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Estimating tree survival: a study based on the Estonian Forest Research Plots Network

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Tree survival, as affected by tree and stand variables, was studied using the Estonian database of permanent forest research plots. The tree survival was examined on the basis of remeasurements during the period 1995–2004, covering the most common forest types and all age groups. In this study, the influence of 35 tree and stand variables on tree survival probability was analyzed using the data of 31 097 trees from 236 research plots. For estimating individual tree survival probability, a logistic model using the logit-transformation was applied. Tree relative height had the greatest effect on tree survival. However, different factors were included into the logistic model for different development stages: tree relative height, tree relative diameter, relative basal area of larger trees and relative sparsity of a stand for young stands; tree relative height, relative basal area of larger trees and stand density for middle-aged and maturing stands; and tree relative height and stand density for mature and overmature stands. The models can be used as preliminary sub-components for elaboration of a new individual tree based growth simulator.

Key words: forest growth, logistic regression, generalized linear mixed model, mortality, survival probability, tree and stand variables

Introduction

Tree mortality is a key factor influencing forest dynamics, and estimating tree survival therefore requires special attention (Yang *et al*. 2003). The accuracy of growth models depends largely on the accuracy of estimating tree survival. The main purpose of survival research is to understand how and why tree mortality occurs. This information is essential for developing strategies of forest management (Hamilton & Edwards 1976). Modelling tree survival is not a trivial task. In her overview Hawkes (2000) highlighted the main problems associated with such models:

Lack of long-term observations. Mortality may be caused by different biotic and abiotic factors which become relevant at different points in time. As a result, the probability of tree survival is usually rather fluctuating and irregular (Gadow 1987).

Improper use of models. Models of tree survival that have been developed on a specific data set and with specific assumptions, should not be used outside the range of their validity. Mortality patterns may differ substantially between different tree species (Dale *et al*. 1985).

Influence of human activity. Human activity is an important factor to natural which complements natural processes and complicates model prediction. It is hard to estimate the effects future management activity, because even in the case of well-defined cutting rules it is difficult to forecast the impact of the real cutting performance in terms of its weight and quality.

According to Vanclay (1994), the causes of tree mortality may be divided into three major groups:

Catastrophic: Large-scale mortality of trees, caused by storms, game damage, insect-pests, flooding or other extraordinary events.

Anthropogenic: Tree mortality caused mostly by harvesting operations, but also by industrial pollution or changes in water tables.

Regular: Tree mortality caused by tree age and competition, but also by pests and diseases and unfavourable weather conditions (storm, drought or flooding).

Catastrophic and anthropogenic mortality are hard to predict and the modeling of such processes requires long-term measurement series on permanent sample plots. Such data are lacking and for this reason, the present study deals only with modeling regular mortality.

A number of models were used to estimate tree survival, including the linear (Moser 1972, Leak & Graber 1976, West 1981), Weibull (Somers *et al*. 1980, Kouba 1989), gamma-distribution (Kobe & Coates 1997), exponential (Moser 1972), Richards (Buford & Hafley 1985), and Gompertz function (Kofman & Kuzmichev 1981). The logistic function has been used mostly for estimating individual tree survival (*see* for example, Hamilton & Edwards 1976, Monserud 1976, Buchman 1979, Hamilton 1986, Vanclay 1991, Vanclay 1995, Dursky 1997, Murphy & Graney 1998, Albert 1999, Monserud & Sterba 1999, Eid & Tuhus 2001, Yao *et al*. 2001, Hynynen *et al*. 2002, Soares & Tomé 2003, Yang *et al*. 2003, Diéguez-Aranda *et al*. 2005). The majority of the more recent survival models have been concentrating on the individual tree level (Mabvurira & Miina 2002). One reason is that the single tree level seems to allow more specific estimates in uneven-aged, species rich forests. In tree survival studies (Hynynen *et al*. 2002, Alenius *et al*. 2003) multilevel logistic regression models for hierarchically structured data are becoming more common.

