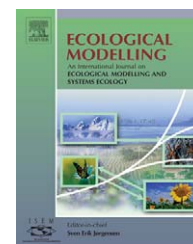


available at www.sciencedirect.comjournal homepage: www.elsevier.com/locate/ecolmodel

Optimisation of tree mortality models based on growth patterns

Jan Wunder^{a,*}, Christof Bigler^{a,b}, Björn Reineking^a, Lorenz Fahse^a, Harald Bugmann^a

^a Forest Ecology, Department of Environmental Sciences, ETH Zurich, CH-8092 Zurich, Switzerland

^b Biogeography Lab, Department of Geography, University of Colorado, Boulder, CO 80309, USA

ARTICLE INFO

Article history:

Received 22 September 2005

Received in revised form 9 February 2006

Accepted 23 February 2006

Published on line 17 April 2006

Keywords:

Forest gap models

Norway spruce

Validation

Forest ecology

Tree death

ABSTRACT

Forest succession is often modelled using “gap models” that simulate the establishment, growth and mortality of individual trees. However, many mortality submodels that are currently used in gap models are based on theoretical assumptions and have not been tested with empirical data sets. Except for disturbance-induced mortality, these models predict the time of individual tree death using stress thresholds (ST). They often include a simple stress memory that keeps track of low diameter growth over the recent growth history of each tree, which may lead to increased mortality. In the present study, we optimised the parameter values for a range of commonly used classical ST models. We used the geometric mean of the averages of the correctly classified living and dead trees as our optimisation and model performance criterion. Furthermore, we compared the performance of the ST models with that of recently derived logistic regression models based on growth patterns as predictor variables. Tree-ring data from dead and living Norway spruce (*Picea abies*) trees of subalpine forests at three study sites in Switzerland were used to calibrate and validate the ST models.

The optimisation increased the performance of the classical ST models by 61–153%. Surprisingly, the model without any stress memory showed the highest performance and thus exceeded the performance of more “realistic” models, i.e., those considering a stress memory. Despite these tremendous improvements, the optimised ST models did not attain the performance of the logistic regression models. Therefore, we conclude that even optimised classical ST models are inferior to regression models with regard to predicting the time of tree death. A considerable change in the simulated forest succession is to be expected if classical ST models that are still used in many gap models are replaced by logistic regression models based on field data.

© 2006 Elsevier B.V. All rights reserved.

1. Introduction

Forests provide numerous economic, environmental, social and cultural benefits and services. Their ability to maintain these functions in the long run is strongly dependent on properties of long-term forest succession. Therefore,

understanding the processes driving succession such as regeneration, growth and mortality of trees under the current as well as a changed climate is of increasing concern (Bugmann, 1997; Fischlin and Gyalistras, 1997; Theurillat and Guisan, 2001; Beniston, 2004; Suarez et al., 2004; van Mantgem and Stephenson, 2005). In this context, model-based projec-

* Corresponding author at: Forest Ecology, Department of Environmental Sciences, ETH-Zentrum CHN G78, Universitätstrasse 16, CH-8092 Zurich, Switzerland. Tel.: +41 44 632 0738.

E-mail address: wunder@env.ethz.ch (J. Wunder).

0304-3800/\$ – see front matter © 2006 Elsevier B.V. All rights reserved.

doi:10.1016/j.ecolmodel.2006.02.037

tions can reveal the likely changes in forest structure and composition and the spatial shift of favourable sites for the main tree species and forest types.

Forest gap models, a widespread subset of forest succession models, simulate establishment, growth and mortality of individual trees on patches of 100–1000 m² as a function of abiotic and biotic factors (Shugart, 1984; Botkin, 1993; Bugmann, 2001). Usually, tree death is modelled as a combination of two or three different sources of mortality: a background mortality at the tree level, a growth-dependent mortality at the stand level and occasionally an exogenous mortality at the landscape level (Keane et al., 2001).

Background mortality is typically modelled as a constant annual mortality, assuming that stochastic events (e.g., lightning) can kill a tree at any time (Botkin et al., 1972). For the growth-dependent mortality, stress thresholds (ST) are commonly applied, i.e., trees whose annual diameter increment falls below a certain absolute or relative threshold are assumed to be stressed and to be subject to an enhanced mortality risk. Exogenous mortality is implemented in some models only, resulting from stochastically occurring large-scale disturbances. In this paper, we focus on models combining background and growth-dependent mortality and refer to them as “stress threshold” (ST) models.

Botkin et al. (1972) introduced a ST model that considers the single tree as a system without memory (i.e., past growth does not affect current mortality probability). Based on this first mortality model, more complex ST models with a simple stress memory were developed in order to reflect known mortality processes more closely. The length of this stress memory is usually defined as the number of years of low growth that need to accumulate before stress mortality starts to act. Stress in a given year results if the annual diameter increment of the tree falls below a threshold.

The available ST models are poorly parameterised (Hawkes, 2000), no matter whether they operate with or without a simple stress memory, and they are largely based on theoretical assumptions (Keane et al., 2001). To improve the mortality formulations in gap models, Hawkes (2000) and Bigler and Bugmann (2004a) have suggested to test the mortality algorithms of succession models against empirical mortality data.

Recent advances of tree mortality models rely mainly on two improvements: they are based on empirical data sets and contain a more complex methodology than ST models, e.g., discriminant analysis (Crow and Hicks, 1990), neuronal networks (Hasenauer et al., 2001), classification and regression trees (Dobbertin and Biging, 1998), Bayesian analysis (Wyckoff and Clark, 2002), survival analysis (Woodall et al., 2005) and logistic regression (Bigler and Bugmann, 2003, 2004b). Implementing these more advanced mortality models into gap models might lead to considerable changes in the modelled succession (Bugmann, 2001; Wyckoff and Clark, 2002). Yet, the fact that ST formulations are still widespread even in “physiology-based” gap models (cf. Price et al., 2001) warrants a more detailed analysis of their performance and possible improvements via model calibration.

Recently, Bigler and Bugmann (2004a) have shown that logistic mortality models based on growth patterns achieve a better performance than ST models with parameters based on theoretical assumptions. However, it is unknown to

what extent the performance of simple ST models could be improved by optimising their parameters. Therefore, the specific objectives of our study are (1) to optimise ST models with empirical tree-ring data from dead and living Norway spruce (*Picea abies* (L.) Karst.) trees of subalpine forests at three study sites in Switzerland, and (2) to compare the performance of the optimised ST models with logistic mortality models based on growth patterns (Bigler and Bugmann, 2004a).

