

Modeling Mortality of Individual Trees in Drained Peatland Sites in Finland

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Multilevel logistic regression models were constructed to predict the 5-year mortality of Scots pine (*Pinus sylvestris* L.) and pubescent birch (*Betula pubescens* Ehrh.) growing in drained peatland stands in northern and central Finland. Data concerning tree mortality were obtained from two successive measurements of the National Forest Inventory-based permanent sample plot data base covering pure and mixed stands of Scots pine and pubescent birch. In the modeling data, Scots pine showed an average observed mortality of 2.73% compared to 2.98% for pubescent birch. In the model construction, stepwise logistic regression and multilevel models methods were applied, the latter making it possible to address the hierarchical data, thus obtaining unbiased estimates for model parameters. For both species, mortality was explained by tree size, competitive position, stand density, species admixture, and site quality. The expected need for ditch network maintenance or re-paludification did not influence mortality. The multilevel models showed the lowest bias in the modeling data. The models were further validated against independent test data and by embedding them in a stand simulator. In 100-year simulations with different initial stand conditions, the models resulted in a 72% and 66% higher total mortality rate for the stem numbers of pine and birch, respectively, compared to previously used mortality models. The developed models are expected to improve the accuracy of stand forecasts in drained peatland sites.

Keywords *Betula pubescens*, generalized linear mixed models, mortality, multilevel models, *Pinus sylvestris*, peatlands, simulation

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1 Introduction

Mortality is one of the main processes of forest succession. Severe inter-tree competition throughout stand development gradually decreases the growth of individual trees and finally leads to the death of some trees. A distinction is usually made between regular competition-related mortality and more irregular catastrophic mortality (Vanclay 1994), the latter not being clearly related to specific stand or site conditions.

In growth simulators applied in forest management, mortality processes are described by empirical models. To predict the probability of a tree dying or surviving during the following growth period due to regular mortality, several probability models in terms of logistic regression have been developed (e.g., Monserud 1976, Hamilton 1986, Avila and Burkhart 1992, Monserud and Sterba 1999, Shen et al. 2000, Eid and Tuhus 2001, Fridman and Ståhl 2001, Yao et al. 2001). To control the maximum density at stand level, models based on the self-thinning concept (Reineke 1933) are applied (e.g. Hynynen 1993, Newton and Weetman 1993). In individual-tree models, it has been shown that in addition to the effect of competition, the rate of mortality varies among sites (Eid and Tuhus 2001, Yao et al. 2001).

In Finland, most of the original peatland area has been made suitable for timber production by means of active peatland drainage operations during the years 1950–1990 (Hökkä et al. 2002). Since peatland sites differ considerably from mineral soil sites with respect to the water and nutrient regimes, specific growth models have been developed to predict the growth of peatland trees (Hökkä et al. 1997). We assumed that these differences would show up as differences in the mortality process as well. Uneven size and spatial distributions of trees may also influence competition-induced mortality. Furthermore, more varying site water status may directly result in higher mortality due to frequent anaerobic conditions in the peat soil (see Kobe and Coates 1997, Shen et al. 2000, Fridman and Ståhl 2001). Consequently, a higher general level of mortality in drained peatland sites may be common, when they are compared to mineral soil sites.

An individual tree-based stand growth simulator MELA (Siitonen et al. 1996) is used in Finland to forecast the development of forest stock at any scale ranging from a single stand to the whole country. All processes (regeneration, growth, ingrowth and mortality) are predicted in 5-year periods. In the MELA simulator the model predicting individual-tree mortality (Hynynen et al. 2002) does not distinguish between mineral soil sites and peatlands, and may thus result in biased mortality estimates for peatland stands.

This study aimed at constructing logistic regression models for the 5-year mortality of Scots pine (*Pinus sylvestris* L.) and pubescent birch (*Betula pubescens* Ehrh.) growing in drained peatland sites. Only regular competition-related mortality and minor sporadic mortality due to insects and diseases were accounted for. The models should be applicable to stand growth simulation systems and thus be based on tree, stand, and site attributes that are generally recorded in forest management planning and forest inventories. Furthermore, they should give reliable predictions in varying conditions with as low bias as possible.

2 Materials

2.1 Modeling Data

Since the key to successful mortality modeling is a large and representative sample of re-measured trees (Monserud and Sterba 1999), we used the SINKA permanent growth plot data, which provide an objective sample of drained peatland stands in northern Finland. The SINKA plots were established in 1984–1988 for the purposes of peatland growth studies (Penttilä and Honkanen 1986). The plots were selected by stratified systematic sampling from those 7th National Forest Inventory sample plots that were located on drained peatlands. The sampling units were stands that were considered to be in satisfactory silvicultural condition (stands with damages were excluded) and homogeneous with respect to site and the stage of stand development. Birch-dominated stands were sampled only from the southern part of northern Finland, but birch was commonly

growing over the whole study area in good sites as an admixture.

The SINKA stand is composed of a cluster of three circular plots located 40 m apart. The size of the plots was adjusted according to stand density. The whole SINKA cluster contained approximately 100 tally trees, which were mapped and measured for diameter at breast height (DBH), species, and canopy class. For these trees, the minimum DBH was 4.5 cm if the stand was past pole stage, and 2.5 cm otherwise. A sub-plot with a smaller radius was superimposed on every plot, and all trees on that plot were treated as sample trees. Additional tree attributes, like height, growth during the past 5-years and damages, were recorded from these sample trees. The first re-measurement of the SINKA data was done in 1988–1994 following a period of 5 growing seasons on each plot. Trees that had died between the measurements were identified at that time. For a more detailed description of the data, see Hökkä et al. (1997).

For the purposes of this study, the data were restricted to stands that had not been thinned or fertilized during the last 5-year period preceding the first measurement or between the measurement occasions. Furthermore, all stands which had been subject to any ditching operations between the measurements were excluded. There was, on the whole, no need of ditch network maintenance (59%). The majority of the stands were early development stands: i.e., pole-size sapling stands and young thinning stands represented 24% and 56% of the stands.

The distribution into fertility classes (Huikari 1952, 1974) 2–4 was almost even: class 2 (mesotrophic) 28%, class 3 (meso-oligotrophic) 29%, and class 4 (oligotrophic) 30%. Eutrophic sites (class 1) were less frequent (13%). The most commonly occurring peatland site types (Laine and Vasander 1990) were tall-sedge pine fens (VSR), which accounted for 13% of the stands, *Carex globularis* pine swamps (PsR) and herb-rich sedge birch-pine fens (RhSR) with 11% each, paludified pine forests (KgR) and herb-rich hardwood-spruce swamps (RhK), with 10% each.