Until recently, the research covering tree survival in Estonia has not been very extensive. Noteworthy is the model for estimating mortality on the stand level by Jõgiste (1998) and the research by Nilson (2006) about the relation between number of trees and mean stand diameter. Models for estimating individual tree survival are still lacking in Estonia. Only recently it has been possible to use the data from the network of permanent forest growth plots, which covers entire Estonia. Thus, the objective of the present study is to identify from that database variables which influence tree survival. We will present a first attempt to model individual tree survival in Estonia.

Our specific hypotheses were that (i) different sets of driving variables influence tree survival at different stand development stages; (ii) at the tree level, variables of relative size (e.g. ratio of tree and stand diameter) describe tree survival better than variables of absolute size; (iii) at the stand level, variables of maximum density influence survival the most; and (iv) shade-tolerant tree species are more vital than light-demanding, and fast growing species have lower rates of survival.

Factors influencing tree survival

In modeling tree survival, a variety of variables have been considered. Hamilton (1986) classified the factors that affect tree survival into four groups: tree size, tree competition status in the stand, tree viability and stand density. In the present analysis, the main factors that influenced tree survival in other studies, are considered. For that purpose, more than 20 logistic models of tree survival and mortality were analyzed. The logistic models for estimating tree survival can be presented in the following general form:

$$P=\left(1+e^{-f(X)}\right)^{-1}=\frac{1}{1+e^{-f(X)}}=\frac{e^{f(X)}}{1+e^{f(X)}} \quad (1)$$

where P is the probability of tree survival, $(1 - P)$ is the probability of tree mortality, and $f(X)$ is the function (mostly linear) of diverse influencing factors (Vanclay 1994). Several authors have used Eq. 1 for different tree species, where every species has a specific set of coefficients (Hamilton 1986, Vanclay 1991, Monserud & Sterba 1999, Eid & Tuhus 2001, Hynynen *et al.* 2002). Factors, influencing mortality may be regarded at the single tree or stand level. The most frequently used variables are listed in Table 1.

Material and methods

Data set

The network of permanent forest growth research plots, established during the period 1995–2004 and covering entire Estonia was used in the present study. The first forest growth research plots of the network were established in the nemoral forests and mesotrophic forests of central Estonia in 1995–1996 and in the heath forests of northern Estonia in 1997–1998 (Kiviste & Hordo 2002). Since 1999, the network of forest research plots has been extended, representing the most common forest types and age groups in Estonia. For extension of the network of forest research plots, sample grid of International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (Karoles *et al.* 2000) was used for placement centres of plot groups. The plot locations in the field were selected randomly on a map.

Generally, the permanent forest growth plots are circular with radii of 15, 20, 25 or 30 meters. The plot size depends on the forest age and density, such that, as a rule, on every plot there are at least 100 trees of the upper tree storey. Trees of the second storey and shrub layer were measured in a smaller concentric circle with a radius of eight (at plot radius 15 m) or 10 meters (at plot radius more than 15 m). On each plot, the polar-coordinates (azimuth and distance from the plot centre), the diameter at breast height, and defects were assessed for each tree. The tree height and height to crown base were measured in every fifth tree and also on dominant and rare tree species. The height to the first dry branch of old coniferous trees was also assessed (*see* Kiviste & Hordo 2002 for more details).

In 2004, the network consisted of 730 of permanent forest growth plots. The tree coordinates and breast height diameters of 101 311 living trees were measured. The total tree height and the height to crown base was assessed on 33 045 trees. During 2000–2004, altogether 380 sample plots were re-measured. It was then found, that of 49 814 trees measured during the previous survey, 4658 trees (9.4%) had been harvested and 2883 trees (5.8%) had died (broken or fallen down) during the period between the two measurements.

During the period between the measurements, trees were harvested on 134 plots; 130 of these were excluded from the analysis because the condition of the trees at the time of harvest was not known. Fourteen plots, where the period between the measurements was not exactly five years, were also excluded from the analysis. Thus, the data set used in the present study contains 31 097 trees from 236 plots. Their locations are shown in Fig. 1.