2. Materials and methods

2.1. Study sites and sampling of trees

The data used in this study are from Bigler and Bugmann (2003). For Norway spruce, the dominant tree species in the European Alps, 105 living and 97 dead trees with more than 10 cm minimum DBH (diameter at breast height) were sampled at the three study sites Davos, Böldmeren and Scatlé (Switzerland). All sites are located in the subalpine zone (1500–2000 m a.s.l.) and are characterised by mature near-natural or primeval forests dominated by Norway spruce. The sites are influenced by a suboceanic climate (Davos: annual precipitation sum = 1075 mm, annual mean temperature = 2.4 °C; Böldmeren: ≈2500 mm, ≈3–4 °C; Scatlé: 1440 mm, 2.2 °C). The geological substrate varies from silicate-gneiss (Davos) and limestone-karst (Böldmeren) to silicate-verrucano (Scatlé). These climatologically and geologically different sites were separated into a training data set and two test data sets. The training data set “Davos” containing 60 living and 59 dead trees was used for the optimisation of the parameter values (model calibration). The two independent test data sets “Böldmeren” (23 living trees and 18 dead trees) and “Scatlé” (22 living trees and 20 dead trees) were used to test the optimised models (model validation). For a more detailed description of the study sites and the field sampling, see Bigler and Bugmann (2003).

Since some ST models use the theoretical maximum growth of Norway spruce at any given age, each measured tree ring was assigned to the corresponding age corrected by the estimated number of missing rings between pith and the first tree ring, which resulted from imprecise coring. Applying this procedure reduced the data to 72 dead and 78 living trees with a reliable estimation of age (Davos: 43 dead and 47 living trees; Böldmeren: 12 dead and 15 living trees; Scatlé: 17 dead and 16 living trees). To assure comparability between ST models, this reduced data set was used for all models. Additionally, we used the full data set for those ST models not depending on tree age information, which allowed for a comparison with the analysis of Bigler and Bugmann (2004a) who had used the same data set.

2.2. Mortality models based on stress thresholds (ST models)

Among the five selected classical ST models described by Botkin et al. (1972), Solomon (1986), Kienast (1987), Keane et al. (1996) and Bugmann (2001), the first four have been implemented in the succession models JABOWA (Botkin et al., 1972), FORENA (Solomon, 1986), FORECE (Kienast, 1987) and FIRE-

Table 1 – Formulations of the stress threshold models (ST models)

ST model	Equation
ST _{abs} (Botkin et al., 1972)	$\Pr(\text{surv})_{i,t} = \begin{cases} p & \text{if } RW_{i,t} < th_{abs} \\ q & \text{else} \end{cases}$
ST _{rel} (Solomon, 1986)	$\Pr(\text{surv})_{i,t} = \begin{cases} p & \text{if } (RW_{i,t} < th_{rel}) \wedge (RW_{i,t-1} < th_{rel}) \\ q & \text{else} \end{cases}$
ST _{comb} (Kienast, 1987)	$\Pr(\text{surv})_{i,t} = \begin{cases} p & \text{if } (RW_{i,t} < th_{abs}) \wedge (RW_{i,t-1} < th_{abs}) \wedge (RW_{i,t-2} < th_{abs}) \\ p & \text{if } (RW_{i,t} < th_{rel}) \wedge (RW_{i,t-1} < th_{rel}) \wedge (RW_{i,t-2} < th_{rel}) \\ q & \text{else} \end{cases}$
ST _{stress} (Keane et al., 1996)	$\Pr(\text{surv})_{i,t} = q - a[1 - \exp(-b \times SC_{i,t})]^c \text{ with } \begin{cases} SC_{i,t} = 0 & \text{if } (RW_{i,t} \geq th_{abs}) \wedge (RW_{i,t-1} \geq th_{abs}) \\ & \wedge (RW_{i,t-2} \geq th_{abs}) \\ SC_{i,t} = SC_{i,t-1} + \Delta SC_{i,t} & \text{else} \\ \Delta SC_{i,t} = 1 & \text{if } (RW_{i,t} < th_{abs}) \\ \Delta SC_{i,t} = 0 & \text{else} \end{cases}$
ST _{sev} (Bugmann, 2001)	$\Pr(\text{surv})_{i,t} = q - a[1 - \exp(-b \times SC_{i,t})]^c \text{ with } \begin{cases} SC_{i,t} = 0 & \text{if } (RW_{i,t} \geq th_{abs}) \wedge (RW_{i,t-1} \geq th_{abs}) \\ & \wedge (RW_{i,t-2} \geq th_{abs}) \\ SC_{i,t} = SC_{i,t-1} + \Delta SC_{i,t} & \text{else} \\ \Delta SC_{i,t} = 10 \times \frac{th_{abs} - RW_{i,t}}{th_{abs}} & \text{if } (RW_{i,t} < th_{abs}) \\ \Delta SC_{i,t} = 0 & \text{else} \end{cases}$

Notes: $\Pr(\text{surv})_{i,t}$ = survival probability of tree i in a given year t , p = annual survival probability in a stress year, q = annual survival probability ($=1 -$ probability of background mortality), $RW_{i,t}$ = ring width of tree i in year t , th_{abs} = absolute growth threshold, th_{rel} = threshold in relation to the age-specific maximum growth (Moore, 1989), $SC_{i,t}$ = stress counter for tree i in year t , Weibull probability distribution parameters for ST_{stress} and ST_{sev} ($a=0.15$, $b=0.15$ and $c=2.5$) adapted for Norway spruce. “ \wedge ” denotes the Boolean “and” operator.

BGC (Keane et al., 1996). In all these stochastic ST models, an individual tree dies if an annually calculated, uniformly distributed random number in the interval $[0,1]$ is larger than the survival probability.

For the background mortality, the annual mortality (Botkin et al., 1972) used in all ST models can be expressed as a constant annual survival probability:

$$\Pr(\text{surv}) = q = \frac{\text{age max}}{\sqrt{0.02}} \quad (1)$$

This reflects the assumption that 2% of the saplings reach the maximum age of that species. For example, an estimated maximum age of 930 years for Norway spruce (mean of several literature sources, see Bugmann, 1994) results in an annual survival probability of approximately 99.6%.

For the growth-dependent mortality, stress thresholds (ST) were applied in all models, i.e., trees falling below a certain threshold of diameter growth experience a reduced, constant survival probability ($\Pr(\text{surv}) = p$). The models by Botkin et al. (1972), Solomon (1986) and Kienast (1987) are based on absolute or relative increment thresholds of DBH increments, or a combination of both, as explained below.

Botkin et al. (1972) assumed that trees growing very slowly for a decade will most likely die. Consequently, every year in which the annual diameter increment $RW_{i,t}$ (ring width of tree i in year t) of an individual tree falls below an absolute threshold of 0.1 mm, the survival probability was assumed to drop to 0.632, indicating that only 1% of trees growing so slowly would survive a decade ($[0.632]^{10} \approx 0.01$). Because the threshold represents an absolute value, we refer to this formulation as the ST_{abs} model (Table 1).