Separate modelling data sets were formed for pine and birch by combining all plots that had at least one pine or one birch growing in them.

Table 1. The number of living and dead trees in the modeling and test data sets.

	Modeling data		Test data	
	Pine	Birch	Pine	Birch
Number of trees	17293	12480	5022	1938
Number of living trees	16821	12108	4844	1882
Number of dead trees	472	372	178	56
Proportion of dead trees (%)	2.73	2.98	3.54	2.89
Number of stands	295	296	47	39

Altogether, the number of trees and plots in the pine data were clearly larger than those in the birch data (Table 1). The mortality proportion for pine was slightly lower (2.73%) than for birch (2.98%).

Since the pine and birch data sets did not show much difference as far as stand-level characteristics were concerned, we calculated those only from the merged data set. The concentration of the data in young stands was also reflected by the stand-level variable means, measured at the beginning of the five-year period (Table 2). The average tree diameter at breast height (DBH) for pine was 9.1 cm (2.5–44.5 cm) and for birch 8.1 cm (2.5–39.5 cm). The strongest limitation in the data was related to the poor representation of large trees; DBH larger than 30 cm was represented by only 27 pine trees and 10 birch trees.

2.2 Test Data

To test the developed models, we used an independent data set of unthinned control plots from 15 peatland thinning experiments located in central and northern Finland. Mortality was obtained from two successive measurements at an interval of 5 years. In each experiment, there were two to five control plots, thus resulting in a total of 47 and 39 plots for pine and birch test data, respectively. In these data sets, the observed rate of 5-year mortality was clearly higher for pine (3.54%), but almost the same for birch (2.89%) as in the modeling data (Table 1). Stand-level variable means (Table 2) revealed some differences compared to the modeling data, probably due to the higher proportion of advanced stands in the test data. The low number of experiments

Table 2. Means of some stand and site attributes in the modeling and test data. Minimum and maximum values are given in parentheses.

Attribute	Modeling data	Test data
N (ha ⁻¹)	1776 (274–7500)	2144 (1161–3467)
G (m ² ha ⁻¹)	12.4 (0.7–34.2)	20.0 (10.8–31.9)
V (m ³ ha ⁻¹)	63.3 (1.8–234.2)	111.8 (43.5–225.8)
D _W (cm)	12.0 (4.9–23.7)	12.9 (8.9–18.9)
H ₀₀ (m)	10.4 (3.3–21.8)	12.0 (8.5–16.6)
TS (dd°C)	956 (735–1070)	949 (767–1080)
N _{coord} (km N)	7250 (7043–7504)	7273 (7060–7478)
E _{coord} (km E)	456 (324–646)	452 (346–614)
Elevation (m.a.s.l.)	122 (2–300)	118 (30–198)
First year of drainage	1966 (1930–1987)	1957 (1930–1972)
Peat thickness (cm)	8 →100	10 →100

N = Number of stems H₀₀ = Height of the hundred thickest trees
 G = Basal area TS = Average temperature sum (with threshold +5°C)
 V = Volume N_{coord} = Northern coordinate
 D_W = Quadratic mean diameter E_{coord} = Eastern coordinate

Table 3. Stand characteristics of the simulation data.

Attribute	Pine, high density	Pine, low density	Birch, high density	Birch, low density	Mixed, high density	Mixed, low density
G (m ² ha ⁻¹)	14.1	10.6	13.6	7.1	22.3	11.4
N (ha ⁻¹)	1775	652	2612	986	3276	881
G _{Pp}	1	1	0	0	0.71	0.69
G _{Bp}	0	0	1	1	0.29	0.31
Fertility class	2	2	3	3	2	2

G_{Pp} = Relative proportion of pine of basal area (0–1)
 G_{Bp} = Relative proportion of birch of basal area (0–1)

gave a lower variability in stand characteristics. The representation of the fertility classes was quite different compared to the modeling data: i.e., mesotrophic sites represented 53% of the stands and oligotrophic sites only 7%. Meso-oligotrophic (27%) and eutrophic sites (13%) were represented in comparable proportions. The average DBH measurements for pine and birch were 10.6 cm (2.9–30.5 cm) and 8.5 cm (4.2–28.0 cm).

For simulations, we selected two plots, one heavily thinned and one control, from three (pure pine, mixed, pure birch stand) thinning experiments. The corresponding stand characteristics are given in Table 3.

3 Methods

3.1 Variable Selection

From numerous variables measured in the field we selected those which were biologically connected to the mortality process of a tree: i.e., size, competition, and vigor (Hamilton 1986, Monserud and Sterba 1999). Tree size is described by DBH because it is the most easily available and precise tree size measurement coming from forest inventory plots. Monserud and Sterba (1999) have shown that transformations such as inverse (DBH⁻¹) and the second power of DBH may be necessary to better fit the non-linear relationship of diameter and mortality probability.

Tree vigor is generally described in terms of diameter increment or crown ratio, which both

have been proven to explain mortality, too (Hamilton 1986, Dobbertin and Biging 1998, Monserud and Sterba 1999, Yao et al. 2001). In our data these variables were available only for sample trees, and thus they were not used.

A tree's social status is considered a good descriptor of individual tree competition, here expressed by BAL (m^2ha^{-1}), the cumulative basal area of the trees larger than the target tree within the same stand. This variable is strongly correlated with the basal area of the stand (G , m^2ha^{-1}). We decided to eliminate the relationship between the two variables in order to be able to use each of them independently. We computed a new ratio variable simply as follows: $\text{BAL}_R = \text{BAL}/G$ (see Vanclay 1991). BAL_R is always located between 0 and 1, a number close to 0 describing a dominant tree within the stand and a number close to 1 describing a suppressed tree within the stand.

As an indicator of stand-level competition, basal area (see Yao et al. 2001) has been shown to influence mortality. The fact that most of the stands were mixed stands suggested that the proportion of the basal area covered by other species (birch – G_{Bp} , pine – G_{Pp} , and spruce – G_{Sp}) is a possible variable to describe one aspect of competition. The quadratic mean diameter (D_W), the mean height of the 100 thickest trees (H_{00}), and the number of stems (N) were other stand-level variables examined. All tree and stand variables used in models had values corresponding to the first measurement occasion.

