

Predicting tree death for *Fagus sylvatica* and *Abies alba* using permanent plot data

Wunder, Jan^{1*}; Reineking, Björn¹; Matter, Jean-François^{1,2};
Bigler, Christof¹ & Bugmann, Harald¹

¹Forest Ecology, Institute of Terrestrial Ecosystems, Department of Environmental Sciences, ETH Zurich, CH-8092 Zurich, Switzerland; ²formerly: Institute of Silviculture, Department of Forest Sciences, ETH Zurich, CH-8092 Zurich, Switzerland; * Corresponding author: Fax: +41446321358; E-mail: wunder@env.ethz.ch

Abstract

Question: How well can mortality probabilities of deciduous trees (*Fagus sylvatica*) and conifers (*Abies alba*) be predicted using permanent plot data that describe growth patterns, tree species, tree size and site conditions?

Location: *Fagus* forests in the montane belt of the Jura folds (Switzerland).

Method: Permanent plot data were used to develop and validate logistic regression models predicting survival probabilities of individual trees. Backward model selection led to a reduced model containing the growth-related variable 'relative basal area increment' (growth-dependent mortality) and variables not directly reflecting growth such as species, size and site (growth-independent mortality).

Results: The growth-mortality relationship was the same for both species (growth-dependent mortality). However, species, site and tree size also influenced mortality probabilities (growth-independent mortality). The predicted survival probabilities of the final model were well calibrated, and the model showed an excellent discriminatory power (area under the receiver operating characteristic curve = 0.896).

Conclusion: Mortality probabilities of *Fagus sylvatica* and *Abies alba* can be predicted with high discriminatory power using a well calibrated logistic regression model. Extending this case study to a larger number of tree species and sites could provide species- and site-specific tree mortality models that allow for more realistic projections of forest succession.

Keywords: Calibration; Discrimination; Ecoinformatics; European beech; Forest ecology; Forest inventory, Forest reserve; Mortality model; Restricted cubic spline; Silver fir; Tree mortality.

Abbreviations: AUC = Area under ROC curve; BAI = Basal area increment; *relbai* = Relative basal area increment; ROC = Receiver operating characteristic.

Introduction

Tree mortality is a key element of forest dynamics that strongly influences the biological and structural diversity of forest ecosystems (Franklin et al. 1987). Quantitative estimates of the risk of tree mortality contribute to our understanding of forest dynamics and increase the reliability of forest modelling in general. Particularly with regard to climate change, improved projections of future forest structure and composition are of increasing significance (Bugmann 1997; Fischlin & Gyalistras 1997; Theurillat & Guisan 2001; Beniston 2004; Suarez et al. 2004; Huber et al. 2005).

Impending tree death can be modelled using two different components of mortality. First, growth-dependent mortality generally relates radial stem growth to mortality probabilities. In stressed trees, carbon allocation to stem growth has a lower priority than the crown or root system (Waring & Pitman 1985). Therefore, a reduction in stem growth is considered a phenotypic reaction to environmental stress that may lead to increased mortality (Dobbertin 2005). Second, growth-independent mortality comprises mortality causes that cannot directly be explained by changes in tree growth. For example, the longevity of trees is influenced by different factors such as the specific site conditions or the tree species itself, and therefore this component is not directly related to growth. Other causes of growth-independent mortality are related to disturbances such as wildfires (e.g. Lampainen et al. 2004) or wind storms (e.g. Nishimura 2006), which lead to sudden tree death, described as disturbance related mortality. Here, we focus on long-term mortality processes and explore them with models combining growth-dependent and growth-independent causes of mortality without consideration of disturbance-related mortality.

Tree mortality models need to be based on large data sets covering species-specific growth histories from trees of different size and age classes which extend over long time periods to reflect the highly variable nature of mortality in space and time (Hawkes 2000; Keane et al. 2001).

However, analysis of tree mortality is often restricted to data sources that are relatively small regarding either a) the number of sampling units such as tree-ring series from several living and dead trees or b) the number of measurement periods, such as in the case of permanent plots that typically have only been measured over a few decades (Biondi 1999).

Tree-ring series provide high resolution records of tree growth, but difficulties with the coring of dead trees and the time consuming measuring of ring widths often do not allow for large data sets (Wyckoff & Clark 2000; Bigler & Bugmann 2004; Bigler et al. 2004). Furthermore, destructive or semi-destructive sampling of trees in the few remaining primary or old growth forests is often restricted, at least in Europe. Although the role of coring as a mortality factor has been shown to be negligible for some tree species (van Mantgem & Stephenson 2004), it remains unclear how coring influences tree growth and mortality.

Permanent plot data are usually characterised by a coarse temporal resolution of tree growth information (typically 5-15 years) but they are often available in large sample sizes, because of the conveniently measurable diameter at breast height (DBH) (Monserud & Sterba 1999; Fridman & Ståhl 2001; Temesgen & Mitchell 2005; Bravo-Oviedo et al. 2006). Since the longevity of trees often exceeds the time span of forest inventories, only partial tree growth information is available from trees in different life stages.

In both cases (tree-ring and permanent plot data), the relative importance and the interaction of growth-dependent mortality (linked to e.g. stem growth) and growth-independent mortality (linked to e.g. site conditions) is not well known. Moreover, many mortality models feature a high discriminatory power between dead and living trees, but it remains unclear how well the predicted survival probabilities agree with the observed probabilities in the test data (calibration). Thus, the specific objectives of our study are (1) to compare the growth-dependent and growth-independent mortality of two case study species (*Fagus sylvatica* and *Abies alba*) based on permanent plot data from near-natural forests and (2) to validate species-specific mortality models that eventually will allow – in combination with disturbance-related mortality models – for an implementation into forest succession models.

Material and Methods

Database

We used data from the forest reserve network of the Swiss Federal Institute of Technology Zurich (ETH Zu-

rich) currently maintained jointly by the Chair of Forest Ecology (ETH Zurich) and the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL Birmensdorf). The network was initiated in the late 1940s to observe the long-term dynamics of unmanaged, near natural forests in Switzerland (Leibundgut 1957). The former Institute of Silviculture (ETH Zurich) directed the successive expansion of the network, currently comprising 39 forest reserves with a total area of 1018 ha and including ca. 150000 individual trees measured during two to five inventories.