Solomon (1986) changed this formulation by introducing a stress memory. He assumed – according to earlier observa-

tions by Nichols (1968) – that a simple stress memory (with k years of low growth) of a tree would improve the calculation of the mortality probability. Consequently, as soon as the annual diameter increment ($RW_{i,t}$) of two consecutive years ($k=2$) falls below the threshold, the survival probability drops to 0.632. In addition, Solomon (1986) assumed the threshold to be equivalent to 10% of the age- and species-specific maximum growth rate. Because a relative threshold was employed, we refer to this model with a simple stress memory as the ST_{rel} model (Table 1).

Kienast (1987) extended the simple stress memory to 3 years ($k=3$) and combined the absolute and the relative threshold (Table 1). The survival probability of a tree in this ST_{comb} model is reduced ($\Pr(\text{surv})_{i,t} = 0.632$) as soon as the annual diameter increment ($RW_{i,t}$) of three consecutive years falls below the absolute threshold of 0.3 mm or below the relative threshold of 10% of maximum growth according to Solomon (1986).

In contrast to ST_{abs} , ST_{rel} and ST_{comb} , the models by Keane et al. (1996) and Bugmann (2001) additionally consider a species-specific shade tolerance, i.e., they assume a link between shade and stress tolerance. This results in tree species having very different capabilities to survive periods of low growth depending on their shade tolerance. Furthermore, the survival probability does not suddenly decrease to 0.632 after 1 year (ST_{abs}), 2 years (ST_{rel}) or 3 years (ST_{comb}) of stress. Similarly, the survival probability does not jump immediately from a reduced level to $q=0.996$ ($=1 -$ probability of background mortality) after 1 year of stress-free growth, as explained below.

Keane et al. (1996) incorporated these ideas in the ST_{stress} model (Table 1) by introducing a stress counter (SC) that is incremented by 1 ($=\Delta SC_{i,t}$) when the annual diameter incre-

ment ($RW_{i,t}$) falls below a threshold of 0.3 mm. Stressed trees become healthy ($SC=0$) after experiencing three consecutive years of growth above the threshold. The stress counter is used in a three-parameter Weibull probability function that is also a function of the shade tolerance of the tree species (Table 1). Thus, the survival probability of tree i at time t depends only on $SC_{i,t}$; the parameters of the Weibull probability distribution ($a=0.15$, $b=0.15$ and $c=2.5$, Table 1) were adapted for Norway spruce as a medium shade-tolerant species (Ellenberg, 1996).

Bugmann (2001) added the severity of stress to the formulation by Keane et al. (1996): in his ST_{sev} model, the stress counter is incremented by a linearly interpolated value in the interval (0,10] (Table 1), reflecting the idea that stress is gradual, rather being a binary result of the growth performance.

Only the ST_{abs} model considers a tree as a system without memory, indicating that the current state is conditionally independent of past states. All other ST models have a simple stress memory. For all models, the thresholds, parameters and resulting probabilities are based on theoretical assumptions that have not been tested with empirical data sets. A more detailed discussion of these mortality models can be found in Bigler and Bugmann (2004a).

2.3. Model performance criterion

The performance of the different ST models was evaluated using a criterion that measures the proportion of correctly classified trees (CCP). A tree is considered to be classified correctly if a living tree is predicted to be alive at the time of sampling, or if a dead tree is predicted to be dead, respectively.

For each living tree i , we calculated the correct classification probability ($\Pr(CCL)_i$) given a certain set of parameter values q and p as

$$\Pr(CCL)_i = q^{L(i)} \times p^{S(i)} \quad (2)$$

where q is the survival probability in “non-stress” years (background mortality), and p is the survival probability in stress years (growth-dependent mortality). $L(i)$ is the lifespan (for dead trees) or the time until sampling (for living trees) of tree i , and $S(i)$ is the number of stress years. For example, in the ST_{abs} model with the original set of parameter values ($q=0.996$, $p=0.632$), a living 60-year-old tree without any stress years would be classified correctly with a probability of 79% ($\Pr(CCL)_i = 0.996^{60} \times 0.632^0 \approx 0.79$).

For each dead tree j , we calculated the correct classification probability ($\Pr(CCD)_j$) given a certain set of parameter values q and p as

$$\Pr(CCD)_j = q^{L(j)} \times p^{S_1(j)} \times (1 - q^{15} \times p^{S_2(j)}) \quad (3)$$

Here, we allowed for a prediction error of 15 years according to Bigler and Bugmann (2004a), i.e. for each dead tree we calculated the survival probability up to 15 years before the actual time of death in the same way as for the living trees. The product of this term and the mortality probability in the following 15 years reveals the correct classification probability

$\Pr(CCD)_j$ for each dead tree j , where $L(j)$ is the lifespan, $S_1(j)$ is the number of stress years during the lifespan except the last 15 years, and $S_2(j)$ is the number of stress years during the last 15 years of tree j . For example, in the ST_{abs} model with the original set of parameter values ($q=0.996$, $p=0.632$), a 100-year-old dead tree with ten stress years in the last 15 years of its life would be classified correctly with a probability of 66% ($\Pr(CCD)_j = 0.996^{100} \times 0.632^0 \times (1 - 0.996^{15} \times 0.632^{10}) \approx 0.66$).

The following model performance criterion (CCP) was used as a measure of the correct classification of any tree in the data set: the “correct classification product” (CCP) was calculated as the geometric mean of the averages of the correctly classified living and dead trees per data set:

$$CCP = \sqrt{\overline{\Pr(CCL)} \times \overline{\Pr(CCD)}} \times 100 \quad (4)$$

with $\overline{\Pr(CCL)}$ denoting the mean of the correct classification probabilities over all living trees (Eq. (2)), and $\overline{\Pr(CCD)}$ denoting the mean of the correct classification probabilities over all dead trees (Eq. (3)). The equal treatment of correctly classified living and dead trees was assured by calculating the geometric mean of $\overline{\Pr(CCL)}$ and $\overline{\Pr(CCD)}$. For example, a CCP of 62 would indicate that on average, all living and dead trees (of a given data set) are classified correctly with a probability of 62%.

We tested whether our measure CCP is related to a ranking system of multi-performance criteria (Reynolds and Ford, 1999) as used by Bigler and Bugmann (2004a, 2004b). In that study, multiple criteria, e.g., the percentage of actually dead trees with a prediction error of up to 15 years, up to 60 years, etc., were calculated for each mortality model and data set. Each criterion of the different mortality models was ranked within a given data set with highest performances having lowest ranks. We found a strong negative relationship between this ranking by Bigler and Bugmann (2004a) and the CCP when applied to their analyses, i.e., low ranks correspond to high CCP values (R^2 for Davos = 0.96, Bødmeren = 0.83, Scatlé = 0.89).

2.4. Optimisation procedure

A maximum likelihood approach did not improve the CCP values of the ST models since it is not robust due to the high influence of single events (i.e., the peculiar growth history of each observed tree): all events must have a probability greater than zero, and every single observed tree growth history has a maximum influence on the optimum parameter values. As a consequence, even one observed dead tree with a life-long high growth rate might lead to unrealistic parameter values and therefore to a poor classification performance.