In earlier studies, sites with different productivity have shown differences in mortality (Eid and Tuhus 2001, Yao et al. 2001). Based on this, we tested the fertility classes as expressed in Huikari's (1952, 1974) classification scheme of peatlands, because those classes are compatible with the MELA simulator (Siitonen et al. 1996). In the data, four fertility classes were represented and described by dummy variables F_1 – F_4 , while the poorest sites (ombrotrophic) were missing, and thus not considered in the analysis. The problem with Huikari's classification system is that it pools together sites which are ecologically very different. Alternatively, we tried the traditional peatland site type classification system as described by Laine and Vasander (1990), which permitted more detailed separation of the ecologi-

cally different forested and composite peatland sites (Ruuhijärvi 1982). Temperature sum (TS) reflects a country-scale site effect and was thus listed as a possible explanatory variable.

In drained peatland sites water regime may cause mortality through a periodically or constantly high ground-water table. This effect was studied with the help of two dummy variables. First, the need for ditch network maintenance (NEED, 0 = no need, 1 = present need or expected need within the next five years) was used, and second, a variable describing the potential regressive development of the site drainage (STA, 0 = satisfactory status, 1 = re-paludified status) was used.

The SINKA sample covered undamaged stands, but some minor damages had occurred during the 5-year period. These damages were recorded tree-wise for coniferous sample trees only. We calculated the percentage of damaged sample trees in every stand based on field recordings to test whether the observed mortality was explained by the damages.

3.2 Model Specification

3.2.1 Logistic Regression

To construct the mortality equations, logistic regression models have been commonly applied as the modeling method. The definition of logit function and the model is formulated as follows (McCullagh and Nelder 1989):

$$\log \text{it}(\pi) = \log [\pi / (1 - \pi)] = \alpha + \beta x \quad (1)$$

where the parameter π is binomially distributed and generally represents the probability of success. Logistic regression models with a binomial stochastic component can provide adequate models specifically for data with binary responses. The final fitted model will predict values on the logit scale.

To see which variables were important to consider in the model building, we first estimated the standard stepwise logistic regression model for both species. The analyses were done with the SAS/LOGISTIC procedure (SAS Institute, Inc.), and the variable selection was based on the standard test of this procedure.

3.2.2 Multilevel Model with Binary Response

The SINKA sample plots formed a three-level hierarchy with several trees measured in each plot and three plots measured in each cluster. Consequently, tree-level observations in every stand were not independent of each other. Since standard logistic regression does not consider this correlation, we used the generalized linear mixed model approach to correctly address the hierarchical structure of the data and insure unbiased tests for all model parameters. However, we did not consider variation within clusters because of the rather limited plot size and probable bias in plot-level stand characteristics calculations (see Hynynen and Ojansuu 2001). Consequently, only tree and stand levels were addressed in this study.

The observed responses y_{ij} – the status of the i :th tree of the j :th stand at the end of the 5-year period – are binary ($0 = \text{live} / 1 = \text{dead}$). With the standard assumptions of the dependent variable, the distribution for the response is $y_{ij} \sim \text{Bin}(\pi_{ij}, 1)$. A 2-level model with random effect can be written in general form:

$$\pi_{ij} = f(X_{ij}^T \beta + u_j) \quad (2)$$

where π_{ij} is the expectation of the response for the i :th tree in stand j , vector X_{ij}^T is the transposed vector of the independent fixed variables, β is the vector of the estimated parameters, and u_j represents the random departure for the j :th stand with $u \sim N(0, \sigma_u^2)$. The link function f is a nonlinear logit function. For total variance we have

$$\text{var}(y_{ij} | \pi_{ij}) = \pi_{ij}(1 - \pi_{ij}) \quad (3)$$

The logit link function for the probability that i :th tree in j :th stand is dead after a 5-year period is as follows:

$$\pi_{ij} = \{1 + \exp(-[X_{ij}^T \beta + u_j])\}^{-1} \quad (4)$$

$$\sigma_e^2 = 1 \quad (5)$$

All parameters of the multilevel model were estimated simultaneously using the first order marginal quasi-likelihood (MQL) procedure (Goldstein et al. 1998). We alternatively tried

penalized quasi-likelihood (PQL) estimation, but that resulted in highly biased parameter estimates (see Alenius et al. 2003). The tree-level variance was assumed to be 1 and tested for over- and under-dispersion (Goldstein 1995). We used the SAS/GLIMMIX macro (SAS Institute Inc.) to build the initial model and MLwiN (Goldstein et al. 1998) to estimate the final models.

3.3 Methods of Model Evaluation

Residual plots, which are commonly used in model diagnostics in traditional regression analysis, cannot be applied to multilevel logistic regression. Moreover, the likelihood-ratio test is unreliable in multilevel logistic regression because the quasi-likelihoods are approximations (Goldstein 1995). In general, the evaluation of multilevel logistic regression models is problematic, as discussed in more detail by Alenius et al. (2002). Consequently, in choosing the best models, we emphasized logical and reliable model behavior from the point of view of prediction. Statistically, we based the models' evaluation on two criteria: 1) the significance of the parameter values of the candidate explanatory variables ($p < 0.05$), and 2) the value of the stand-level variance, which we tried to minimize. The latter was used only as a rough indication of model improvement. We also assessed the models' ability to predict mortality close to the observed mortality rate in the modeling data and test data. The models were applied to the modeling and test data sets to predict the mortality probability for each tree, and the average probabilities were calculated. The observed proportion of dead trees in both data sets and the average predicted probabilities were compared. Furthermore, the observed and predicted mortalities in the modeling data were compared graphically as a function of different tree and stand variables after categorizing the variable values and comparing the class means.

Finally we made simulations to study mortality at stand level using six sample stands (see Section 2.2) representing varying stand conditions with respect to density and species (Table 3). The simulations were done with the Motti stand simulator (Salminen and Hynynen 2001) by incorporating the new models as alternatives for the old models

to predict individual-tree mortality. Besides tree-wise mortality, the growing stock level is also controlled by a self-thinning model (see Hynynen et al. 2002). For the selected stands, the total number of dead stems and mortality basal area, and the resulting development of stem number and basal area over a 100-year simulation period were calculated and compared. In the simulation, no stand management measures were permitted.

4 Results

4.1 Logistic Regression

In Tables 4 and 5, PMODEL0 and BMODEL0 are the standard stepwise logistic regression models for pine and birch, respectively. For pine, the square root of the DBH described tree size (Table 4). There was no variable expressing tree-level competition, but at stand level G and G_{BP} described competition effects. Two site classes were significant, as well as the STA.