For the sampling design, three levels of forest reserve observations with increasing accuracy were distinguished (Leibundgut 1959, 1962, 1966): compartment, permanent plot and strip transect. The compartments comprise the total area of the forest reserve. Within this area, for all trees > 4cm DBH, species, condition (alive or dead) and DBH (calliper measurement to the nearest cm) were recorded; these data were merged to stand scale variables (e.g. diameter distributions). Within the compartment, areas of 0.3ha to 1ha with a homogenous forest community type, microtopography, stage of development and stand structure were defined as permanent plots. Within each permanent plot and for each individual tree, species, DBH (calliper measurement to the nearest mm), Kraft's crown class (Kraft 1884) and the 'social' position of the tree (i.e. stratum, vigour and dynamic tendency; Assmann 1961) were recorded. The third level, the strip transects located within the compartments, were used to illustrate selected structural features of the forest in a three dimensional manner.

Due to financial cutbacks, only a part of the data have been digitized and quality checked until now. Therefore, some inventories of forest reserves are currently unavailable for analysis. Since analyses of forest dynamics require at least two inventories, we focus in this paper on two data sets from the same area fulfilling this condition.

Study sites and sample size

We selected two forest reserves near St. Ursanne (Switzerland, Table 1) in the Jura folds, a calcareous mountain belt in western central Europe. Both forest reserves, the southeast-facing 'Bois Banal' and the northwest-facing 'Haute Côte', are located on opposite slopes of the river Doubs. They are influenced by a maritime west coast climate (Köppen & Geiger 1930-1939). The predominant soil types are Rendzic Leptosols (Anon. 1998) on late Jurassic substrate, i.e. Malm (Diebold et al. 1963, Table 1). In this study, we focused on the dominant tree species, *F. sylvatica* and, the most abundant co-dominant species, *A. alba*. The selected eight permanent plots (Bois Banal: 5, Haute Côte: 3) belong

to the *Cardamino-Fagetum* (Ellenberg & Klötzli 1972) as classified by Burger (1976). They represent a *Fagus*-dominated forest in all strata, except for the smallest DBH class at Haute Côte (Fig. 1).

Derivation of growth variables

For the growth-dependent mortality, we used relative basal area increment (*relbai*) to quantify the percentage of newly created wood that is assuring water transport within the tree. Recently, *relbai* has been successfully applied to predict tree mortality using tree rings (Bigler & Bugmann 2004; Bigler et al. 2004). We calculated *relbai* by dividing the basal area increment (BAI) of tree *i* between t_1 and t_2 by its basal area (BA) at t_2 :

$$relbai(i, t_1, t_2) = \frac{BAI(i, t_1, t_2)}{BA(i, t_2)} \quad (1)$$

with $BAI(i, t_1, t_2) = BAI(i, t_2) - BAI(i, t_1)$ and $t_1 < t_2$.

Thus, for growing trees, *relbai* is restricted to an interval between zero and one, representing the growth increment relative to actual tree size. Consequently, low values indicate low vigour and thus should be related to an increased risk of mortality. The DBH values measured at our sites were converted into basal area by assuming a circular outline of stem cross sections, and the DBH increment between inventories was used to calculate BAI. Based on this transformation, we obtained two *relbai* values per tree, one for each inventory interval.

Since we observed negative BAI values for a few living trees possibly due to measurement errors (ca. 1.6% of all living trees), we reduced our data set to trees with positive increments that were living at the first and second inventory. The *relbai* values calculated between these two inventories were used to explain whether a tree was alive at the third inventory. We also excluded trees < 10cm DBH and trees with broken stems to avoid potentially different mortality processes in the regeneration phase and disturbance mortality, respectively.

Model development

Our mortality model consisted of a growth-dependent and a growth-independent mortality component. The growth-dependent mortality component reflects the relationship between tree growth and mortality. The growth-independent mortality component is independent of growth rates, i.e. vigour, but flexible to take into account differences between tree species (*F. sylvatica* and *A. alba*), sites (Bois Banal and Haute Côte) and tree size. We used a logistic regression model with a binary response variable describing the condition of the tree at the end of the last inventory period (alive or dead). For

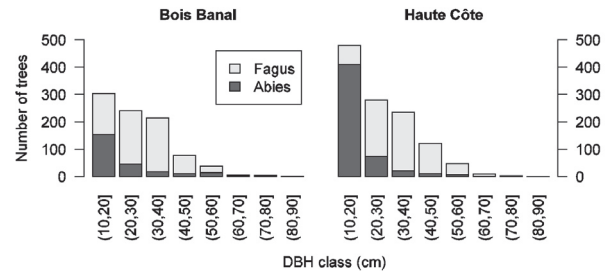


Fig. 1. Diameter distribution of *F. sylvatica* (grey) and *A. alba* (black) at the two sites Bois Banal ($n_{F. sylvatica} = 634$ trees, $n_{A. alba} = 251$ trees) and Haute Côte ($n_{F. sylvatica} = 654$ trees, $n_{A. alba} = 527$) in 1998/1999 (cf. Table 1).

the growth-dependent mortality, the explanatory variable was *relbai* of each growing tree calculated from the first and the second inventory. For the growth-independent mortality, we used the factors ‘species’ (two levels, ‘*F. sylvatica*’ and ‘*A. alba*’) and ‘site’ (two levels, ‘Bois Banal’ and ‘Haute Côte’). Additionally, we included the variable DBH as an indicator of tree size, which can be considered as a proxy for tree age.

The variable *relbai* was transformed using restricted cubic splines with four knots (Hastie & Tibshirani 1990). Restricted cubic splines are composed of piecewise third-order polynomials within intervals determined by the knots. The connections between the polynomials

Table 1. Site information of the analysed forest reserves.