For this reason, we used the CCP as the optimisation criterion (i.e., model performance criterion). All parameters (stress thresholds, th ; survival probabilities of background mortality, q , and of growth-dependent mortality, p ; length of the simple stress memory, k) were optimised by applying the modified simplex method (Nelder and Mead, 1965). To check the optimised parameters, we screened the array of values around the respective optimum. All analyses were performed using the function “optim” in the “R” software (R for windows 2.1.0, R Development Core Team, 2005).

Table 2 – Original and optimised (calibrated) parameter values and corresponding model performance criterion (CCP) of those ST models that do not take into account shade tolerance

Model	Parameter and model performance criterion (CCP)				
	Name	Units	Original	Optimised	Change (%)
ST _{abs}	th _{abs}	mm × 10 ⁻²	10.00	9.02 (9.35)	-9.8 (-6.5)
	p	%	63.2	0.0 (0.0)	-100.0
	q	%	99.6	100.0 (100.0)	+0.4
	k	Years	1	1 (1)	0.0
	CCP		33.4 (31.4)	56.5 (55.7)	+69.2 (+77.4)
ST _{rel}	th _{rel}	%	10.00	3.80	-62.0
	p	%	63.2	0.0	-100.0
	q	%	99.6	100.0	+0.4
	k	Years	2	1	-50.0
	CCP		21.3	51.1	+139.9
ST _{comb}	th _{abs}	mm × 10 ⁻²	30.00	9.02	-69.9
	th _{rel}	%	10.00	0.00	-100.0
	p	%	63.2	0.0	-100.0
	q	%	99.6	100.0	+0.4
	k	Years	3	1	-66.7
	CCP		22.3	56.5	+153.4

Notes: Results shown for Davos data set (*n* dead = 43 trees, *n* alive = 47 trees). Values in parentheses are derived using the extended data set of 119 trees (60 living and 59 dead individuals). th_{abs} = absolute growth threshold, th_{rel} = threshold in relation to the age-specific maximum growth (Moore, 1989), *p* = annual survival probability in a stress year, *q* = annual survival probability (=1 – probability of background mortality), *k* = length of the simple stress memory.

3. Results

3.1. Model calibration

On average, the optimised models correctly classified 32.1–56.5% of the trees (CCP = 32.1 respectively 56.5, Tables 2 and 3), thus increasing the performance of the original mortality models by 61–153%.

The models ST_{abs}, ST_{rel} and ST_{comb} performed better than models that consider shade tolerance, i.e., ST_{stress} and ST_{sev} (Tables 2 and 3). Moreover, the models ST_{abs} and ST_{comb} showed the highest performance (CCP = 56.5), but the ST_{comb} model was turned into a special case of a model with an abso-

lute threshold only and the same optimised parameters as the ST_{abs} model (Table 2).

In general, the optimisation simplified the ST models. The stress memories and the stochastic character were eliminated, which is expressed by survival probabilities *p* = 0 in stress years and *q* = 1 in all other years (Tables 2 and 3). Consequently, the maximum CCP values for the three optimised ST models with the highest performance were achieved without any stress memory (Table 2). Also, the original increment thresholds were reduced in all ST models: slightly in the ST_{abs} model (-9.8%), more in the ST_{stress} (-37.5%), to about half in the ST_{sev} model (-53.3%) and to about a third in the ST_{rel} model (-62.0%, Tables 2 and 3). These reductions occurred also in the ST_{comb} model, the only

Table 3 – Original and optimised (calibrated) parameter values and corresponding model performance criterion (CCP) of ST models that take into account shade tolerance

Model	Parameter and model performance criterion (CCP)				
	Name	Units	Original	Optimised	Change (%)
ST _{stress}	th _{abs}	mm × 10 ⁻²	30.00	18.75 (15.82)	-37.5 (-47.3)
	q	%	99.6	100.0 (100.0)	+0.4 (+0.4)
	CCP		19.9 (22.2)	32.1 (36.6)	+61.3 (+64.9)
ST _{sev}	th _{abs}	m × 10 ⁻²	30.00	14.00 (14.15)	-53.3 (-52.8)
	q	%	99.6	100.0 (100.0)	+0.4 (+0.4)
	CCP		17.3 (23.8)	35.3 (42.3)	+104.0 (+77.7)

Notes: Results shown for Davos data set (*n* dead = 43 trees, *n* alive = 47 trees). Values in parentheses are derived using the extended data set of 119 trees (60 living and 59 dead individuals). th_{abs} = absolute growth threshold, *q* = annual survival probability (=1 – probability of background mortality).

model applying two thresholds, where the absolute threshold was reduced slightly and the relative threshold was set to zero (i.e., the relative threshold is not relevant any more, Table 2).

The performance of the optimised and original ST_{abs} and ST_{rel} models applied to the growth curve of one exemplary 235-year-old dead tree is shown in Fig. 1. According to the optimised models, the survival probability function drops from 1 to 0 (Fig. 1b and d) as soon as the growth rate falls below the threshold (Fig. 1a and c).

The optimised ST_{abs} model predicts the tree to die after 221 years (prediction error of 14 years), ST_{rel} after 230 years (prediction error of 5 years). In contrast, the survival probabilities of the original model show an exponential decline with some discontinuities. Consequently, it is very likely that the original models predict the tree to die many years prior to its real death date.

3.2. Model validation

Applying the optimised ST models to the independent test data sets Bödmeren and Scatlé increased the CCP values by up to 173 and 272%, respectively (Table 4). In accordance with the results of the model calibration, the models without consideration of shade tolerance showed the highest performance (ST_{abs} , ST_{rel} , ST_{comb}).

3.3. Neighbourhood of the optimum parameter combination

For the ST_{abs} , ST_{rel} and ST_{comb} models (i.e., the models without shade tolerance), increasing the length of the stress memories led to lower CCP values (Fig. 2). However, noticeable are the relatively high CCP values for the ST_{abs} and ST_{comb} models at a memory length of 3 years and for ST_{rel} at a memory length of 4 years (Fig. 2). Furthermore, these three models were more susceptible to threshold changes than to changes of the annual stress survival probabilities (cf. the ST_{abs} model in Fig. 3). The ST_{stress} and ST_{sev} models (i.e., those models considering shade tolerance) were also susceptible to threshold changes (cf. the ST_{stress} model in Fig. 4).

3.4. Comparison with logistic regression models based on growth patterns

We compared the performance of the five optimised ST models with four empirical models based on logistic regression (Bigler and Bugmann, 2004a) at the two validation sites Bödmeren and Scatlé using the same dendrochronological data set and the same model performance criterion (CCP). The four models introduced by Bigler and Bugmann (2004a) differ in terms of the growth variables used, with three of the models relying on the variable “relative basal area increment” (two of them on additional growth variables) and one model relying on the variable “ring width” only (Table 5).