For birch, the model was quite different. The inverse of DBH and BAL_R were selected as tree-level predictors (Table 5). Numerous stand attributes (G , G_{BP} , D_W , H_{00} , N) were also significant. Of those, mortality appeared to decrease as N increased, which is illogical.

4.2 Multilevel Analysis

We estimated several alternative multilevel models for both species in order to compare them. In general, the inverse of tree DBH and BAL_R were the most important explanatory variables in all models (Tables 4–5). Mortality decreased as tree DBH increased. For tree size, many other additional transformations were tried (see Vanclay 1994), but those effects were either insignificant or, when applied, showed unrealistically high mortality for large trees. High BAL_R , which is connected to suppressed trees, was also related to higher mortality.

At stand-level, a higher overall basal area increased the probability of mortality for both species (Tables 4–5). Increasing G_{BP} significantly increased pine mortality. For birch, the

effect was consistent: greater G_{BP} increased the probability of birch survival. For pine, D_W was also significant; higher mortality was related to lower mean diameter.

Site fertility as expressed according to Huikari (1952, 1974) had a significant effect on the mortality of pine, giving the lowest mortality rate for site F_4 and the highest for F_1 , which was the most productive one. F_2 did not differ from F_4 . Of all the candidate models using Huikari's classification system, PMODEL1 gave the lowest stand-level variance and was thus considered the primary one. With PMODEL2, we aimed to better account for site effects as well as damages. Composite pine mires (PM_C) and a large site group of spruce mire sites (SM) were distinguished from forested pine mires (PM_F). PMODEL2 also accounts for the slightly increased mortality rate as a function of increased proportion of damages in sample trees. With this model the highest mortality was found on spruce mires and the lowest on forested pine mires. As judged by the lowest stand level residual variance, PMODEL2 performed the best in describing mortality. We also estimated PMODEL3, in which the site quality effects were excluded.

For birch, the site effects were different (Table 5). With BMODEL1, the highest mortality rate was found in F_4 , but only F_2 showed a significantly lower mortality rate. Distinguishing between composite and forested mires (BMODEL2) did not improve the results, because classes PM_C and SM were both insignificant, and the stand-level variance remained virtually unchanged (Table 5). BMODEL3, which did not account for the site quality effect, showed higher stand-level variance. Mortality appeared to be greater in more southern locations, as indicated by the significance of TS (Table 5). Since damages were determined only for coniferous trees, we did not consider that effect for birch.

Table 4. Models for 5-year mortality of Scots pine in drained peatland sites. Standard errors are given in parentheses.

Variables	PMODEL0	Multilevel models		
		PMODEL1	PMODEL2	PMODEL3
Constant	-1.183 (0.123)	-6.372 (0.467)	-6.906 (0.517)	-5.855 (0.043)
DBH ⁻¹	–	36.35 (12.66)	37.81 (12.60)	37.64 (12.78)
DBH ^{1/2}	-0.411 (0.015)			
BAL _R	–	2.060 (0.355)	2.132 (0.353)	2.020 (0.355)
G	0.120 (0.004)	0.116 (0.021)	0.107 (0.020)	0.107 (0.022)
G _{Bp}	1.906 (0.117)	1.812 (0.438)	1.773 (0.488)	2.007 (0.435)
D _w	–	-0.103 (0.041)	-0.103 (0.041)	-0.110 (0.043)
F ₁	0.706 (0.053)	1.042 (0.331)	–	
F ₂	-0.220 (0.049)	0.226 (0.275)	–	
F ₃	-0.038 (0.040)	0.545 (0.244)	–	
PM _C			0.488 (0.220)	
SM			1.054 (0.343)	
STA = 0	-0.382 (0.055)	–	–	
Damage (%)			0.014 (0.005)	
Tree variance	1.000 (0.000)	1.000 (0.000)	1.000 (0.000)	1.000 (0.000)
Stand variance	–	1.682 (0.207)	1.541 (0.197)	1.985 (0.231)

DBH = Tree diameter at breast height, cm
 STA = Dummy variable with 1 indicating re-paludified sites
 F₁–F₃ = Dummy variables referring to Huikari's fertility classes 1–3
 PM_C = Dummy variable for composite pine mire sites

SM = Dummy variable for spruce mire sites
 Damage = Proportion of sample trees with recorded damages
 For other notations, see Tables 2–3.

Table 5. Models for 5-year mortality of pubescent birch in drained peatland sites. Standard errors are given in parentheses.

Variables	BMODEL0	Multilevel models		
		BMODEL1	BMODEL2	BMODEL3
Constant	-13.65 (0.800)	-11.58 (2.196)	-12.15 (2.027)	-12.34 (2.050)
DBH ⁻¹	73.21 (6.848)	92.52 (13.97)	94.42 (14.03)	93.18 (14.12)
BAL _R	2.330 (0.265)	1.885 (0.523)	1.814 (0.525)	1.847 (0.525)
G	0.108 (0.010)	0.091 (0.020)	0.080 (0.021)	0.083 (0.021)
G _{Pp}	-1.328 (0.141)	-1.972 (0.452)	-1.049 (0.546)	-1.414 (0.384)
D _w	-0.228 (0.024)	–		
H ₀₀	0.220 (0.019)			
N	-0.00036 (0.0001)			
F ₁	0.197 (0.089)	-0.616 (0.544)		
F ₂	-0.355 (0.048)	-1.035 (0.420)		
F ₃	-0.080 (0.049)	-0.696 (0.397)		
PM _C			-0.697 (0.388)	
SM			0.085 (0.468)	
TS	0.0065 (0.001)	0.0047 (0.002)	0.0046 (0.002)	0.0048 (0.002)
Tree variance	1.000 (0.000)	1.000 (0.000)	1.000 (0.000)	1.000 (0.000)
Stand variance	–	2.246 (0.315)	2.200 (0.308)	2.656 (0.354)

For notations, see Tables 2–4.

Table 6. Observed and predicted number of dead trees in the modeling and test data with corresponding mortality percentages in parentheses.

