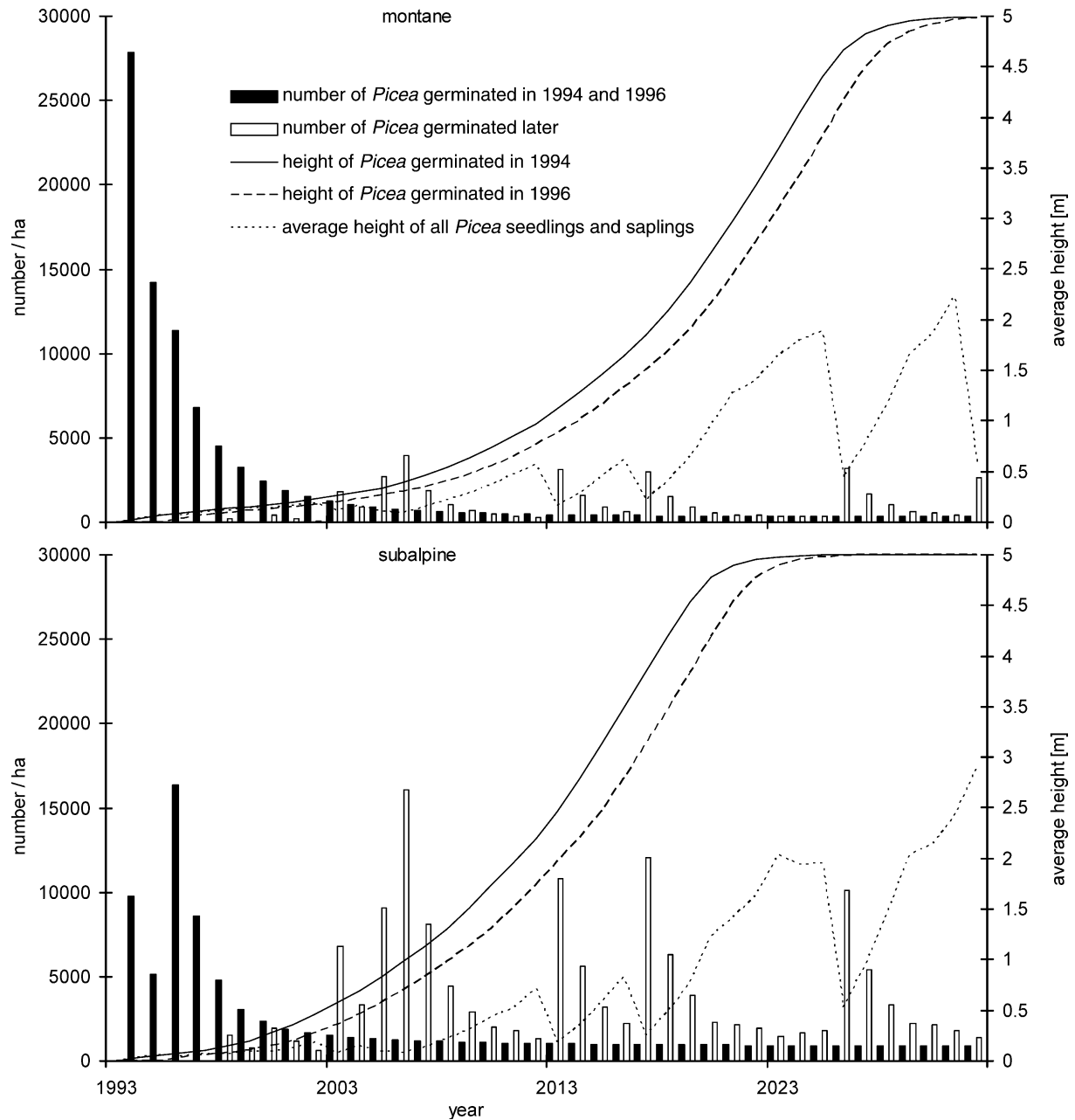
Fig. 6 Simulated numbers and average height of *Picea abies*. Simulations were performed with microsite-specific germination, mortality and growth rates (gs-ms-rs, cf. Table 2), with the estimated browsing intensities (cf. Table 3) and seed inputs (cf. Table 1). Amounts and heights of the *Picea abies* saplings germinated in 1994 and 1996 were calculated in two separate simulation runs where only these cohorts germinated