Figure 2 presents distributions of permanent sample plots analyzed in this study by forest site types, dominant species and stand development stages. Most plots are located in the nemoral and mesotrophic forest types. The site type 'others' includes alvar, transition bog, and fen forests. Pine stands are more represented than stands with other tree species. The alder forests include four black alder plots and five grey alder plots. Almost all groups by site type and by main species include stands of all development stages. Regarding stand age, it appears that the distribution of plots is quite balanced between the ages of 20 and 80 years (Fig. 3). Four plots stocked with pine forests have an age of 150 years or more.

Variables investigated

The list of variables which are assumed to influence tree survival and their statistical characteristics are presented in Table 2. The majority of the variables are continuous (age, height, diameter, etc.), but there are also some nominal variables (storey, tree species, forest site type) and binary variables as a transformation of nominal variables (tree species indicator, sign of moose damage, etc.) in the data set. The investigated data set was hierarchical, some of the variables were appointed at tree level (storey, tree species, tree diameter, tree height, etc.) and others at plot level (dominant tree species, forest site type, age of the first storey, mean diameter, mean height, etc.).

Table 1. Most frequently used tree and stand variables for estimating tree survival.

Individual tree		Forest stand	
Tree status	Source	Stand variable	Source
Tree diameter at breast height (*D*)	Monserud (1976), Hamilton & Edwards (1976), Hamilton (1986), Vanclay (1991), Dursky (1997), Monserud & Sterba (1999), Eid & Tuhus (2001), Yao *et al.* (2001), Mabvurira & Miina (2002), Hynynen *et al.* (2002), Soares & Tomé (2003), Yang *et al.* (2003)	Stand basal area	Hamilton & Edwards (1976), Hamilton (1986), Vanclay (1991), Eid & Tuhus (2001), Yao *et al.* (2001), Hynynen *et al.* (2002), Yang *et al.* (2003), Diéguez-Aranda *et al.* (2005)
Tree relative diameter (the ratio of tree diameter and stand mean diameter)	Hamilton (1986), Eid & Tuhus (2001), Mabvurira & Miina (2002)	Stand dominant height	Palahi & Grau (2003), Diéguez-Aranda *et al.* (2005)
The estimated tree diameter increment for a specified time	Monserud (1976), Hamilton (1986), Vanclay (1991), Yao *et al.* (2001), Yang *et al.* (2003)	Stand age	Hynynen *et al.* (2002), Diéguez-Aranda *et al.* (2005)
Tree height	Hamilton & Edwards (1976), Dursky (1997), Palahi & Grau (2003)	Stand mean diameter	Hamilton (1986), Eid & Tuhus (2001), Mabvurira & Miina (2002)
Tree age	Hynynen *et al.* (2002)	Relative proportion of tree species in stand (measured interms of basal area, volume or number of trees)	Yao *et al.* (2001), Eid & Tuhus (2001)
Relative length of tree crown	Hamilton & Edwards (1976), Monserud & Sterba (1999)	Stand site quality	Dursky (1997), Eid & Tuhus (2001), Yao *et al.* (2001), Mabvurira & Miina (2002)
The sum of basal area of larger trees (BAL index)	Vanclay (1991), Monserud & Sterba (1999), Eid & Tuhus (2001), Hynynen *et al.* (2002), Palahi & Grau (2003)	Number of trees per ha	Eid & Tuhus (2001), Soares & Tomé (2003), Diéguez-Aranda *et al.* (2005)
The sum of basal area of larger broadleaf trees	Yang *et al.* (2003)		
Tree defects caused by game, insects or some other damages	Hamilton & Edwards (1976)		