Species	Models	Modeling data	Test data
Pine	Observed	472 (2.73)	178 (3.53)
	PMODEL0	733 (4.24)	–
	PMODEL1	491 (2.84)	357 (7.09)
	PMODEL2	490 (2.83)	–
	PMODEL3	490 (2.83)	283 (5.61)
	Old model	237 (1.37)	114 (2.26)
Birch	Observed	372 (2.98)	56 (2.89)
	BMODEL0	350 (2.81)	–
	BMODEL1	391 (3.13)	43 (2.20)
	BMODEL2	380 (3.04)	–
	BMODEL3	396 (3.17)	54 (2.77)
	Old model	465 (3.73)	81 (4.16)

5 Model Evaluation

5.1 Model Fit and Performance in Predicting Mortality

In general, the predictions of the multilevel models PMODEL1 and PMODEL3 showed good correspondence with the observed mortality rate in the modeling data (Fig. 1). PMODEL0 overestimated mortality, while the old mortality model used in simulators greatly underestimated mortality. There was much less variation in the predictions of birch models BMODEL0, BMODEL1, and BMODEL3, which all gave mortality rates which were close to observed rate of mortality (Fig. 2). The observed mortality of both species showed some variability for large trees for which none of the models were able to account in prediction. With respect to BALRAT and G, the predicted mortality rate followed closely that of the observed rate (Figs. 1–2). With respect to the proportional basal area of other species (G_{Bp} and G_{Pp}), the harmful effect of birch on pine survival was more important than the favorable effect of pine on birch survival.

For pine, all multilevel models resulted in almost equal accuracy in predicting the overall proportion and number of dead trees in the modeling data (Table 6). The least biased were PMODEL2 and PMODEL3, and the most biased PMODEL0. In the test data PMODEL3 was

again the best, but PMODEL1 the worst with a 100% overestimated mortality rate. For birch, BMODEL2 showed the best fit in the modeling data, and the old model the poorest fit, with high over-estimation of mortality. In the test data, BMODEL3, without site effects, showed the best fit. PMODEL2 and BMODEL2 were omitted from further testing, because of the need for detailed information concerning damages and site classification.

5.2 Results from Simulation

The simulations were done with PMODEL1 and PMODEL3 for pine and BMODEL1 and BMODEL3 for birch because the site type classification used in these models was compatible with the simulator input information. Simulations with the old models were carried out to provide a point of comparison. Temporal development of basal area mortality is shown only for mixed stands. These results include models of mortality due to tree-level competition and mortality due to self-thinning.

Depending on stand conditions, stem number mortality was –1–72% and basal area mortality 6–122% higher with the new models than with the old ones over the simulation period (Table 7). In a dense pine stand, the new models produced 4–6 m^2ha^{-1} lower live basal area and a correspondingly higher mortality rate than the old model (Table 7). In a low-stocked pine stand, in relative terms there is an even bigger difference when PMODEL1 and PMODEL3 are compared with the old models but both new models gave almost identical results.

In the dense birch stand, all the models resulted in almost identical basal area and stem number mortality, but in the low-density stand BMODEL1 resulted in a clearly higher mortality rate, compared to the other models (Table 7). Because the coefficients of BMODEL1 and BMODEL3 were nearly equal, the difference was due to the dummy variable F_2 , which had a large coefficient (see Table 5).

In the dense mixed stand, combinations of the new models (PMODEL1 & BMODEL1 and PMODEL3 & BMODEL3) gave slightly higher stem number and basal area total mortality than

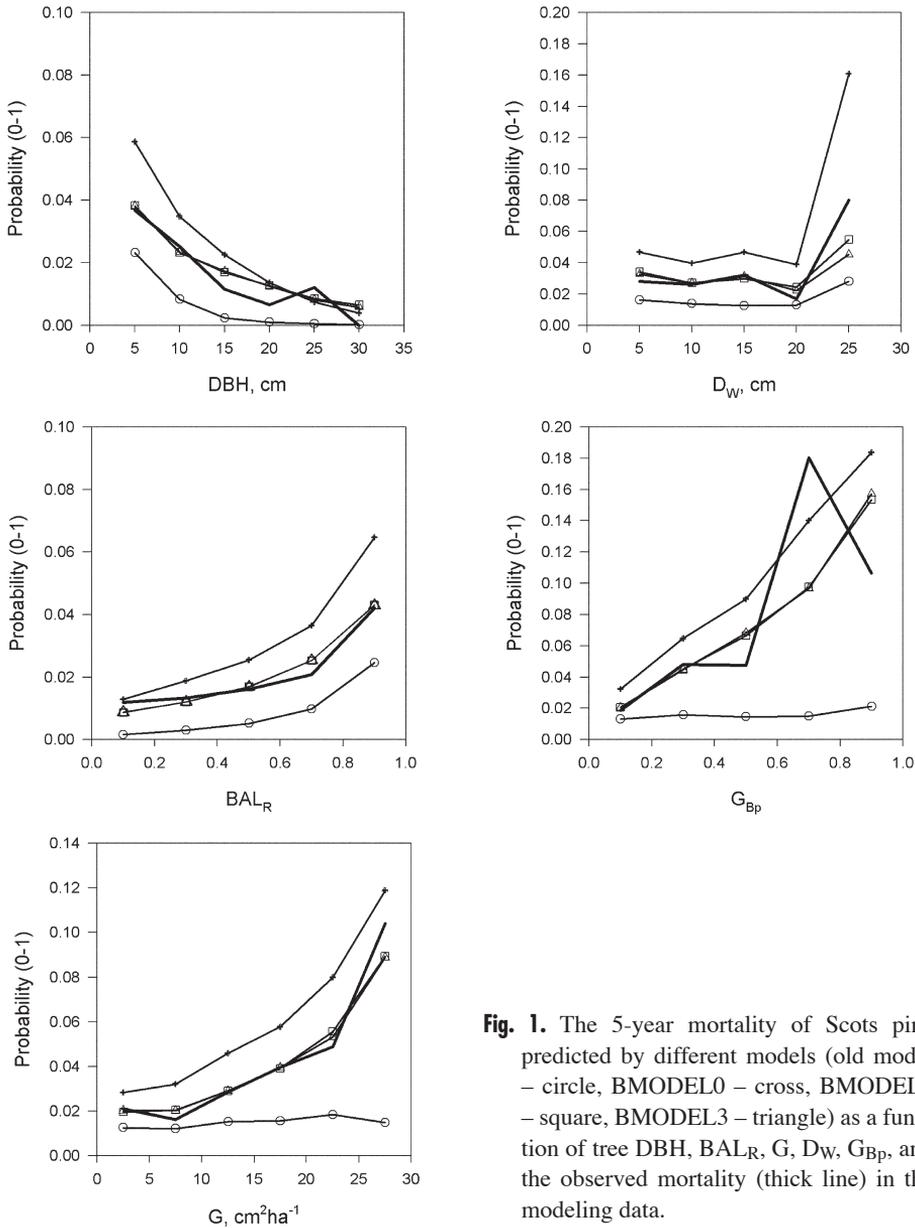


Fig. 1. The 5-year mortality of Scots pine predicted by different models (old model – circle, BMODEL0 – cross, BMODEL1 – square, BMODEL3 – triangle) as a function of tree DBH, BAL_R , G , D_W , G_{Bp} , and the observed mortality (thick line) in the modeling data.

the old models (Table 7). The pattern of basal area development was almost identical in all models (Fig. 3). The peak in the curves of the basal area of dead trees was a result of exceeding the self-thinning limit (Hynynen 1993), which took place at the same time for all models. The difference among the models was the different allocation of

mortality to species: i.e., the new models showed more dead pine but less dead birch than the old models, thus probably resulting in different stand composition at the end of the simulation period.