It should be kept in mind here that we modelled only the average height of the trees in a height class, and that the height growth increment in each height class is reduced according to the browsing intensities of the classes. Therefore, no tree can grow up without having been browsed if browsing intensities are non-zero. Thus, if browsing amounts to 40 and 20% on the montane and subalpine level, respectively, and height growth without browsing is 7.2 and 6.6 cm, respectively, the simulated average trees actually grow 60% of 7.2 cm and 80% of 6.6 cm, i.e. 4.32 cm on the montane and 5.28 cm on the subalpine level.

Future species composition

In the model, the succession of the microsite types has a direct influence on the future rates of germination, mortality and growth, and an indirect influence on the future tree number and species composition. Conversely, tree growth has a direct effect on the frequency of microsite types, as microsite types with trees taller than 1.3 m change into one of the four tree microsite types ('Betula', 'Sorbus', 'Acer' or 'Picea'). Thus, future tree growth is altered by microsite type changes, and tree growth in turn alters the frequency of the microsite types.

Montane level

According to the long-term simulations, the microsite types 'Betula', 'Sorbus', and 'Acer' together are anticipated to cover only 1.6% of the area about 30 years after the *Picea* die-back (cf. bar for 'Betula/Sorbus/Acer' in Fig. 7). According to our rating (Table 2), *Betula pendula*, *Sorbus aucuparia* and *Acer pseudoplatanus* thickets are among the 'favourable' microsite types for *Picea* establishment. Hence, after 30 simulation years about 6.4% of the *Picea* seedlings and saplings were found on these microsite types (cf. diamonds in Fig. 7).

Furthermore, because trees that are taller than 1.3 m (i.e., size classes 6–8) were assumed to dominate their microsite type and therefore to represent a microsite type of their own (i.e., 'Betula', 'Sorbus', 'Acer' or 'Picea'), we conclude that in the snag stands on the montane level, somewhat higher numbers of the deciduous tree species will establish compared to *Picea* (i.e., 1.6 vs. 1.3% microsite cover, Fig. 7). This is mostly due to their good germination ability on open sites during the first years after *Picea* die-back and the absence of browsing in the case of *Betula* saplings. However, the simulated frequencies of single microsite types for the future cannot be taken literally because the proportion of the area which changes into a tree microsite type when a tree reaches the height of 1.3 m (i.e. 0.125–0.5 m^2) was probably underestimated. For example, the anticipated ca. 3.3 *Picea* saplings per 100 m^2 ($= 330$ trees ha^{-1}) that are taller than 1.3 m in the year 2023 (cf. white bar and dotted line in Fig. 6) would probably occupy more space than only about 1.3 m^2 (i.e. 1.3% of the area, cf. white bar in Fig. 7).

Nevertheless, the long-term simulations show that coarse woody debris ('CWD'), logs and *Rubus idaeus* will probably cover the largest fraction of the area about 30 years after the *Picea* die-back (bars in Fig. 7). Coarse woody debris will become one of the most if not the most important microsite type for *Picea* regeneration at that time (diamonds in Fig. 7).

Subalpine level

Microsite types such as 'Fern', 'MossFern', 'CWD', 'Log', 'Grass' and—to a lower extent—also 'Polytrichum' will probably still dominate the subalpine level of the Gandberg forest about 30 years after the *Picea* dieback, besides the new *Picea* thickets (cf. bars in Fig. 7). The most favourable microsite types for *Picea* regeneration will be 'CWD', 'Polytrichum', 'MossFern' and 'Fern' (cf. diamonds in Fig. 7).