Site	Bois Banal	Haute Côte
Conditions		
Co-ordinates (N, E)	47°20'15", 7°9'5"	47°20'5", 7°9'53"
Altitude (m a.s.l.)	450-680	700-800
Exposition	SE	NW
Slope (%)	20-100	80
Geology	Malm (Kimmeridgien, Séquanien, Rauracien)	Malm (Kimmeridgien, Rauracien)
Annual precipitation (mm)	900 (Delémont)	
Mean annual temperature (°C)	8.7 (Delémont)	
Inventory		
Permanent plot area (ha)	1.65	2.13
Inventory campaign	1975 1986 1999	1973/1974 1985 1998/1999
Sample trees (1998/1999)		
- <i>Fagus sylvatica</i> (alive/dead)	885 634 (604/30)	1181 654 (647/7)
- <i>Abies alba</i> (alive/dead)	251 (237/14)	527 (477/50)

Notes: Annual precipitation sum and mean annual temperature were derived from the climate station Delémont, ca. 18 km west of both sites (415 m a.s.l.). Bois Banal: inventories of all permanent sample plots in 1975, 1986, 1999 were conducted midyear; Haute Côte: 1973 (end of year) / 1974 (beginning of the year), 1985 (midyear), 1998 (end of year) / 1999 (beginning of the year). Sample trees: from all trees at the two sites (Bois Banal: 1603 trees; Haute Côte: 2569 trees) we selected those that (1) were growing and alive at the first and second inventory campaign, (2) exceeded 10 cm DBH at the second inventory campaign, and (3) had no broken stem.

are forced to be smooth and the composite function is constrained to be linear in the tails (Stone & Koo 1985; Harrell 2001). Applying restricted cubic splines allows for a nonlinear relationship between *relbai* and the logits of the survival probabilities to be fitted, which is accomplished by including two nonlinear terms *relbai'* and *relbai''* in the equation. The variable DBH was log-transformed to decrease the weight of the large number of trees found in the smaller DBH classes.

In the full model, we allowed for the most meaningful two-way interactions, i.e. all interactions between *relbai*, site and species and additionally the interaction between DBH and site. We reduced this model by applying a fast backward selection method (Harrell 2001) to identify a more parsimonious description of the key patterns in the data.

Model performance

Model performance was assessed using a combination of calibration and discriminatory power measures (Pearce & Ferrier 2000). Calibration measures express how well the predicted survival probabilities agree with the observed probabilities in the test data. The discriminatory power indicates how well the model is able to discriminate between living and dead trees. Model performance (calibration and discrimination) was assessed using bootstrapping techniques (Guisan & Harrell 2000; Harrell 2001; Steyerberg et al. 2001). Bootstrapping allows for correcting the overoptimism that results when evaluating a model on the same data to which it was fitted. In a first step, a reduced predictive model was fitted to the original sample (2066 trees) using backward selection. The model performance of this original model on the original sample is called *apparent* model performance (e.g. R^2_{apparent}). In a second step, 1500 bootstrap samples of equal size to the original sample were drawn with replacement from the original sample. For each bootstrap sample, a reduced predictive model was fitted using the same backward selection method. Predictions of the bootstrap models for the original sample led to new values of performance indices, whose means resulted in the *bias-corrected* model performance (e.g. $R^2_{\text{bias-corrected}}$). The difference between the apparent and bias-corrected model performance is considered to be a 'stable estimate of the overoptimism' (Moons et al. 2004). Overoptimism occurs when the model is fitted too closely to the original data set, possibly due to a large number of predictors (overfitting). The model's expected performance on new data equals its performance on the original data reduced by the amount of overoptimism.

Calibration was quantified with calibration curves that relate predicted to observed probabilities. Ideal calibration, i.e. no difference between predicted and observed probabilities, is expressed by a 45° line (Har-

rell 2001). Deviations from this perfect calibration curve indicate model overfitting: slope angles < 45° are typical for models that are fitted too closely to the original data set, whereas slope angles > 45° indicate excessive regularisation, i.e. an insufficient flexibility of the model (Reineking & Schröder 2006).

Discrimination was visualised with the receiver operating characteristic (ROC) curve and measured by AUC (the area under the ROC curve; Fielding & Bell 1997). The ROC curve is derived by plotting all true positive values (sensitivity) against all false positive values (1-specificity). The AUC is a nonparametric and threshold-independent measure that can be interpreted as the probability that a randomly selected tree that survived between the second and third inventory has a higher predicted probability to survive than a randomly selected tree that died during that period (Fielding & Bell 1997).

All analyses were performed using R, a language and environment for statistical computing (R Development Core Team 2006). Logistic regression models were fitted, calibrated and validated using the Design package (R-package version 2.0-12; Harrell 2005), ROC graphs were plotted using the ROCR package (R-package version 1.0-1; Sing et al. 2005).

Results

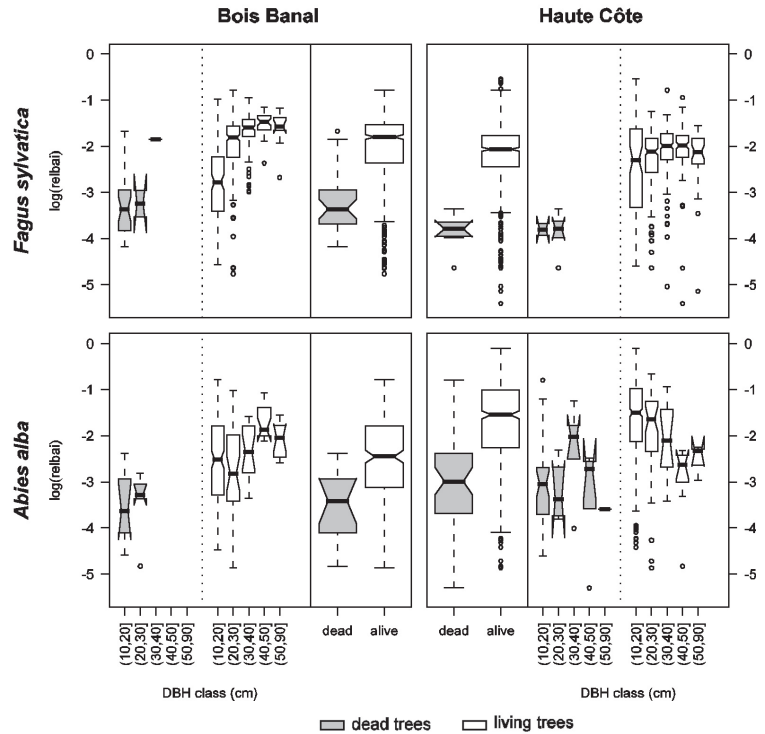
Distribution of relative basal area increments

Prior to tree death, *relbai* was considerably lower than that of surviving trees (Fig. 2). The respective time period covered the first inventory interval, representing an 11 year growth history of each tree (Bois Banal: 1975–1986, Haute Côte: 1973/74–1985, Table 1). Overall, trees that died during the last inventory interval (Bois Banal: 1986–1999, Haute Côte: 1985–1998/99) showed a strongly reduced *relbai*, with the clearest differences between living and dead *F. sylvatica* at Haute Côte (pooled box plots in Fig. 2). Generally, larger dead trees (DBH > 30cm) were found only at Haute Côte. For living *F. sylvatica*, *relbai* increased with size to a maximum between 30cm and 50cm DBH, and the largest trees showed a slight decrease of *relbai*. For living *A. alba* at Bois Banal, the *relbai* – DBH relationship was qualitatively similar to that of *F. sylvatica*, but at Haute Côte, *relbai* decreased with increasing DBH, with a minimum between 40cm and 50cm DBH, i.e. at sizes where all other living trees showed highest *relbai*.