In the low-stocked mixed stand, there were more differences among the models in simulated development (Fig. 3). With the new models, the

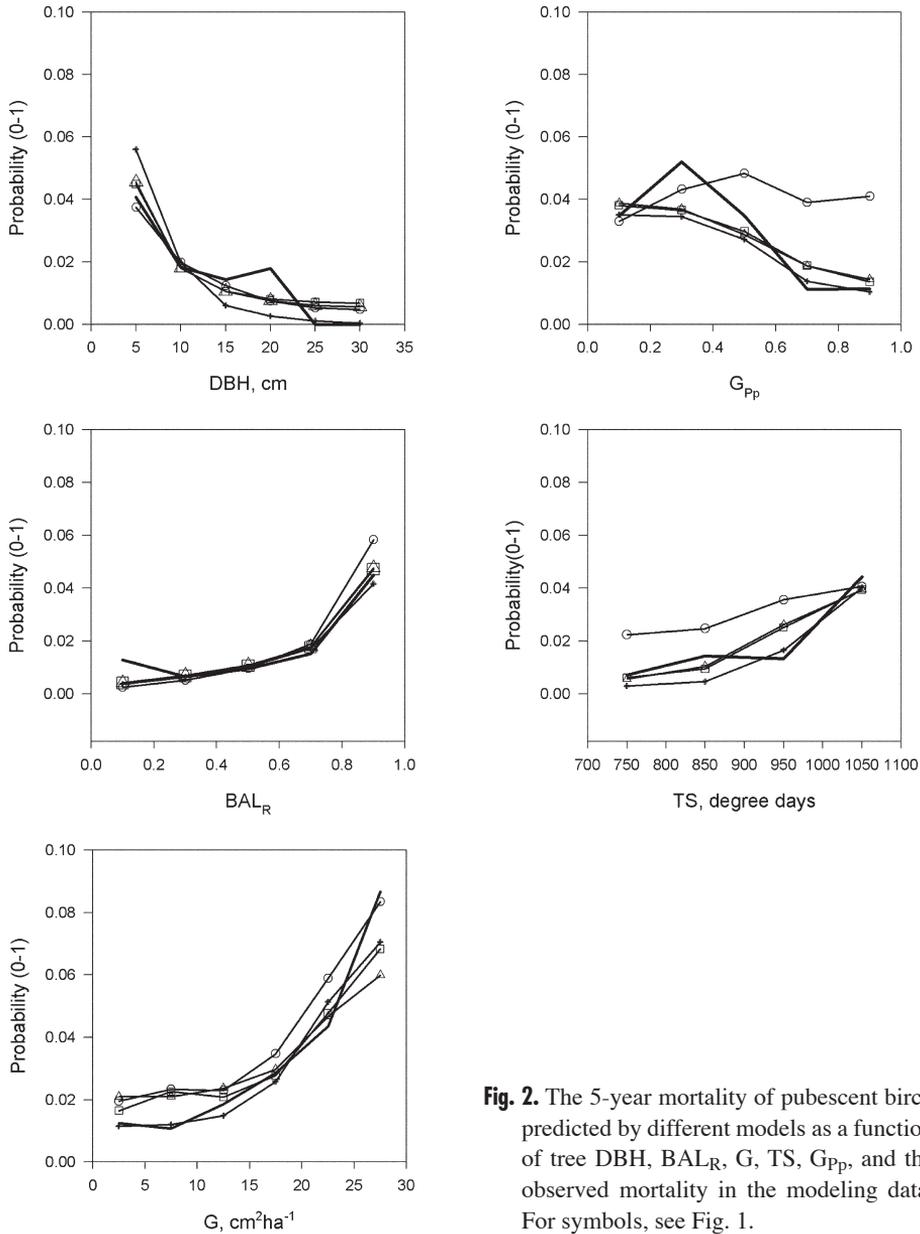


Fig. 2. The 5-year mortality of pubescent birch predicted by different models as a function of tree DBH, BAL_R , G , TS, G_{Pp} , and the observed mortality in the modeling data. For symbols, see Fig. 1.

self-thinning limit was not achieved during the simulation period, while with the old models the stand reached the self-thinning limit at simulation age 70 years. In general, pine mortality was higher with the new models (Table 7), and there was also more temporal variation (Fig. 3). Birch mortality with the new models showed a convex pattern

over time, while the old models resulted in a very high mortality rate at the end of the period when the stand exceeded the self-thinning limit.