In contrast to the results for the montane level, our simulations for the subalpine level suggest that the microsite types 'Sorbus' or 'Acer' will be more scarce (0.9% of the area) than the microsite type 'Picea' (5.4%) at that time (cf. Fig. 7). This low amount of deciduous trees that will reach the height of 1.3 m is caused by (1) the estimated low seed inflow rates (Table 1) and (2) the assumed high browsing rates of ungulates on *Sorbus* and *Acer* (Table 3).

Discussion

Importance of microsites

We developed a new tree regeneration model for snag stands ('RegSnag') that considers microsite-specific differences in germination, mortality and growth rates. The model is based on the assumption that microsite types are crucial for explaining the establishment and viability
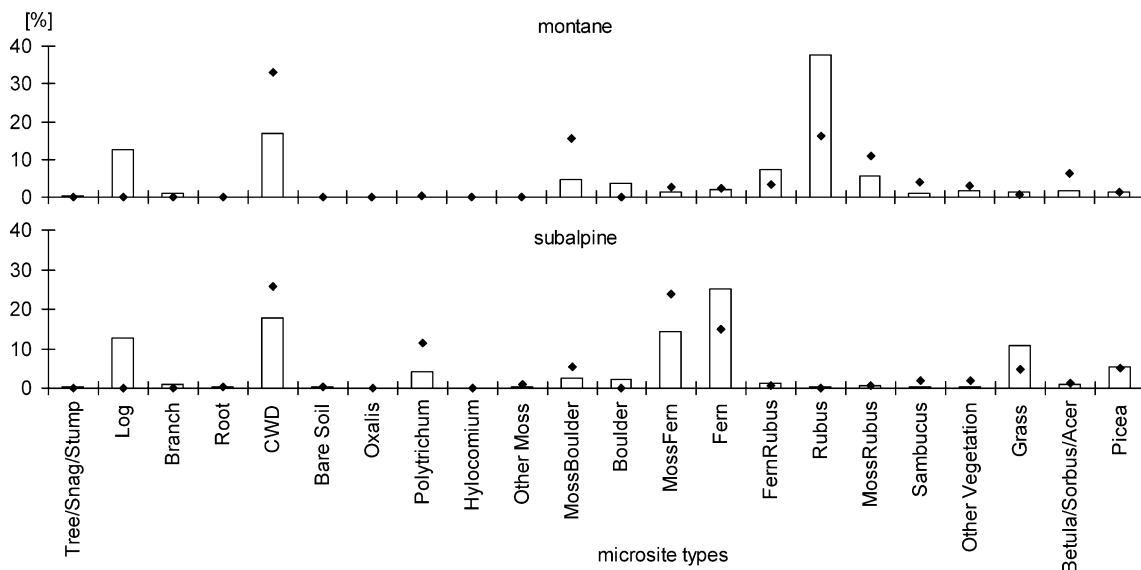

Fig. 7 Simulated future microsite composition of the Gandberg site in the year 2023. *Bars* represent the frequencies of microsite types, while *diamonds* show the frequency of *Picea* on each microsite type in percent of all *Picea* seedlings and saplings in height classes 1–5

of tree regeneration in mountain forests (e.g. Kinnaird 1974; Brang 1996a, Hörnberg et al. 1997; Holeksa 1998; Frehner 2000). This could be confirmed by comparing simulation outputs with independent field data (cf. Model evaluation). Simulations in which germination, mortality and growth rates were equal on all microsite types deviated to a much higher extent from the independent field data than simulations with microsite-specific rates (Fig. 4, Table 6). Therefore, we conclude that our model projected tree regeneration in the first 8 years after *Picea* die-back more accurately when microsite-specific rates were used. This was true for both the montane and subalpine levels (cf. Table 6).

Nevertheless, in reality the microsite-specific parameters probably differ more strongly between the most 'unfavourable' and the most 'favourable' sites than we assumed in the model (i.e. more than 50–150% of the average, cf. section Height increment). The microsite 'FernRubus', to give only one example, was assumed to be unfavourable for *Picea* regeneration, with low germination and growth rates and high mortality rates (cf. Table 2). Nonetheless, our simulation overestimated the amount of saplings on 'FernRubus' by a factor of about 3 on the montane level (cf. Fig. 4). This indicates that microsites are probably even more important than we assumed.