Model development

Backward selection of the full model (Table 2) led to a reduced model with clearly distinct growth-dependent

Fig. 2. Relative basal area increment (*relbai*) of *F. sylvatica* and *A. alba* measured between 1973/74 and 1985 at the two sites Bois Banal and Haute Côte. Condition of the trees in 1998/1999: grey boxes = dead trees, white boxes = living trees. *relbai* values are shown for all dead and living trees (large box plots in the inner parts of the graph) and also for different DBH classes (small box plots, outer parts). Tree numbers: see notes in Fig. 1. Box plots: the box length covers the first and third quartile of the data, the median is marked with a bold line. Notches define an approximate confidence interval of the median, 'whiskers' are extended to the most extreme data point between the box and 1.5 times of the box length (R Development Core Team 2006).



and growth-independent components, i.e. there were no significant interactions between *relbai* and the other variables (Table 3, App. 1). *Relbai* was treated as a single

entity together with the newly created nonlinear terms *relbai'* and *relbai''* that had been derived by the restricted cubic spline transformation.

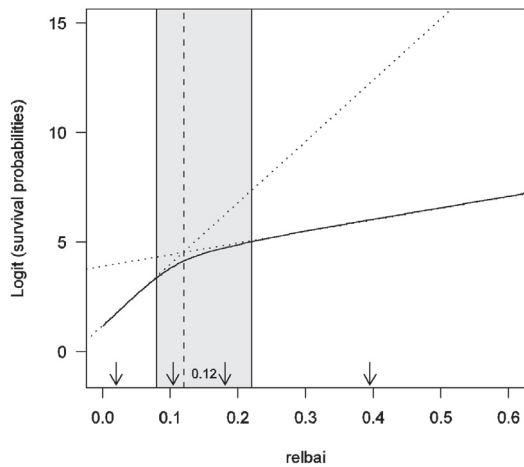


Fig. 3. Growth-mortality relationship according to the variable *relbai* (growth-dependent mortality) expressed in logits, i.e. the logarithm of the ratio of survival probabilities to mortality probabilities. Transition zone (grey) around the inflexion point at *relbai* 0.12 (intersection of the two slope tangents). Arrows locate the four knots of the restricted cubic spline transformation (*relbai* values of 0.020, 0.104, 0.181 and 0.395, corresponding to the 5%-, 35%-, 65%- and 95%-quantiles of the observed *relbai*). Tangents were fitted with linear regression of the segments below and above the transition zone.

Table 2. Full logistic regression model for the survival probabilities of individual trees (n dead = 101 trees, n alive = 1965 trees). $AUC_{\text{apparent}}: 0.910$, $AUC_{\text{bias-corrected}}: 0.901$, Nagelkerke's $R^2_{\text{apparent}}: 0.381$, Nagelkerke's $R^2_{\text{bias-corrected}}: 0.355$.

Predictor	Coefficient	S.E.	Wald Z	P
Intercept	5.12	1.70	3.01	0.003
<i>relbai</i>	18.96	13.02	1.46	0.145
<i>relbai'</i>	-15.05	132.75	-0.11	0.910
<i>relbai''</i>	65.13	532.04	0.12	0.903
species	-24.29	4.10	-5.93	<0.001
site	-2.09	0.64	-3.25	0.001
log(DBH)	-0.69	0.32	-2.17	0.030
<i>relbai</i> × species	22.98	15.74	1.46	0.144
<i>relbai'</i> × species	-282.26	166.36	-1.70	0.090
<i>relbai''</i> × species	1131.89	774.69	1.46	0.144
<i>relbai</i> × site	12.11	14.12	0.86	0.391
<i>relbai'</i> × site	-59.86	137.82	-0.43	0.664
<i>relbai''</i> × site	77.95	539.99	0.14	0.885
species × site	2.47	0.60	4.09	<0.001
species × log(DBH)	4.50	0.80	5.60	<0.001

Notes: S.E. = standard error, factor coding for species (*A. alba* = 0, *F. sylvatica* = 1) and site (Bois Banal = 0, Haute Côte = 1), restricted cubic splines with additional nonlinear terms *relbai'* and *relbai''*, the four knots are located at *relbai* values of 0.020, 0.104, 0.181 and 0.395, corresponding to the 5%-, 35%-, 65%- and 95%-quantiles of the observed *relbai*.

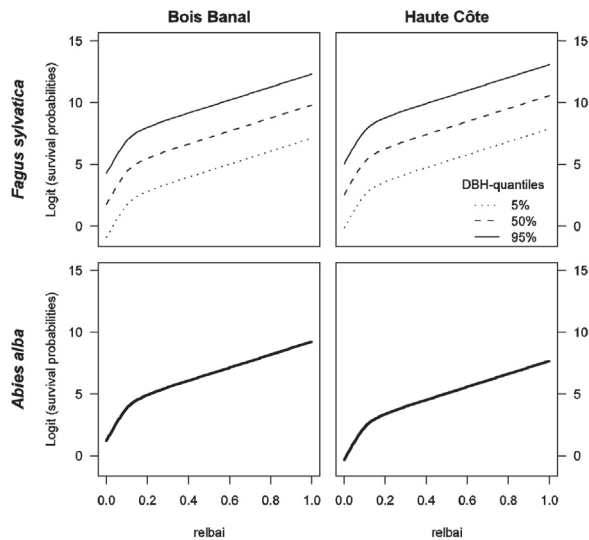


Fig. 4. Survival probabilities of *Fagus sylvatica* and *Abies alba* for a range of growth conditions at the two sites Bois Banal and Haute Côte expressed in logits, i.e. the logarithm of the ratio of survival probabilities to mortality probabilities. The curves indicate the survival probabilities for trees with 10.8, 22.9 and 46.3 cm DBH corresponding to the 5%-, 50%- and 95%-quantiles of the observed DBH. Upper panels (*F. sylvatica*): DBH quantile curves indicate different survival probabilities. Lower panels (*A. alba*): DBH-quantile curves are superimposed.