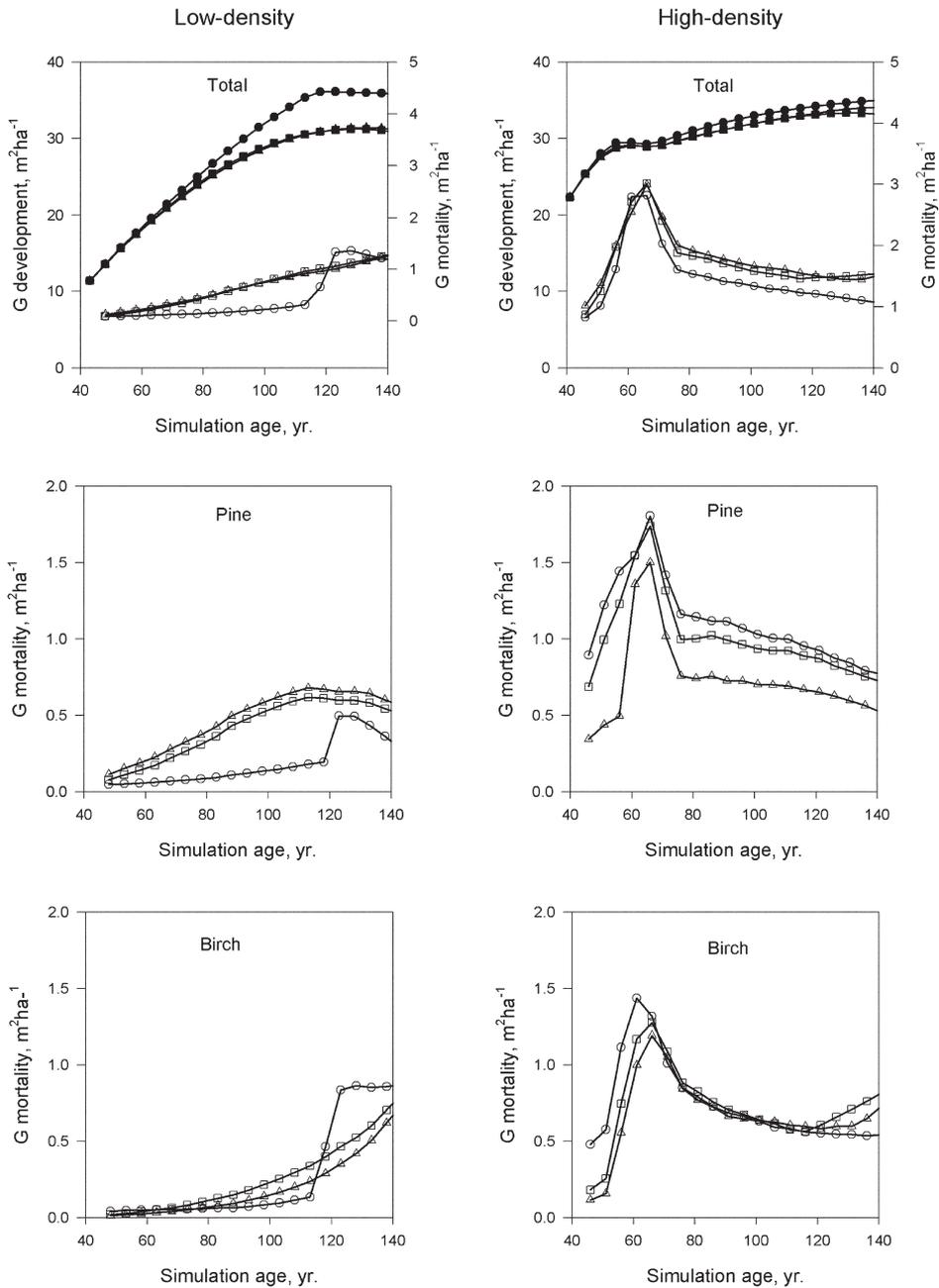


Fig. 3. The development of live (filled symbols) and dead (open symbols) basal area predicted by the old Scots pine and birch models (circle) and the combination of PMODEL1 & BMODEL1 (square) and PMODEL3 & BMODEL3 (triangle) (see Tables 4 and 5), and the development of dead basal area by species in a high-density and low-density mixed stand (see Table 3).

Table 7. Total mortality (number of stems and basal area) over a 100-year simulation produced by different models in different stand conditions and relative difference in mortality compared to that predicted by the old models.

Stand	Model	N_{dead} (ha^{-1})	Relative difference (%)	G_{dead} (m^2ha^{-1})	Relative difference (%)
Pine high density	Old model	678		7.52	
	PMODEL1	788	+16	11.54	+53
	PMODEL3	830	+22	12.06	+60
Pine low density	Old model	66		1.36	
	PMODEL1	100	+51	2.67	+97
	PMODEL3	114	+72	3.01	+122
Birch high density	Old model	1848		30.26	
	BMODEL1	1972	+7	32.11	+6
	BMODEL3	1828	-1	31.95	+6
Birch low density	Old model	291		8.14	
	BMODEL1	483	+66	13.50	+66
	BMODEL3	321	+11	9.49	+17
Mixed high	Old models	2503		29.38	
	Models1	2566	+3	34.68	+18
	Models3	2523	+1	35.51	+21
Mixed low	Old models	263		9.44	
	Models1	398	+52	13.81	+46
	Models3	404	+54	13.72	+45

6 Discussion

In this study, we constructed multilevel logistic regression models to predict the probability of individual trees dying in an up-coming five-year growth period. The designed use of the models in growth simulators emphasized the necessity of obtaining reliable predictions with variables generally available. One important element affecting reliability is representative modeling data. Our data was based on an objective sample of drained peatland forest in northern Finland. Because pine mortality was not influenced by large-scale climatic factors, the models may be applicable to conditions in southern Finland, as well. However, this assumption may not be valid for the birch models. Since the data mostly covered young stands and small-dimension trees, the models are expected to be least accurate for large trees, which were very poorly represented. Furthermore, there was no evidence of the models' performance for the smallest trees with DBH < 2.5 cm, because those trees were excluded from the DBH measurements.

In the model construction, we applied multilevel models methods to obtain unbiased estimates for the parameters (Goldstein 1995). In connection with binary response the method has been applied in forestry, e.g., by Jalkanen (2001). However, in the estimation of previous individual-tree mortality equations, the two-level structure of forest tree data has been ignored so far. We used the MQL estimation method, because it gave fairly unbiased models, compared to the results of the PQL method (Alenius et al. 2003). In this study, the random component at stand level was significant in all the multilevel models, and the fixed part was quite different compared to that of the stepwise logistic regression model. Most of the differences were related to the stand-level variables in the fixed part, many of those being significant in logistic regression but insignificant in the multilevel models. For pine the stepwise logistic regression resulted in a clearly biased prediction of the mortality rate in the modeling data. To prevent misconceptions, Monserud and Sterba (1999) did not consider any stand-level variables in mortality models for trees in Austria.

This leads to more stable and robust models that are, however, not able to respond to differences in stand conditions. The multilevel logistic models have the standard advantage of random parameter models: with observations of the response variable available, the models can be calibrated for specific stands.

The inverse of DBH is the most common expression for the relationship between mortality and tree size (Monserud and Sterba 1999, Shen et al. 2000, Eid and Tuhus 2001), and it is rather flexible in fitting varying shapes specific to different species (e.g., Monserud and Sterba 1999). In our data, pine and birch showed rather similar form with respect to tree DBH. For both species, there was evidence of increasing mortality for big trees, too (Fig. 1–2), which could be interpreted as age-related senescence as tree size increases (see e.g., Yao et al. 2001). This effect could not be accounted for by additional transformed forms of DBH for pine, and for birch the second power of DBH resulted in a mortality rate which was too high for large trees. Subsequently, we entered only DBH^{-1} in our models, and simultaneously accepted some bias for large trees. To model the slight increase in mortality of big trees accurately would have required a better sample of large trees in the modeling data.