On the montane level, the most suitable microsites for *Picea* establishment were 'Root', 'Coarse Woody Debris', moss cushions, and—surprisingly—'MossRubus', whereas the most unfavourable sites were 'Fern', 'FernRubus' and 'Rubus' (cf. Fig. 4). While on the subalpine level 'Root' and 'CWD' were also suitable sites, 'Polytrichum' and all sites dominated by ferns, raspberries and grasses were unfavourable (Fig. 4). It is likely that similar findings would have been obtained if we had merged some microsite types (e.g. 'FernRubus' and 'Rubus') in the tree regeneration model. Such a reduction in the number of microsites would simplify the model, but any grouping of microsite types would have to be made with care, so as to maintain the variability in site conditions that was found to be so important.

Limitations of the RegSnag model approach

Obviously, a height-structured model of forest dynamics also has limits. In particular, the average height of the trees in a class is crucial for determining the transitions between the height classes. Irregular seed input caused the average height of trees in a certain class to drop dramatically when saplings of a good seed year became part of this class. An opposite effect was found when saplings of a bad seed year became part of a class (cf. Fig. 6). Consequently, such events affected the transition probabilities because these probabilities changed sharply, e.g. as average height approaches maximum height (cf. Eq. 2). This made it difficult to predict the future height of trees. Nevertheless, we were able to circumvent this problem by simulating the development of single tree cohorts with our model (cf. Fig. 6).

A further limitation of the model approach is that browsing by ungulates can only be integrated by reducing the growth rates of all trees in a given height class, but not of individual trees (see section Browsing intensity). In the case that browsing affects all individual trees similarly over time, e.g. if all trees are browsed twice during a certain time period, this general reduction in growth is not a problem. In this case, instead of being browsed twice as strongly, each tree simply experiences a reduced terminal shoot growth every year. However, the approach would cause large deviations between reality and model simulations when ungulates browse some trees repeatedly (e.g. Eiberle and Nigg 1987; Gill 1992a) while they spare others. We have, however, no evidence that this latter effect would be the case on the Gandberg forest, which is congruent with the findings by Ducan et al. (1998).

Browsing by deer may also cause changes in the ground vegetation. Gill (1992b) summarised in his review that shrub and herbaceous plant biomass often decreases while the biomass of grasses, ferns and mosses increases. Such effects were, however, neglected in our model, and could be considered in future model versions.

Speed of reforestation and impact of herbivory

The most noticeable effect of heavy browsing is a change in the tree species composition due to a partial or even complete prevention of the establishment of certain species (e.g. Gill 1992b; Wasem and Senn 2000). In the living stands on the Gandberg site, *Abies alba* and *Acer pseudoplatanus* have already been scarce. In the future, they will probably be absent (*Abies*) or at least very rare (*Acer*) if browsing by ungulates continues at the present intensity. In contrast, *Betula pendula* quickly established after the *Picea* die-back, which is congruent with findings in other snag stands (Baker and Kemperman 1974) and in windtrow areas (Peterson and Pickett 1995; Schmidt-Schütz 1999). However, the density of *Betula* regeneration is much too low to form a pioneer stand on the Gandberg site, probably because the large extent of the snag stands minimized seed inflow (cf. limited long distance dispersal of *Betula*, Cameron 1996). Thus, the formerly dominant species *Picea* and neither the rare *Abies* and *Acer* (< 3%) nor the potentially abundant *Betula* or *Sorbus* trees will replace the current herbaceous vegetation in the snag stands on the Gandbeg site. This is in agreement with the findings of Schmid and Frye (1977) in the Rocky Mountains, where spruce-dominated snag stands with less than 10% fir in the overstory remained spruce forests.