Survival probabilities

We expressed the survival probabilities by their logits, i.e.

$$\log\left(\frac{p}{1-p}\right) \quad (1)$$

where p is the survival probability. The general shape of all resulting survival probability curves was the same, i.e. the growth-mortality relationship was independent of species, site and tree size (Figs. 3 and 4). Thus, the restricted cubic splines fit of $relbai$ suggests that the functional relationship of $relbai$ is non-linear (Fig. 3). We found two areas of $relbai$ that were characterised by different

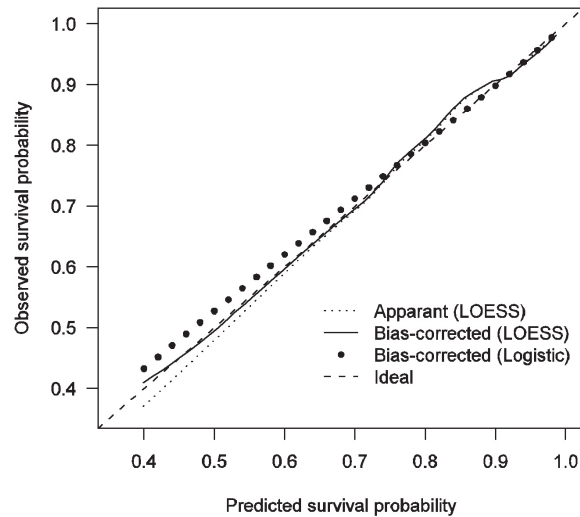


Fig. 5. Calibration plot of the reduced mortality model (Table 3) based on 1500 bootstrap samples of the original data set. Relations between predicted and observed survival probabilities were obtained using a smooth nonparametric calibration ('LOESS', Harrell 2001) and a linear logistic calibration ('Logistic', Harrell 2001). 'Apparant' curve: original model applied to the original sample. 'Bias corrected' curves: bootstrap model applied to the original sample. 'Ideal' curve: predicted survival probabilities equal observed survival probabilities.

sensitivities to changes in $relbai$; they were separated by a transition zone around the inflexion point of $relbai \approx 0.12$ (intersection of the two slope tangents, Fig. 3).

Thus, for a slowly growing tree ($relbai < 0.12$), small changes in growth lead to relatively large changes in the survival probability. For example, an increase of $relbai$ by 0.01 would lead to an increase of the logit by 0.28, corresponding to an odds ratio of 1.3 (i.e. such an increase of $relbai$ leads to a 1.3 fold increase in the chance of survival). In contrast, for a fast growing tree ($relbai > 0.12$), the same growth increase of $relbai$ (0.01) changes the logit by only 0.053 (odds ratio = 1.05).

In contrast, differences in the factors not directly related to growth led to different survival probabilities

Table 3. Reduced logistic regression model for the survival probabilities of individual trees after backward selection (n dead = 101 trees, n alive = 1965 trees). AUC_{apparent} : 0.903, $AUC_{\text{bias-corrected}}$: 0.896, Nagelkerke's R^2_{apparent} : 0.367, Nagelkerke's $R^2_{\text{bias-corrected}}$: 0.344 (for representation of the model see App. 1).

Model component	Predictor	Coefficient	S.E.	Wald Z	P
Growth-independent mortality	Intercept	1.16	0.34	3.42	0.001
	species	-18.79	3.53	-5.32	<0.001
	site	-1.56	0.34	-4.58	<0.001
	species \times site	2.33	0.58	4.01	<0.001
	species \times log(DBH)	3.57	0.70	5.11	<0.001
Growth-dependent mortality	$relbai$	29.17	5.43	5.37	<0.001
	$relbai'$	-72.92	39.17	-1.86	0.063
	$relbai''$	146.10	102.00	1.43	0.152

See notes in Table 1 for further detail.

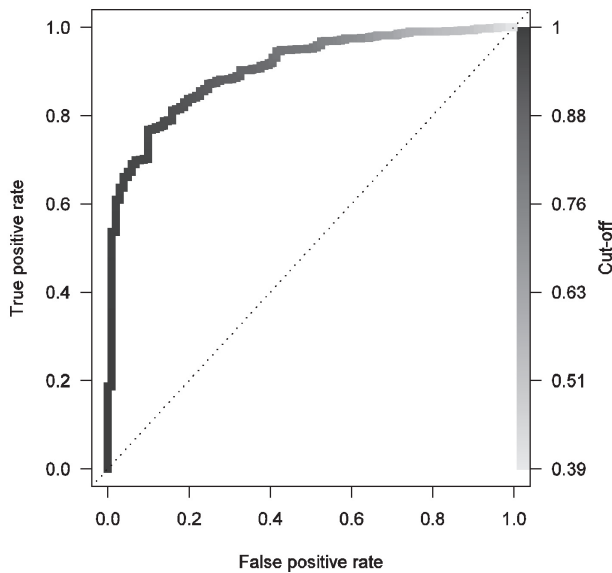


Fig. 6. ROC (Receiver Operating Characteristic) curve for the original data set (reduced model). True positive rate = sensitivity, false positive rate = 1 - specificity. Grey scale code (right y axis): Cut-off points ranging from 0.39 (light grey) to 1.00 (black). $AUC_{\text{bias-corrected}} = 0.896$.

depending on species, site and tree size due to a vertical shift of the general survival probability curve (Fig. 4). Only for *F. sylvatica*, did tree size contain significant information for predicting mortality, i.e. tree size was not significant for *A. alba*. Generally, the larger the DBH of *F. sylvatica* at both sites, the higher the corresponding survival probabilities. The highest survival probabilities were predicted for *F. sylvatica* at Haute Côte and the lowest for *A. alba* at the same site. For *A. alba* at Haute Côte, the survival probability was nearly equal to that of small *F. sylvatica* (5%-quantile of DBH, Fig. 4), whereas for *A. alba* at Bois Banal, the corresponding survival probability was similar to that of intermediate-sized *F. sylvatica* (50%-quantile of DBH, Fig. 4).

Model performance

The calibration plot indicated a good match of predicted and observed probabilities in the interval [0.7, 1], as revealed by the apparent and bias-corrected (optimism-corrected) curves (Fig. 5). Below that interval, our model underestimated slightly the survival probabilities, i.e. the predictions were slightly too pessimistic (Fig. 5).

