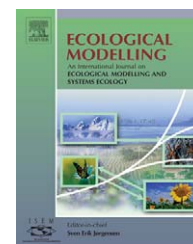


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# Optimisation of tree mortality models based on growth patterns

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## 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.

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## 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-

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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 m<sup>2</sup> 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-

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