Generally, browsing often reduces height growth of coniferous species (Eiberle 1975; Kristöfel and Poll-anschütz 1995; McLaren 1996; Hester et al. 2004), thus prolonging the phase where seedlings and saplings are

susceptible to damage by other factors such as pathogenic fungi or snow pressure (cf. Ott et al. 1997). This indirectly reduces the number of tree saplings both in reality and in our model, in which they remain longer in the lower height classes that have higher mortality rates.

However, our long-term simulations suggest that *Picea* regenerates rather quickly in the snag stands on the Gandberg site, regardless of the high browsing intensities (Fig. 6). Eiberle and Nigg (1986) observed that in closed high montane *Picea–Abies* forests, heavily browsed *Picea* saplings required on average 22 years to reach the height of 1.3 m and thus to grow above the height that chamois are normally able to reach. Lüscher (1990) determined between 25–85 years at the montane level and 35–105 years at the subalpine level until *Picea* reached a height of 5 m. Brang and Duc (2002) estimated (based on a literature review) that it takes an average of 68 years for tree regeneration in small gaps of subalpine and high montane *Picea* forests to grow to a height of 5 m. Mayer and Ott (1991) and Ott et al. (1997) suggest that it takes about 50 to 80 years until tree regeneration in the subalpine level reaches the status of 'protective regeneration' (i.e. trees that have a height and dbh sufficient to effectively protect against snow avalanches or rockfall). Probably the higher light availability in snag stands leads to relatively large height increments compared to otherwise comparable closed forests (Brang 1996a; Frehner 2000). Therefore this difference may reduce the period that a tree is exposed to ungulate browsing and until it reached the status of a protective regeneration (cf. 5 m) at the Gandberg site.

Conclusions

Our study confirms the commonly held assumption that microsite effects on tree regeneration in mountain snag stands are quite important, not only on the subalpine but also on the montane level. Our rather simple model was able to capture these effects and to accurately simulate the development of tree regeneration over the first 8 years after the *Picea* die-back. The model showed that microsite types and microsite-specific effects on germination, mortality and height increment of trees should receive more attention when tree regeneration in mountain forests is modelled. This applies particularly in snag stands or other heavily disturbed sites, where light availability under a closed tree canopy is not limiting any more, but where competitive effects from ground vegetation and other site conditions become crucial for the growth and survival of tree regeneration.

References

Baker BH, Kemperman JA (1974) Spruce beetle effects on a white spruce stand in Alaska. J Forest 72:423–425

Beudert B (1999) Veränderungen im Stoffhaushalt eines abgestorbenen Fichtenökosystems im Forellenbachgebiet des Nationalparks Bayerischer Wald. Einzugsgebiet Grosse Ohe - 20 Jahre hydrologische Forschung im Nationalpark Bayerischer Wald, Symposiumsbericht. Nationalparkverwaltung Bayerischer Wald, pp 83–106

Bossel H, Krieger H (1991) Simulation model of natural tropical forest dynamics. Ecol Model 59(1–2):37–71

Brang P (1996a) Experimentelle Untersuchungen zur Ansamungsökologie der Fichte im zwischenalpinen Gebirgswald. Beih Schweiz Z Forstwes 77:1–375

Brang P (1996b) Ansamungsgunst und Verteilung der Direktstrahlung in schlitzförmigen Bestandesöffnungen zwischenalpiner Fichtenwälder. Schweiz Z Forstwes 147(10):761–784

Brang P (1997) Ecological niches of seedling establishment in high-elevation forests. In: Hollstedt C, Vyse A (eds) Sicamous Creek Silvicultural Systems Project: Workshop proceedings. Research Branch, B.C. Ministry of Forests, Victoria, B.C, Kamloops, Biritish Colombia, Canada, pp 144–153

Brang P, Schönenberger W, Ott E, Gardner B (2001) Forests as protection from natural hazards. In: Evans J (ed) The forest handbook. Blackwell, Oxford, pp 53–81

Brang P, Duc P (2002) Zu wenig Verjüngung im Schweizer Gebirgs-Fichtenwald: Nachweis mit einem neuen Modellansatz. Schweiz Z Forstwes 153(6):219–227