The logistic regression models showed a high performance that generally exceeded those of the optimised ST models (Table 4). An analysis of variance revealed a significant difference between the performance of the five opti-

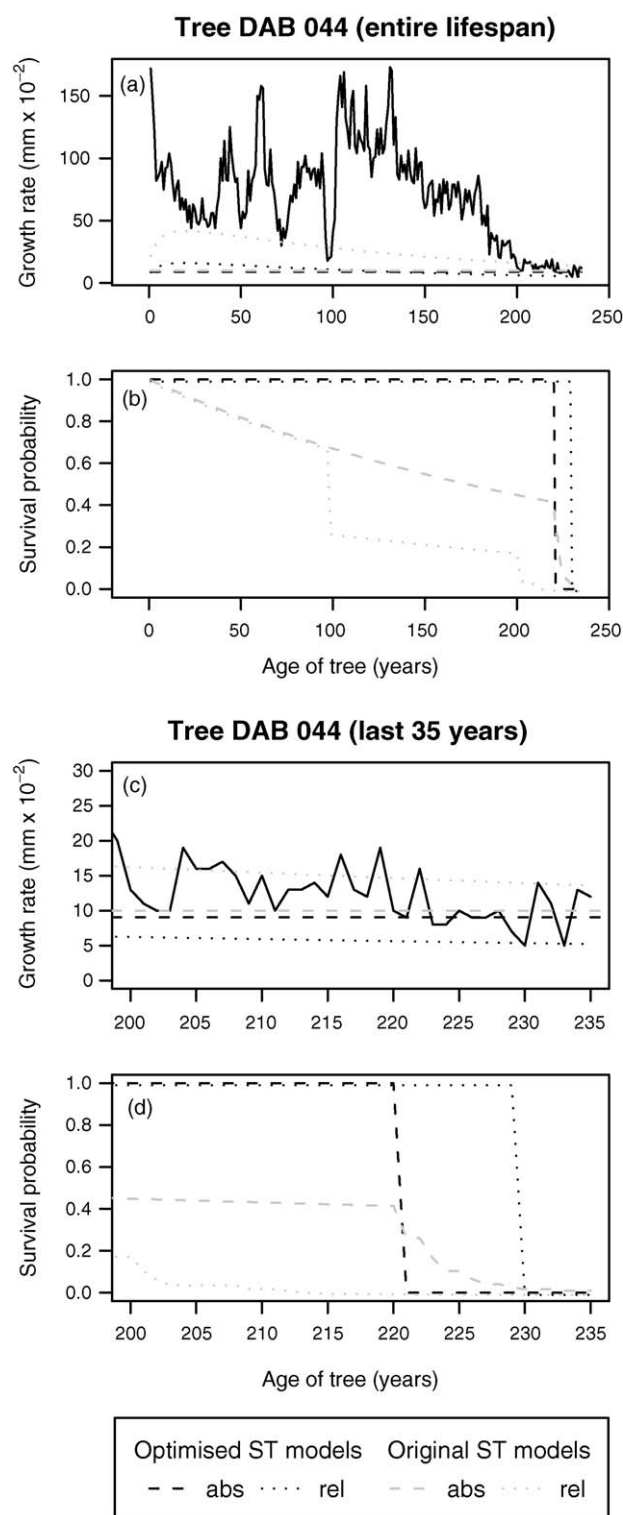


Fig. 1 – Application of the original and optimised ST_{abs} and ST_{rel} models to the growth curve of a single dead tree (DAB 044) from the Davos data set (continuous black line) for the entire lifespan (a and b) and an extended section of the last 35 years (c and d). Shown are the absolute and relative growth thresholds (a and c) and the annual survival probabilities (b and d) of ST_{abs} and ST_{rel} (dotted and dashed lines).

Table 4 – Validation of original and optimised ST models and corresponding model performance criterion (CCP) for the data sets Bödmeren (n dead = 12 trees, n alive = 15 trees) and Scatlé (n dead = 17 trees, n alive = 16 trees)

Model	Site					
	Bödmeren			Scatlé		
	Original	Optimised	Change (%)	Original	Optimised	Change (%)
ST _{abs}	22.8 (19.4)	42.8 (38.1)	+87.7 (+96.4)	25.4 (24.2)	42.9 (38.4)	+68.9 (+58.7)
ST _{rel}	15.7	31.6	+101.3	11.7	36.4	+211.1
ST _{comb}	19.2	42.8	+122.9	11.8	42.9	+263.6
ST _{stress}	14.7 (17.6)	21.8 (30.2)	+48.3 (+71.6)	17.2 (17.7)	29.8 (27.2)	+73.3 (+53.7)
ST _{sev}	9.2 (14.0)	25.1 (34.2)	+172.8 (+144.3)	9.0 (11.0)	33.5 (32.4)	+272.2 (+194.5)

Note: Values in parentheses are derived using the extended data sets of Bödmeren (n dead = 18, n alive = 23) and Scatlé (n dead = 20, n alive = 22).

Table 5 – Logistic regression models by Bigler and Bugmann (2004a)

Logistic regression models (Bigler and Bugmann, 2004a)	Growth variable(s)	Model performance (CCP)	
		Bödmeren	Scatlé
Model 1	RW ₃	44.0	39.9
Model 2	log(BAI/BA)	47.9	50.4
Model 3	log(BAI/BA), locreg ₅	46.7	55.4
Model 4	log(BAI/BA), locreg ₅ , log(BAI ₃)	45.3	50.4

Notes: Growth variables of the four models and corresponding model performance (CCP) for the two validation sites Bödmeren (n dead = 18, n alive = 23) and Scatlé (n dead = 20, n alive = 22). RW₃ = average of the ring widths of the last 3 years, log(BAI/BA) = log-ratio of basal area increment and basal area (relative basal area increment), locreg₅ = slope of a local, linear regression of the basal area increment over the last 5 years, log(BAI₃) = logarithmic basal area increment over the last 3 years.

mised ST models versus the four logistic regression models (Bigler and Bugmann, 2004a) at the two validation sites ($n = 18$, $F_{1,15} = 16.04$, $P < 0.001$). Furthermore, there was no significant difference between the two validation sites Bödmeren and

Scatlé ($F_{1,15} = 1.44$, $P = 0.249$), indicating site-independent mortality processes.

4. Discussion

4.1. Performance of optimised ST models

The optimised ST models showed a strongly improved performance, which was expected because their original parameters had been estimated arbitrarily (Tables 2 and 3). Analogous to the results of Bigler and Bugmann (2004a), the ST_{abs} model (the only model without a simple stress memory) showed high optimised CCP values and thus a good performance. Similarly high CCP values were achieved by the optimised ST_{rel} and ST_{comb} models, which were reduced to models without memory. In addition, the optimised ST_{comb} model was reduced to ST_{abs}, thus showing the same performance as ST_{abs} and indicating that the optimisation algorithm found the global maximum. The other models with a simple stress memory predicted mortality much less reliably. However, the inferior performance of the ST_{rel} model might be a result of its strong dependency on the accuracy of the maximum growth function (Moore, 1989): for all sites, the predicted theoretical maximum growth used in the ST_{rel} model was often exceeded by the tree-ring data, thus questioning the optimised relative threshold as determined here (results not shown).