The bias-corrected (=optimism-corrected) discriminatory power of the reduced model yielded an AUC of 0.896 (Fig. 6). Thus, with a probability of nearly 90%, a randomly selected tree that survived between the second and third inventory has a higher predicted probability to

survive than a randomly selected tree that died during that period. Therefore, the selected variables *relbai*, site, species and DBH allow the differentiation of the survival probabilities of dead and surviving trees of *F. sylvatica* and *A. alba* at the two sites Bois Banal and Haute Côte (Fig. 6). The applied bootstrap techniques estimated the optimism in AUC to be lower than 0.01 (reduced model).

Discussion

Development and interpretation of the mortality model

The analogous behaviour of *Fagus sylvatica* and *Abies alba* may be a result of similar life history strategies as expressed by their shade tolerance (Ellenberg 1996). However, the different DBH-frequency distributions of both species suggested a bell shape for *F. sylvatica* and an inverse J-shape for *A. alba* (Fig. 1), indicating higher recruitment and mortality rates for *A. alba*. Nishimura et al. (2005) found similar DBH patterns in an old-growth coniferous forest in central Japan with bell shapes for *Picea jezoensis* var. *hondoensis* and *Tsuga diversifolia* and inverse J-shapes for *Abies mariesii* and *Abies veitchii*, which were interpreted as a trade-off between recruitment and interspecific competition.

F. sylvatica and *A. alba* also show some crucial ecological differences concerning their stress reaction: *F. sylvatica* has an extraordinary plasticity of crown architecture, as it can form long shoots to optimise the exploitation of crown space and short shoots to optimise light exploitation (Bartels 1993). In addition to regular shoot formation, shoots can be formed either proleptically (from preformed dormant buds, facultative) or sylleptically (without bud dormancy, young individuals only). Consequently, the growth of *F. sylvatica* with a primary plagiotropic and secondary orthotropic axis (tree architecture type TROLL; Hallé et al. 1978) allows for an extremely flexible exploitation of crown space. Furthermore, the storage tissue in the large rays of *F. sylvatica* exceeds that of *A. alba*'s uniseriate rays (Sachsse 1984) and allows for a faster stress reaction. For *A. alba*, crown architecture is less flexible, i.e. growth is restricted to long shoots optimised for survival in the shade. The species shows a strict monopodial growth with regularly structured levels of plagiotropic branches (tree architecture type MASSART; Hallé et al. 1978) and a high plasticity of leaf formation ranging from bifacial to equifacial needles (Kaplan 2001). This structure leads to an extreme shade tolerance, which even exceeds that of *F. sylvatica* and allows for the survival of still longer periods of low growth by *A. alba* (Leibundgut 1984). However, such ecological differences are not evident

in our model, suggesting that shade tolerance is not important for trees exceeding 10cm DBH. Additionally, the relatively low number of dead trees in the larger size classes may mask possible differences.

The growth-independent mortality differs between species, sites and size (DBH). For *A. alba*, the conditions at Haute Côte are predicted as being less favourable, which may be explained by the slightly different microclimate characterised by lower temperatures due to the northwest-facing slope and the higher altitude of that site. According to Ellenberg (1996), *F. sylvatica* benefits from the limestone in the upper montane belt (900-1250 m a.s.l.), which generally promotes deciduous trees and thus allows for the dominance of *F. sylvatica*. This phenomenon may be reflected in the observed higher vitality with increasing altitude of *F. sylvatica* vs. *A. alba*, even if the site Haute Côte is located slightly below the upper montane belt (Table 1). *A. alba* is more competitive than *F. sylvatica* only on heavy clay soils (Mayer 1992).

Additional factors, such as the successional stage of the forest, could also influence the observed growth-independent mortality. Young, dense stands often show high mortality rates because of the effect of self-thinning (Yoda et al. 1963). Mature forests experience relatively low mortality rates, which may increase again in the old-growth stage (Franklin et al. 1987). Even if the eight permanent sample plots used here cover a range of successional stages of *Fagus* forests, it is unlikely that they reflect all possible stages of that forest community type. For example, the high mortality of older *A. alba* with larger DBH at Haute Côte may indicate a starting decay stage in some patches within the permanent sample plots representing Haute Côte.

Model performance and limitations

The estimated survival probabilities of the reduced model appear reliable, since the amount of overfitting is very small according to the results of the bootstrap method (Harrell 2001). Overfitting might be caused by the high number of predictors in the full model ($n=15$, see Table 2), which exceeded the recommended ratio of 1:10 (Peduzzi et al. 1996), i.e. the relationship between the predictors and the smallest group of the binary response variable (101 dead trees) should not exceed 1:10. However, in the case of an uneven distribution of the levels of the binary response variable, this rule appears very conservative, and a slight deviation may be acceptable (Reineking & Schröder 2006).

The reduced model seems to be calibrated well in the interval [0.7, 1], i.e. predicted survival probabilities between 70 and 100 percent equal observed probabilities (Fig. 5). This range comprises ca. 96% of all predicted survival probabilities (data not shown). Consequently,

the slight deviation from the ideal line between predicted and observed probabilities below the specified interval can be explained with a slight model overfitting. According to the classification scheme by Hosmer & Lemeshow (2000), the reduced mortality model shows excellent discriminatory power (AUC = 0.896, Fig. 6). The performance slightly exceeded the AUC calculated for single species mortality models of *Pinus pinaster* and *P. sylvestris* in Spain based on permanent plots that were re-measured every five years (AUC: 0.796 resp. 0.754 for the fitting data set, Bravo-Oviedo et al. 2006). Thus, a good model performance was achieved in spite of the relatively large inventory interval of more than 11 years, which is far from an optimal annual resolution. Using a reasonably complex model, the overfitting turned out to be negligible according to the applied bootstrap techniques. Therefore, we suggest to calibrate mortality models with bootstrap techniques, which are a powerful tool to assure that predicted survival probabilities match observed probabilities, especially in the case of relatively small data sets.

However, our model assumes an identical growth-mortality relationship for all individuals of one tree species; therefore it is 'blind' for variations caused by different genotypes (Mölleken et al. 1994). Also, the aggregation of the eight permanent plots within the *Cardamino-Fagetum* may have led to a systematic error, because heterogeneity within the sites is not reflected (Burger 1976). Furthermore, for some sites the time interval between the inventories varied slightly, as the time of the corresponding measurements varied partially with the seasons (Table 1). This effect could result in an increased variance of tree growth histories. However, these limitations did not seriously affect model performance.