Bugmann H, Marti F, Wallimann K (1989) Auswirkungen eines Phosphorsäureesters (Insektizid Ekamet) auf die Planktonbiozönose des Greifensees. Diplomarbeit, ETH Zürich, EAWAG Dübendorf, Schweiz, 232 p

Burkart A (2001) Einschätzung - Samenbehang. interner Bericht, Eid. Forschungsanstalt WSL, Birmensdorf, 8 p

Cameron AD (1996) Managing birch woodlands for the production of quality timber. Forestry 69(4):357–371

Chauvin C, Renaud J-P, Rupé C, Leclerc D (1994) Stabilité et gestion des forêts de protection. Bull tech 27(27):37–52

Ducan AJ, Hartley SE, Iason GR (1998) The effect of previous browsing damage on the morphology and chemical composition of Sitka spruce (*Picea stichensis*) saplings and on their subsequent susceptibility to browsing by red deer (*Cervus elaphus*). For Ecol Manage 103:57–67

Eiberle K (1975) Ergebnisse einer Simulation des Wildverbisses durch den Triebschnitt. Schweiz Z Forstwes 126:821–839

Eiberle K, Nigg H (1986) Untersuchung über den Verbiss durch die Gemse (*Rupicapra rupicapra* L.) an Fichte (*Picea abies*). Ber Bot-Zool Ges Liecht-Sargans-Werdenberg 15:15–36

Eiberle K, Nigg H (1987) Grundlagen zur Beurteilung des Wildverbisses im Gebirgswald. Schweiz Z Forstwes 183:747–785

Frehner M (2000) Untersuchungen über den Einfluss unterschiedlicher Kleinstandorte und der Pflanztechnik auf Fichtenpflanzungen in subalpinen Lawinenschutzwäldern. Beih Schweiz Z Forstwes 92:1–227

Gill RMA (1992a) A review of damage by mammals in north temperate forests: 1. Deer. Forestry 65(2):145–169

Gill RMA (1992b) A review of damage by mammals in North Temperate forests: 3. Impact on trees and forests. Forestry 65(4):363–388

Golser M, Hasenauer H (1996) Height growth development of Norway spruce, fir and common beech regeneration in uneven-aged mixed species stands. In: Skovsgaard JP, Johannsen VK (eds) IUFRO Conference. Danish Forest and Landscape Research Institute, Copenhagen, pp 493–503

Golser M, Hasenauer H (1997) Predicting juvenile tree height growth in uneven-aged mixed species stands in Austria. For Ecol Manage 97(2):133–146

Hasenauer H, Stampfer E, Rohrmoser C, Sterba H (1994) Solitärdimensionen der wichtigsten Baumarten Östereichs. Österr Forsztg 105(3):28–29

Hester AJ, Millard P, Gordon J, Wendler B, Wendler R (2004) How does timing of browsing affect above- and below-ground growth of *Betula pendula*, *Pinus sylvestris* and *Sorbus aucuparia*? OIKOS 105(3):536–560

Heurich M (2001) Waldentwicklung im montanen Fichtenwald nach grossflächigem Buchdruckerbefall im Nationalpark Bayerischer Wald. In: Heurich M (ed) Waldentwicklung im Bergwald nach Windwurf und Borkenkäferbefall. Nationalparkverwaltung Bayerischer Wald, Grafenau, Deutschland, pp 99–176

High Performance Systems Inc (2001) Stella research software. Hanover, Germany

Holeksa J (1998) Rozpad drzewostanu i odnowienie swierka a struktura i dynamika karpackiego boru gornoreglowego (Breakdown of tree stand and spruce regeneration versus structure and dynamics of a Carpathian subalpine spruce forest). Monogr Bot 82:1–201 (English summary 201–209)

Hörnberg G, Ohlson M, Zackrisson O (1997) Influence of bryophytes and microrelief conditions on *Picea abies* seed regeneration patterns in boreal old-growth swamp forests. Can J For Res 27:1015–1023