The ST_{stress} and ST_{sev} models, which consider the relationship between stress tolerance and shade tolerance as a physiologically plausible mechanism, revealed relatively low CCP values (Table 3). Therefore, a strict link between stress

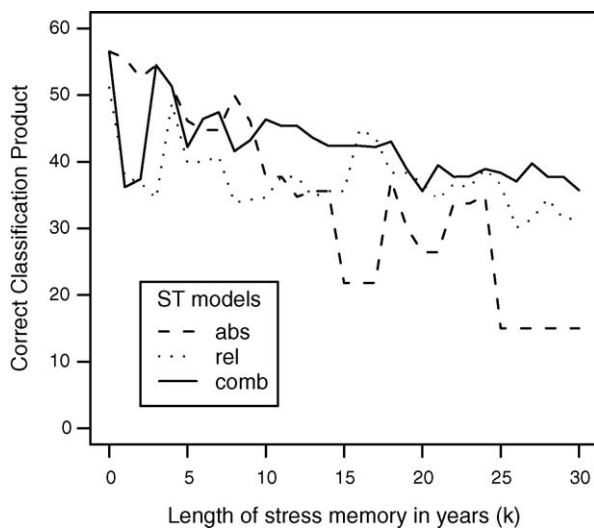


Fig. 2 – Neighbourhood zone for the models ST_{abs}, ST_{rel} and ST_{comb} for the Davos data set (n dead = 43 trees, n alive = 47 trees). Model performance (CCP) vs. length of a simple stress memory (number of years with low growth before stress mortality starts to act). Note: for all ST models, the optimum performance is achieved without any stress memory.

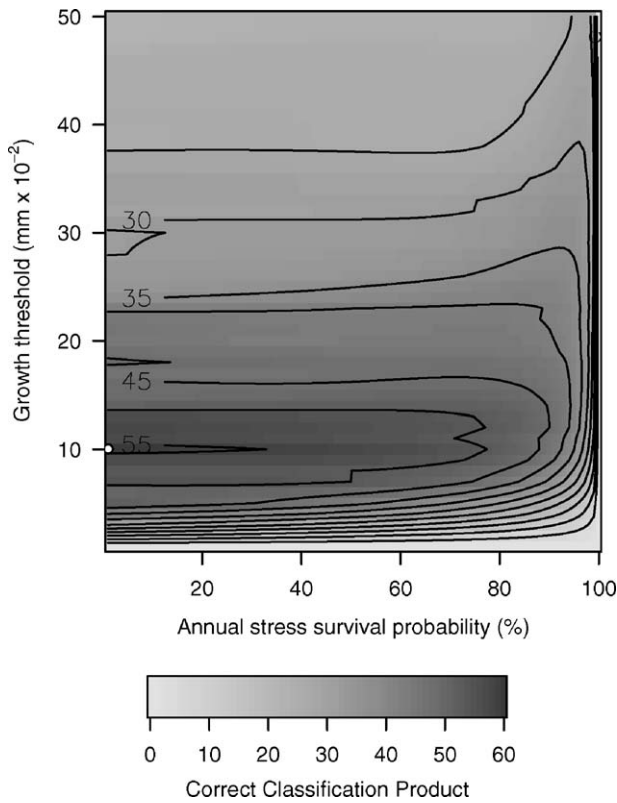


Fig. 3 – Neighbourhood zone for the ST_{abs} model for the Davos data set (n dead = 43 trees, n alive = 47 trees). Background mortality probability is zero (see Table 3). Calculated CCP values are based on the growth threshold and the annual stress survival probability. White circle: optimum parameter combination.

tolerance and shade tolerance as hypothesised by Keane et al. (1996) and Bugmann (2001) does not appear to be realistic, at least not for Norway spruce. For example, species like Scots pine (*Pinus sylvestris* L.) or European larch (*Larix decidua* Mill.) are shade intolerant, but they are quite stress tolerant with respect to drought in the case of pines and to low temperatures in the case of larch (Ellenberg and Klötzli, 1972; Bartels, 1993). Thus, these model formulations should be revised to separately consider various causes of stress, rather than considering all stresses as being equal. Wehrli et al. (2005) recently detected a strong overestimation of mortality rates in the gap model FORCLIM (V2.9.2) as compared to observed tree mortality rates in forest inventory plots. This may be caused by the fact that this FORCLIM version was based on the ST_{stress} model with the original parameter values, which is not reliable according to our study.

All “improvements” of the structure of the original ST_{abs} model that introduced a more or less sophisticated stress memory did not increase the CCP values (i.e., model performance), supporting the rule of parsimony in modelling (Burnham and Anderson, 2002). Surprisingly, in the group of models not considering shade tolerance, the ecologically plausible original parameter values for the survival probabilities in stress years (p) and “normal” years (q) were optimised to $p=0$ and $q=1$, implying immediate death of all trees falling below

the stress threshold and survival of all other trees (Table 2), and thereby a change from stochastic models to deterministic ones. On average, these parameter values lead to a high number of correctly classified trees of the calibration data set. However, for an individual tree, the sudden death after 1 year of low growth is ecologically implausible, since storage effects are known to buffer trees from short-term, severe stresses (Kozłowski, 1992).

The reduction of the increment thresholds in the optimised ST models suggests that Norway spruce trees are able to survive at lower DBH increment levels than previously expected (Tables 2 and 3). For the optimised ST_{abs} model (the model with the highest performance), the slightly reduced threshold and particularly the strongly reduced survival probability in stress years indicate that the succession of Norway spruce might be faster than suggested by projections of succession models using the original parameter values. For the optimised ST_{abs} model, the (theoretical) annual survival probability of an average tree of the calibration data set (Davos) equals 97.9% compared to 98.8% for the original ST_{abs} model. As a consequence, the resulting higher turnover rates may affect various ecosystem properties, including total forest carbon storage (Stephenson and van Mantgem, 2005).