Perspectives

Because the observed growth-mortality relationship was independent of tree species, size and site conditions, it may be feasible to group tree species into functional groups that are characterised by similar growth-dependent mortality patterns. Research on additional tree species would be required to classify major tree species in functional groups. Also, the importance of the site variable in our study raises the question whether mortality processes are specific to each site, or whether they can be grouped according to site types.

As a step towards comprehensive tree mortality models, a combination of already existing mechanistic approaches to model disturbance related mortality (e.g. Peltola et al. 1999) and phenomenological mortality models as presented here could cover a wide range of mortality causes. These combined models could be implemented

into forest succession models (e.g. FORCLIM; Risch et al. 2005) and replace their mortality submodels, which are often based on theoretical assumptions not evaluated with field data (cf. Keane et al. 2001; Wunder et al. 2006). Since the models presented here are probabilistic, they fit well with the stochastic character of succession models. Improved mortality routines in these models will allow for more realistic projections of future forest dynamics.

Acknowledgements. This paper would not have been possible without the huge effort that went into the assembly and maintenance of the ETH forest reserve network. The establishment and support of this network by the former heads of the Institute of Silviculture (ETH Zurich) is gratefully acknowledged. We would like to thank Mathias Wirth for his data survey over nearly 40 years as well as numerous contributors for their field work and data digitisation. We are grateful to Lorenz Fahse, Helge Bruelheide and two anonymous reviewers for valuable comments on an earlier version of the manuscript. BR acknowledges funding by the Swiss Federal Agency for Education and Research under the Integrated Project ALARM of the European Union (GOCE-CT-2003-506675).

References

- Anon. 1998. *World reference base for soil resources*. Food and Agriculture Organization of the United Nations, Rome, IT.
- Assmann, E. 1961. *Waldertragskunde : organische Produktion, Struktur, Zuwachs und Ertrag von Waldbeständen*. BLV, München, DE.
- Bartels, H. 1993. *Gehölkunde: Einführung in die Dendrologie*. Ulmer, Stuttgart, DE.
- Beniston, M. 2004. Climatic change and its impacts. an overview focusing on Switzerland. In: Beniston, M. (ed.) *Advances in global change research*, Kluwer, Dordrecht, NL.
- Bigler, C. & Bugmann, H. 2004. Predicting the time of tree death using dendrochronological data. *Ecol. Appl.* 14: 902-914.
- Bigler, C., Gricar, J., Bugmann, H. & Cufar, K. 2004. Growth patterns as indicators of impending tree death in silver fir. *For. Ecol. Manage.* 199: 183-190.
- Biondi, F. 1999. A comparison between repeated timber inventories and dendrochronological time series for forest monitoring. In: Wimmer, R. & Vetter, R.E. (eds.) *Tree-ring analysis: biological, methodological, and environmental aspects*, CAB International, Wallingford, UK.
- 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. 1997. Sensitivity of forests in the European Alps to future climatic change. *Clim. Res.* 8: 35-44.
- Burger, T. 1976. *Kriterien für die Ausscheidung von Standortseinheiten, dargestellt am Beispiel eines Waldreservates*. Diploma Thesis, Institut für Waldbau, ETH Zürich, Zürich, CH.
- Diebold, P., Laubscher, H.P., Schneider, A. & Tschopp, R. 1963. *Geologischer Atlas der Schweiz*. Blatt 40 (1085) St. Ursanne. Kümmerly & Frey, Bern, CH.
- Dobbertin, M. 2005. Tree growth as indicator of tree vitality and tree reaction to environmental stress: a review. *Eur. J. For. Res.* 124: 319-333.
- Ellenberg, H. 1996. *Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht*. 5th ed. Ulmer, Stuttgart, DE.
- Ellenberg, H. & Klötzli, F. 1972. Waldgesellschaften und Waldstandorte der Schweiz. *Mitteilungen der Eidgenössischen Anstalt für das forstliche Versuchswesen* 48: 587-930.
- Fielding, A.H. & Bell, J.F. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ. Conserv.* 24: 38-49.
- Fischlin, A. & Gyalistras, D. 1997. Assessing impacts of climatic change on forests in the Alps. *Global Ecol. Biogeogr. Lett.* 6: 19-37.
- Franklin, J.F., Shugart, H.H. & Harmon, M.E. 1987. Tree death as an ecological process. *BioScience* 37: 550-556.
- Fridman, J. & Ståhl, G. 2001. A three-step approach for modelling tree mortality in Swedish forests. *Scand. J. For. Res.* 16: 455-466.
- Guisan, A. & Harrell, F.E. 2000. Ordinal response regression models in ecology. *J. Veg. Sci.* 11: 617-626.
- Hallé, F., Oldemann, R.A.A. & Tomlinson, P.B. 1978. *Tropical trees and forests. An architectural analysis*. Springer, Berlin, DE.
- Harrell, F.E. 2001. *Regression modeling strategies*. Springer, New York, NY, US.
- Harrell, F.E. 2005 *Design Package*. R-package version 2.0-12. <http://biostat.mc.vanderbilt.edu/s/Design>; <http://biostat.mc.vanderbilt.edu/rms>
- Hastie, T.J. & Tibshirani, R.J. 1990. *Generalized additive models*. Chapman & Hall, London, UK.
- Hawkes, C. 2000. Woody plant mortality algorithms: descriptions, problems and progress. *Ecol. Model.* 126: 225-248.
- Hosmer, D.W. & Lemeshow, S. 2000. *Applied logistic regression*. 2nd ed. Wiley, New York, NY, US.
- Huber, U.M., Bugmann, H.K.M. & Reasoner, M.A. 2005. Global change in mountain regions. In: Beniston, M. (ed.) *Advances in global change research*. Springer, Dordrecht, NL.
- Kaplan, D.R. 2001. Fundamental concepts of leaf morphology and morphogenesis: a contribution to the interpretation of molecular genetic mutants. *Int. J. Plant Sci.* 162: 465-474.
- 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. *Clim. Change* 51: 509-540.
- Köppen, W. & Geiger, R. 1930-1939. *Handbuch der Klimatologie*. Borntraeger, Berlin, DE.
- Kraft, G. 1884. *Beiträge zur Lehre von Durchforstungen, Schlagstellungen und Lichtungshieben*. Klindworth's, Hannover, DE.