We used BAL_R to indicate the relative competitive status of a tree in every stand (c.f. Vanclay 1991). When stand basal area is included in the model, a better description of the competitive situation is expected to result. Basal area is important because it increases the probability of large trees dying as stand density increases. Otherwise, higher site occupancy would have no effect on the large trees. Both BAL_R and G were significant for both species. For pine, it was also necessary to address variation in D_W , which could be interpreted as another effect of stand-level competition.

The basal area of competing tree species appeared to be an important factor influencing mortality. Scots pine and pubescent birch differ from each other with respect to their tolerance of competition and shade. Scots pine is a shade-intolerant species, while pubescent birch has some shade-tree characteristics (Ferm 1990). In mixed sapling stands, birch is able to dominate in inter-species competition, because it can outgrow pine

due to its faster early growth (Heikurainen 1959, Jakkila and Pohtila 1978). Furthermore, birch easily causes mechanical damage to the crowns of pines through whipping by its branches (Jakkila and Pohtila 1978). This competitive superiority was reflected by the higher probability of mortality of pine as the proportion of birch basal area in the stand increased. The same phenomenon, but to a lesser degree, was detected in the birch model as a higher probability of birches staying alive when the proportion of pine increased. These effects have not been accounted for in previous mortality models in Finland.

In previous studies the site properties have been shown to affect the tree mortality rate. Higher mortality has been related to better productivity by, e.g., Yao et al. (2001) and Eid and Tuhus (2001). Accordingly, the old mortality models used for pine in the MELA system (Siitonen et al. 1996) predict mortality to be highest in the most productive sites. Vanclay (1994) has expressed criticism of this relationship, because, in principle, good sites are expected to support higher stocking than low-productive sites.

In peatland sites, Scots pine covers a much wider range of fertility than pubescent birch, which grows well only on good and medium sites (F_1 – F_3). Huikari's (1952, 1974) classification scheme of peatlands is basically parallel to the Finnish classification of mineral soil sites (Cajander 1909), which arranges sites in order of timber yield, and mostly reflects the availability of nitrogen and calcium in soil (Tamminen 1991). Huikari's classification explained both birch and pine mortality, but mortality did not follow the fertility sequence of sites. Pine mortality was better characterized by the differences among ecological groups of forested and composite pine mires defined in accordance with the original peatland site types. Sparsely forested composite sites showed higher pine mortality than forested pine mires. This was expected, since the composite sites were initially wet, often thick-peated, and subsequently may have more problems related to site nutrition when drained (Kaunisto and Paavilainen 1988). Severe potassium deficiencies have been shown to be critical for Scots pine growth (e.g., Kaunisto 1992). In this way, our findings coincide with the conclusion of Shen et al. (2000), that mortality was related to the avail-

ability of certain key nutrients. It is also possible that instead of being an effect of productivity as such, the higher rate of mortality on good sites is partly an effect of higher local competition, which cannot properly be accounted for by robust stand- or tree-level indicators of competition like G and BAL_R . This effect is thus accounted for by the site quality variables. On the other hand, some site effects are implicitly included in the models through stand variables. Adding spatial information in competition measures may help to some extent, but that was not possible in this study. Based on the results we had, we suggest that site quality effects should be very carefully considered before they are applied in mortality equations.

We initially hypothesized that the status of site drainage would influence mortality in peatland sites. However, the variables that described the need for ditch network maintenance or regressive development with re-paludification proved not to be significant in the multilevel models. The influence may actually be low, or the data may not have covered stands where poor drainage really was a problem. Low influence is supported by the results of Hökkä and Penttilä (1995), which indirectly showed that Scots pine on drained peatland tolerates surprisingly high groundwater levels. What is important is the considerable difference in the observed mortality rate in the Scots pine modeling data and the rate predicted by the old mortality model (Figs 1–4), which, in turn, was derived from data mostly covering mineral soil stands. This demonstrates that mortality in general is higher and has more influence on stand development in peatland sites. One possible cause is site nutrient status (Shen et al. 2000), but even more important may be water status (Kobe and Coates 1997, Shen et al. 2000, Fridman and Ståhl 2001), which is clearly less favorable in peatland sites than in mineral soil sites. Consequently, the inherent risk of mortality in peatlands is higher compared to that of mineral soil sites, but within peatlands, poor drainage and problematic nutrition did not increase the risk so much that they could be distinguished in these data.

The temperature sum was significant for pubescent birch, showing higher mortality in southern latitudes. There is no clear explanation for this result. Partly it may be due to the greater compe-

tion in denser stands in the south. However, we decided to keep the variable in the model because it significantly reduced the bias in predictions.

Simulations showed that the new models generally resulted in a higher rate of mortality compared to the previous models. Consequently, applying the new models resulted in a slower approach to the self-thinning limit, because more mortality occurred before the limit. If self-thinning is not considered, there was more temporal variation in the rate of mortality with the new models. With pine, the new models predicted that most trees would die in the middle of the simulation period, while birch mortality strongly increased at the end of the simulation period. This is in accordance with the knowledge of the character of these species. As a shade-intolerant species, pine easily dies from competition if suppressed. However, in young drained peatland stands, mortality may be rather low, because of the good vigor of young trees (Seppälä 1969) and generally uneven spatial and size distribution, with less severe influence of inter-tree competition on individuals. Pubescent birch, on the other hand, is able to survive in high densities when young (Ferm 1990), but may die as suppression continues and crown length diminishes (Niemistö 1987).

Based on the variable site effects in the models of both species, experiences from the simulations, and possible difficulties in classifying drained peatland sites in the field, we recommend using PMODEL3 and BMODEL3 in simulators to obtain realistic predictions of individual tree mortality in peatland sites. The poor fit of PMODEL1 in the test data may be explained by the different representation of sites in the test data and modeling data (Table 6), but the almost equal performance of PMODEL1 (with site effects) and PMODEL3 (without site effects) in simulation suggests that with pine, site quality effect was marginal. With birch, the site dummy F_2 had a pronounced effect, which could not be explained. Because birch mortality was dependent on the temperature sum, BMODEL3 should be used with caution when applied in southern Finland. We expect that the constructed models will generally improve the accuracy of simulated stand development on drained peatland sites by allocating more wood to the mortality component. The differences are not considerable, but

may become effective in country-scale planning of forest resources. Furthermore, the within-stand species dynamics will change considerably as the new models are applied, because the new models resulted in clearly different mortality rates for Scots pine and pubescent birch.

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