However, some shortcomings in predicting tree mortality are still obvious. For example, the optimised ST_{abs} model predicts the death date of tree DAB 044 very reliably (Fig. 1), but, several other dead trees are misclassified (results not shown). An important reason for such misbehaviour is that neither the original nor the optimised ST models can handle sup-

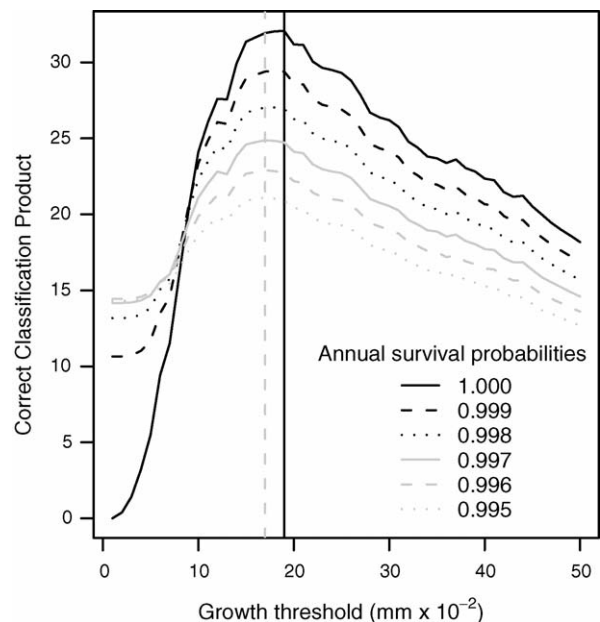


Fig. 4 – Neighbourhood zone for the ST_{stress} model for the Davos data set (n dead = 43 trees, n alive = 47 trees). Calculated CCP values based on the threshold and the annual survival probability ($1 - \text{probability of background mortality}$). Left vertical line (dashed): maximum of the CCP function for the original parameter value (survival probability $q = 0.996$). Right vertical line (continuous): maximum of the CCP function for the optimised parameter value (survival probability $q = 1.000$).

Table 6 – Ranking of the optimised ST models with and without memory (5 models) and the logistic regression models (4 models) sensu Bigler and Bugmann (2004a) based on the average CCP values at the validation sites Bödmeren und Scatlé (Tables 4 and 5)

Mortality model	CCP (average)	Rank
Logistic regression models	47.5	1
Optimised ST models		
Without memory (ST_{abs} , ST_{rel} , ST_{comb})	39.9	2
With memory (ST_{stress} , ST_{sev})	27.6	3

pression periods in the early part of tree life, which do not necessarily lead to tree death (see also Bigler and Bugmann, 2004b).

Surprisingly, an increasing length of the simple stress memory led to lower CCP values (Fig. 2). The local neighbourhood around the optimum parameter combination shows that all ST models are very susceptible to the threshold parameter, but they are much less susceptible to the annual survival probability in stress years (cf. ST_{abs} in Fig. 3). Once the annual diameter growth falls below a very small growth level, the survival probability of the tree is reduced strongly in the model. The fact that the reduction level barely affects model performance in a range from $q=0\%$ to $q=35\%$ indicates a concentration of low growth years towards the end of a tree's lifespan (Fig. 3). Therefore, even with higher annual survival probabilities (e.g., $q=35\%$), the probability for a modelled tree to survive 5 years of low growth is reduced strongly ($\Pr(\text{surv})=(0.35)^5 \approx 0.005$), most likely leading to a correct classification of that tree when the period of low growth occurs towards the end of its life span.

4.2. Ranking of mortality models

We compared the optimised ST models with recently derived logistic regression models based on growth patterns (Bigler and Bugmann, 2004a) by applying them to the same test data set. An ANOVA revealed a better performance of the logistic regression models: only the regression model based on ring width alone as predictor variable performed worse than the ST_{abs} model at one validation site (but still better than the other optimised ST models), whereas all regression models using basal area information as predictor variables performed better than the optimised ST models (models 2–4; Table 5). Among these three models, we found only small performance differences between the models with a memory length of 3–5 years ($\log[BAL_3]$ and \logreg_5 in models 3 and 4; Table 5) and those without memory (model 2; Table 5). Therefore, the better performance of the logistic regression models might be due to the choice of the growth variables (relative basal area increment BAI/BA; Table 5) rather than the presence of a memory, which again is somewhat surprising, at least for model 2 (Table 5).

Based on all these results, we established a ranking system for the performance of the mortality models (Table 6). According to this ranking, the logistic regression models show the highest performance, followed by the optimised memoryless ST models and finally the ST models (considering shade

tolerance) with a simple stress memory. Amazingly, the performance of both model types – ST models and logistic regression models – can increase with lower “biological realism” (i.e., the absence of a memory), which is a striking example that ecological plausibility in modelling does not automatically lead to high performance.

5. Conclusion

In this study, we have shown how an optimisation routine can be used to improve estimates of tree mortality in forest succession models with subsequent consequences for predicting forest succession in general. Surprisingly, the mortality models with an ecologically plausible stress memory showed a lower performance than models without any stress memory. Therefore, our analyses indicate that if classical ST (stress threshold) models are used in forest succession models, optimised models without memory should be preferred over those with a simple stress memory.

Furthermore, the performance of the memoryless ST models based on the explanatory variable “ring width” was exceeded considerably by regression models based on the variable “relative basal area increment”. To improve forest succession models, we suggest to replace the classical ST models with regression models based on relative basal area increment or more complex growth variables than ring width. Especially gap models that include “more advanced” ST models (Kienast, 1987; Keane et al., 1996) are most strongly in need of such replacements due to the weak ST model performance, whereas the oldest and simplest formulation by Botkin et al. (1972) shows acceptable performance, at least for Norway spruce.

In general, the optimisation routine could also be applied to other mortality models used in forest succession models that were not considered here. These models often show a similar structure and their parameters are mostly based on theoretical assumptions. For example, the forest succession model FORCLIM (V2.9.3; Risch et al., 2005), whose mortality model is based on the formulation by Kienast (1987) might be improved considerably by optimising the parameters of the mortality algorithm.

Changing the mortality submodel in forest succession models may in turn require a revision of the formulation or at least an adjustment of the parameters in the growth function. Sensitivity studies of forest succession models including the optimised mortality estimators could elucidate the impact of the submodel improvement on biomass production, stem numbers, turnover rates, and other ecologically important variables.

In our study, the theoretical maximum growth rate that is used in many forest succession models was often exceeded by observed tree-ring data from the sites Davos, Bödmeren and Scatlé. This indicates an underestimation of Norway spruce growth in forest succession models, which is particularly notable since site conditions in subalpine forests tend to be far from optimum. The optimisation routine presented here might be used to calibrate and validate growth submodels and further elements of forest succession models since currently used parameters have often been estimated without much empirical validation (Bugmann, 2001).

Clearly, the optimisation of mortality models, which has been restricted to Norway spruce in our study, should be extended to other tree species or at least functional groups of tree species. To avoid the time-consuming sampling and processing of dendrochronological cores and the measurement of tree rings, long-term inventory data should be used as calibration and validation data sets (see Zhao et al., 2004; Woodall et al., 2005; Bravo-Oviedo et al., 2006).

Considerable improvements in the modelling of forest succession can be expected if the currently implemented ST models in gap models are replaced by empirical regression models, thus leading to more reliable projections of future forest structure and composition.

Acknowledgments

We would like to thank Monika Ferster from the Seminar for Statistics at ETH Zurich for valuable discussions and two anonymous reviewers who provided helpful comments on an earlier version of the manuscript.