- Lampainen, J., Kuuluvainen, T., Wallenius, T.H., Karjalainen, L. & Vanha-Majamaa, I. 2004. Long-term forest structure and regeneration after wildfire in Russian Karelia. *J. Veg. Sci.* 15: 245-256.
- Leibundgut, H. 1957. Waldreservate in der Schweiz. *Schweiz. Zeitschr. f. Forstw.* 108: 417-421.
- Leibundgut, H. 1959. Über Zweck und Methodik der Struktur- und Zuwachsanalyse von Urwäldern. *Schweiz. Zeitschr. f. Forstw.* 110: 111-124.
- Leibundgut, H. 1962. *Richtlinien für die Aufnahme von Waldreservaten*. Unpubl. report. Institut für Waldbau, ETH Zurich, Zürich, CH.
- Leibundgut, H. 1966. *Die Waldpflege*. Haupt, Bern, CH.
- Leibundgut, H. 1984. *Unsere Waldbäume*. Huber, Frauenfeld, CH.
- Mayer, H. 1992. *Waldbau auf soziologisch-ökologischer Grundlage*. 4th ed. Gustav Fischer, Stuttgart, DE.
- Möllerken, H., Eckstein, D., Venne, H. & Scholz, F. 1994. Growth of spruce (*Picea abies* (L.) Karst.) as controlled by genotype and environment. *Dendrochronologia* 12: 23-32.
- Monserud, R.A. & Sterba, H. 1999. Modeling individual tree mortality for Austrian forest species. *For. Ecol. Manage.* 113: 109-123.
- Moons, K.G.M., Rogier, A., Donders, T., Steyerberg, E.W. & Harrell, F.E. 2004. Penalized maximum likelihood estimation to directly adjust diagnostic and prognostic prediction models for overoptimism: a clinical example. *J. Clin. Epidemiol.* 57: 1262-1270.
- Nishimura, N., Hara, T., Kawatani, M., Hoshino, D. & Yamamoto, S.-I. 2005. Promotion of species co-existence in old-growth coniferous forest through interplay of life-history strategy and tree competition. *J. Veg. Sci.* 16: 549-558.
- Nishimura, T.B. 2006. Successional replacement mediated by frequency and severity of wind and snow disturbances in a *Picea-Abies* forest. *J. Veg. Sci.* 17: 57-64.
- Pearce, J. & Ferrier, S. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. *Ecol. Model.* 133: 225-245.
- Peduzzi, P., Concato, J., Kemper, E., Holford, T.R. & Feinstein, A.R. 1996. A simulation study of the number of events per variable in logistic regression analysis. *J. Clin. Epidemiol.* 49: 1373-1379.
- Peltola, H., Kellomäki, S., Väisänen, H. & Ikonen, V.-P. 1999. A mechanistic model for assessing the risk of wind and snow damage to single trees and stands of Scots pine, Norway spruce, and birch. *Can. J. For. Res.* 29: 647-661.
- R Development Core Team. 2006. *R: a language and environment for statistical computing*. R for windows 2.3.1. <http://www.R-project.org>.
- Reineking, B. & Schröder, B. 2006. Constrain to perform: Regularization of habitat models. *Ecol. Model.* 193: 675-690.
- 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.
- Sachsse, H. 1984. *Einheimische Nutzhölzer und ihre Bestimmung nach makroskopischen Merkmalen*. Parey, Hamburg, DE.
- Sing, T., Sander, O., Beerenwinkel, N. & Lengauer, T. 2005. ROCr: Visualizing the performance of scoring classifiers. R-package version 2.0-12. <http://rocr.bioinf.mpi-sb.mpg.de>
- Steyerberg, E.W., Harrell, F.E., Borsboom, G.J.J.M., Eijkemans, M.J.C.R., Vergouwe, Y. & Habbema, J.D.F. 2001. Internal validation of predictive models: efficiency of some procedures for logistic regression analysis. *J. Clin. Epidemiol.* 54: 774-781.
- Stone, C.J. & Koo, C.Y. 1985. Additive splines in statistics. In: *Statistical Computing Section ASA*, pp. 45-48. American Statistical Association, Washington, DC, US.
- 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.
- Temesgen, H. & Mitchell, S.J. 2005. An individual-tree mortality model for complex stands of Southeastern British Columbia. *West. J. Appl. For.* 20: 101-109.
- Theurillat, J.-P. & Guisan, A. 2001. Potential impact of climate change on vegetation in the European Alps: a review. *Clim. Change* 50: 77-109.
- van Mantgem, P.J. & Stephenson, N.L. 2004. Does coring contribute to tree mortality? *Can. J. For. Res.* 34: 2394-2398.
- Waring, R.H. & Pitman, G.B. 1985. Modifying logpole pine stands to change susceptibility to mountain pine beetle attack. *Ecology* 66: 889-897.
- Wunder, J., Bigler, C., Reineking, B., Fahse, L. & Bugmann, H. 2006. Optimisation of tree mortality models based on growth patterns. *Ecol. Model.* 197: 196-206.
- Wyckoff, P.H. & Clark, J.S. 2000. Predicting tree mortality from diameter growth: a comparison of maximum likelihood and Bayesian approaches. *Can. J. For. Res.* 30: 156-167.
- Yoda, K., Kira, T., Ogawa, H. & Hozumi, K. 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions (Intraspecific competition among higher plants XI). *J. Biol. Osaka City Univ.* 14: 107-129.

Received 21 March 2006;

Accepted 19 October 2006;

Co-ordinating Editor: H. Bruelheide.

For App. 1, see also JVS/AVS Electronic Archives;
www.opuluspress.se/

App. 1. Reduced logistic regression model after backward selection. Y_i = status of tree i (dead = 0, alive = 1); factor coding for species (*A. alba* = 0, *F. sylvatica* = 1) and site (Bois Banal = 0, Haute Côte = 1). Restricted cubic splines: the four knots are located at *relbai* values of 0.020, 0.104, 0.181, 0.395, corresponding to the 5%-, 35%-, 65%- and 95%-quantiles of the observed *relbai*.

$$\Pr\{Y_i = 1 | X_i\} = \frac{1}{1 + \exp(-X_i\beta)},$$

where $X_i\beta = 1.161$

+ 29.17	<i>relbai</i>
- 518.37	$(\text{relbai}-0.020)_+^3$
+1038.53	$(\text{relbai}-0.104)_+^3$
-505.01	$(\text{relbai}-0.181)_+^3$
-15.15	$(\text{relbai}-0.395)_+^3$
-18.79	species
-1.56	site
+2.33	species × site
+3.57	species × log(DBH)

with $(x)_+ = x$ if $x > 0$, 0 otherwise.