Huth A, Ditzer T, Bossel H (1998) The rain forest growth model FORMIX 3-model description and analysis of forest growth and logging scenarios for the Dermakot Forest Reserve (Malaysia). Göttinger Beitr Land- und Forstwirtsch Trop Subtrop 124:1–182

Ishizuka M, Toyooka H, Osawa A, Kushima H, Kanazawa Y, Sato A (1998) Secondary succession following catastrophic windthrow in a boreal forest in Hokkaido, Japan: the timing of tree establishment. J Sust For 6(3/4):367–388

Jorritsma ITM, Van Hees AFM, Mohren GMJ (1999) Forest development in relation to ungulate grazing: a modeling approach. For Ecol Manage 120:23–34

Kellomäki S, Väisänen H (1991) Application of a gap model for the simulation of forest ground vegetation in boreal conditions. For Ecol Manage 42:35–47

Kinnaird JW (1974) Effect of site conditions on regeneration of birch (*Betula pendula* Roth and *Betula pubescens* Ehrh). J Ecol 62(2):467–472

Kristöfel F, Pollanschütz J (1995) Entwicklung von Fichtenpflanzungen nach Triebrückschnitten. FBVA-Berichte 85:1–16

Kuoch R (1965) Der Samenfall 1962/63 an der oberen Fichtenwaldgrenze im Sertigtal. Mitt EAFV 41:61–85

Kupferschmid AD (2002) Bark influence on vegetation development in a dead *Picea abies* mountain forest. In: Bottarin R, Tappeiner U (eds) Interdisciplinary mountain research. Blackwell Verlag, Berlin, pp 242–247

Kupferschmid AD, Schönenberger W, Wasem U (2002) Tree regeneration in a Norway spruce snag stand after tree die-back caused by *Ips typographus*. For Snow Landsc Res 77(1/2):149–160

Kupferschmid AD, Bugmann H (2005) Predicting decay and vegetation development in *Picea abies* snag stands. Plant Ecol 197:247–268

Kupferschmid Albisetti AD (2003) Succession in a protection forest after *Picea abies* die-back. PhD thesis, Nr. 15228, E-Collection: < http://e-collection.ethbib.ethz.ch/cgi-bin/show.pl?type = diss&nr = 15228 > , ETH, Zürich, Switzerland, 238 p

Kupferschmid Albisetti AD, Brang P, Schönenberger W, Bugmann H (2003) Decay of *Picea abies* snag stands on steep mountain slopes. For Chron 79(2):247–252

Lässig R, Egli S, Odermatt O, Schönenberger W, Stöckli B, Wohlgemuth T (1995) Beginn der Wiederbewaldung auf Windwurfflächen. Schweiz Z Forstwes 146(11):893–911

Lexer MJ, Hönninger K (2001) A modified 3D-patch model for spatially explicit simulation of vegetation composition in heterogeneous landscapes. For Ecol Manage 144(1–3):43–65

Lüscher F (1990) Untersuchungen zur Höhenentwicklung der Fichtennaturverjüngung im inneralpinen Gebirgswald. Dissertation, ETH, Zürich, Schweiz, 138 p

Mayer H, Ott E (1991) Gebirgswaldbau Schutzwaldpflege; Ein waldbaulicher Beitrag zur Landschaftsökologie und zum Umweltschutz. Gustav Fischer Verlag, Stuttgart

McLaren BE (1996) Plant-specific response to herbivory: simulated browsing of suppressed balsam fir on Isle Royale. Ecology 77(1):228–235

Mencuccini M, Piussi P, Zanzi Sulli A (1995) Thirty years of seed production in a subalpine Norway spruce forest: patterns of temporal and spatial variation. For Ecol Manage 76:109–125

Monserud RA, Ek AR (1977) Prediction of understory tree height growth in northern hardwood stands. For Sci 23(3):391–400