REFERENCES

- Bartels, H., 1993. *Gehölkzkunde: Einführung in die Dendrologie*. Ulmer, Stuttgart, p. 336.
- Beniston, M., 2004. Climatic Change and its Impacts. An Overview Focusing on Switzerland. *Advances in Global Change Research*, vol. 19. Kluwer, Dordrecht, p. 286.
- Bigler, C., Bugmann, H., 2003. Growth-dependent tree mortality models based on tree rings. *Can. J. For. Res.* 33, 210–221.
- Bigler, C., Bugmann, H., 2004a. Assessing the performance of theoretical and empirical tree mortality models using tree-ring series of Norway spruce. *Ecol. Model.* 174, 225–239.
- Bigler, C., Bugmann, H., 2004b. Predicting the time of tree death using dendrochronological data. *Ecol. Appl.* 14, 902–914.
- Botkin, D.B., 1993. *Forest Dynamics: An Ecological Model*. Oxford University Press, Oxford, 309 pp.
- Botkin, D.B., Janak, J.F., Wallis, J.R., 1972. Some ecological consequences of a computer model of forest growth. *J. Ecol.* 60, 849–872.
- Bravo-Oviedo, A., Sterba, H., del Río, M., Bravo, F., 2006. Competition-induced mortality for Mediterranean *Pinus pinaster* Ait. and *P. sylvestris* L. *For. Ecol. Manage.* 222, 88–98.
- Bugmann, H., 1994. On the ecology of mountainous forests in a changing climate: a simulation study. Ph.D. Thesis, Swiss Federal Institute of Technology Zürich, Zürich, p. 258.
- Bugmann, H., 1997. Sensitivity of forests in the European Alps to future climatic change. *Climate Res.* 8, 35–44.
- Bugmann, H., 2001. A review of forest gap models. *Climatic Change* 51, 259–305.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference: A Practical Information—Theoretic Approach*. Springer, New York, p. 488.
- Crow, G.R., Hicks, R.R., 1990. Predicting mortality in mixed oak stands following spring insect defoliation. *For. Sci.* 36, 831–841.
- Dobbertin, M., Biging, G.S., 1998. Using the non-parametric classifier CART to model forest tree mortality. *For. Sci.* 44, 507–516.
- Ellenberg, H., 1996. *Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht*. Ulmer, Stuttgart, p. 1095.
- Ellenberg, H., Klötzli, F., 1972. *Waldgesellschaften und Waldstandorte der Schweiz*. Mitteilungen der Eidgenössischen Anstalt für das forstliche Versuchswesen 48, 587–930.
- Fischlin, A., Gyalistras, D., 1997. Assessing impacts of climatic change on forests in the Alps. *Global Ecol. Biogeogr. Lett.* 6, 19–38.
- Hasenauer, H., Merkl, D., Weingartner, M., 2001. Estimating tree mortality of Norway spruce stands with neural networks. *Adv. Environ. Res.* 5, 405–414.
- Hawkes, C., 2000. Woody plant mortality algorithms: descriptions, problems and progress. *Ecol. Model.* 126, 225–248.
- Keane, R.E., Morgan, P., Running, S.W., 1996. FIRE-BGC—a mechanistic ecological process model for simulating fire succession on coniferous forest landscapes of the northern Rocky Mountains. USDA Forest Service Research Paper INT-RP-484.
- Keane, R.E., Austin, M., Field, C., Huth, A., Lexer, M.J., Peters, D., Solomon, A., Wyckoff, P., 2001. Tree mortality in gap models: application to climate change. *Climatic Change* 51, 509–540.
- Kienast, F., 1987. FORECE—a forest succession model for Southern Central Europe. Report ORNL/TM-10575, Oak Ridge National Laboratory, Oak Ridge, Tennessee.
- Kozłowski, T.T., 1992. Carbohydrate Source and Sinks in Woody Plants. *Bot. Rev.* 58, 107–222.
- Moore, A.D., 1989. On the maximum growth equation used in forest gap simulation models. *Ecol. Model.* 45, 63–67.
- Nelder, J.A., Mead, R., 1965. A simplex method for function minimization. *Comput. J.* 7, 308–313.
- Nichols, J.O., 1968. Oak mortality in Pennsylvania. *J. Forest.* 66, 681–694.
- Price, D.T., Zimmermann, N.E., van der Meer, P.J., Lexer, M.J., Leadley, P., Jorritsma, I.T.M., Schaber, J., Clark, D.F., Lasch, P., McNulty, S., Wu, J., Smith, B., 2001. Regeneration in gap models: priority issues for studying forest response to climate change. *Climatic Change* 51, 475–508.
- R Development Core Team, 2005. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria, <http://www.R-project.org>.
- Reynolds, J.H., Ford, E.D., 1999. Multi-criteria assessment of ecological process models. *Ecology* 80, 538–553.
- Risch, A.C., Heiri, C., Bugmann, H., 2005. Simulating structural forest patterns with a forest gap model: a model evaluation. *Ecol. Model.* 181, 161–172.
- Shugart, H.H., 1984. *A Theory of Forest Dynamics. The Ecological Implications of Forest Succession Models*. Springer, New York, 278 pp.
- Solomon, A.M., 1986. Transient response of forests to CO₂-induced climate change: simulation modeling experiments in eastern North America. *Oecologia* 68, 567–579.
- Stephenson, N.L., van Mantgem, P.J., 2005. Forest turnover rates follow global and regional patterns of productivity. *Ecol. Lett.* 8, 524–531.
- Suarez, M.L., Ghermandi, L., Kitzberger, T., 2004. Factors predisposing episodic drought-induced tree mortality in *Nothofagus*—site, climatic sensitivity and growth trends. *J. Ecol.* 92, 954–966.
- Theurillat, J.-P., Guisan, A., 2001. Potential impact of climate change on vegetation in the European Alps: a review. *Climatic Change* 50, 77–109.
- van Mantgem, P.J., Stephenson, N.L., 2005. The accuracy of matrix population model projections for coniferous trees in the Sierra Nevada, California. *J. Ecol.* 93, 737–747.

- Wehrli, A., Zingg, A., Bugmann, H., Huth, A., 2005. Using a forest patch model to predict the dynamics of stand structure in Swiss mountain forests. *For. Ecol. Manage.* 205, 149–167.
- Woodall, C.W., Gramsch, P.L., Thomas, W., 2005. Applying survival analysis to a large-scale forest inventory for assessment of tree mortality in Minnesota. *Ecol. Model.* 189, 199–208.
- Wyckoff, P.H., Clark, J.S., 2002. The relationship between growth and mortality for seven co-occurring tree species in the southern Appalachian Mountains. *J. Ecol.* 90, 604–615.
- Zhao, D., Borders, B., Wilson, M., 2004. Individual-tree diameter growth and mortality models for bottomland mixed-species hardwood stands in the lower Mississippi alluvial valley. *For. Ecol. Manage.* 199, 307–322.