Mössmer EM (1998) Ohne Schutzwald geht's bergab! Allg. Forsztzg (21):1284–1285

Nüsslein S, Faisst G (1998) Waldentwicklung im Nationalpark Bayerischer Wald 1998: Totholzflächen und Waldverjüngung. Bayerische Landesanstalt für Wald und Forstwirtschaft, Freising, Deutschland, 25 p

Ott E, Lüscher F, Frehner M, Brang P (1991) Verjüngungsökologische Besonderheiten im Gebirgsfichtenwald im Vergleich zur Bergwaldstufe. Schweiz Z Forstwes 142(11):879–904

Ott E, Frehner M, Frey H-U, Lüscher P (1997) Gebirgsnadelwälder: Ein praxisorientierter Leitfaden für eine standortgerechte Waldbehandlung. Verlag Paul Haupt, Bern, Schweiz

Pacala SW, Canham CD, Saponara J, Silander JA, Kore RK, Ribbens E (1996) Forest models defined by field measurements: estimation, error analysis and dynamics. Ecol Monogr 66(1):1–43

Peterson CJ, Pickett STA (1995) Forest reorganization: a case study in an old-growth forest catastrophic blowdown. Ecology 76(3):763–774

Roth I (1996) Untersuchungen über die forstliche Ansamung in einem abgestorbenen Fichtenbestand, Objekt: Gandberg oberhalb Schwanden GL. Diplomarbeit, ETH, Zürich, Schweiz, 99 p

Rüegg D, Schwitter R (2002) Untersuchungen über die Entwicklung der Verjüngung und des Verbisses im Vivian-Sturmgebiet Pfäfers. Schweiz Z Forstwes 135(4):130–139

Schmid JM, Frye RH (1977) Spruce beetle in the Rockies. US Dep Agric For Serv Gen Tech Rep RM 49:1–38

Schmidt A (1983) Der Freiberg Kärpf; Das älteste Wildschutzgebiet der Schweiz in den Glarner Alpen. Buchhandlung Baeschlin, Glarus, Schweiz

Schmidt-Schütz A (1999) Wiederbewaldung von Fichten-Sturmwurfflächen auf vernässenden Standorten mit Hilfe von Pioniergehölzen. Forstl Forsch ber München 176:120–130

Schönenberger W (2000) Silvicultural problems in subalpine forests in the Alps. In: Price MF, Butt N (eds) Forests in sustainable mountain development: a state of knowledge report for 2000. CABI Publishing, UK, pp 197–203

Sterba H, Golser M, Schwiger J, Hasenauer H (1997) Modelle für das Ankommen und das Wachstum der Naturverjüngung. Cent bl gesamte Forstwes 1:11–33

Ulanova NG (2000) The effects of windthrow on forests at different spatial scales: a review. For Ecol Manage 135:155–167

Urban DL, Bonan GB, Smith TM, Shugart HH (1991) Spatial applications of gap models. For Ecol Manage 42:95–110

Veblen TT, Hadley KS, Reid MS, Rebertus AJ (1989) Blowdown and stand development in a Colorado subalpine forest. CJFR 19:1218–1225

Walcher J, Kupferschmid AD (2001) Borkenkäfer-Schadenflächen bei Schwanden. In: Rageth T (eds) Binding Preis für vorbildliche Waldpflege 2001: Vivian als Chance. Gemeinde Schwanden GL. Sophie und Karl Binding Stiftung, Basel, Schweiz, pp 43–45

Wasem U, Senn J (2000) Fehlende Weisstannenverjüngung: Hohe Schalenwildbestände können die Ursache sein. Wald Holz 9(81):11–14

Wohlgemuth T, Kull P (2002) Disturbance of microsites and early tree regeneration after the catastrophic windthrow Vivian 1990 in Swiss mountain forests. For Snow Landsc Res 77(1/2): 17–47

Wunder J (2002) Naturverjüngung in schlitzförmigen Bestandesöffnungen. Erfolgskontrolle in hochmontanen und subalpinen Schutzwäldern des Vorderreintales, Graubünden. Diplomarbeit, Universität Bayreuth, Bayreuth, Deutschland, 67 p