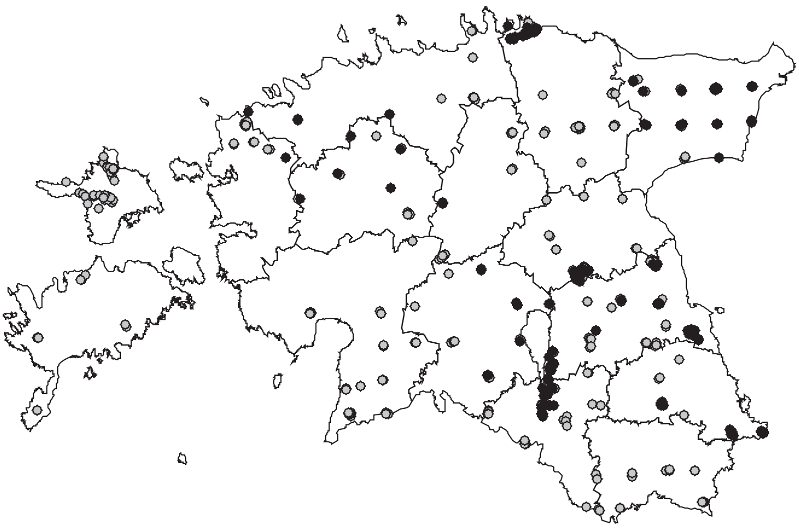


Fig. 1. Location of re-measured permanent sample plots in Estonia. Points in the map indicate locations of 3–6 permanent sample plots. Black dots = plots used in this study, grey dots = other plots in the network.

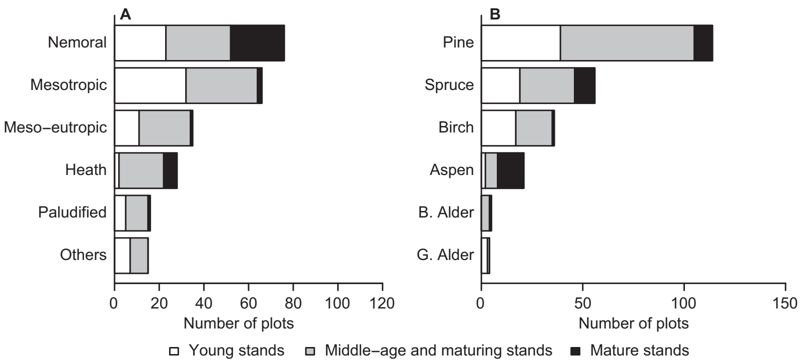


Fig. 2. Distribution of plots by groups of (**A**) forest site types and (**B**) main tree species.

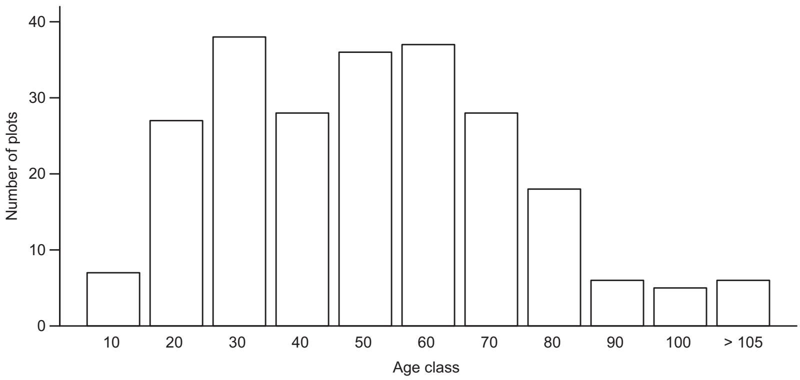


Fig. 3. Distribution of plots by age classes.

The tree storey (RIN) was defined during the field assessment according to the rules of a forest survey. The majority of trees on plots were assigned to the I storey (81.9%). Altogether 17.3% of the trees belong to the second storey (II storey), but substantially less trees were measured from the regeneration and shrub layer (respectively, 0.6% and 0.2%). In some plots, the second story (II storey) and the regeneration trees and the shrub layer were measured in the smaller concentric circle. In some sample plots, the small regeneration and shrub layer trees were not measured at all.

Almost one half of the trees (46.8%) were

Table 2. Variables influencing tree survival and their descriptive characteristics.

Variable code	Description	Unit	Type	Level	Observ. no.	Mean	Min	Max	SD
Tree Level									
RIN	Storey		Nominal	Tree	31097				
PL	Tree species		Nominal	Tree	31097				
D	Breast height diameter	cm	Continuous	Tree	31097	14.5	1.0	74.0	8.0
DS	Relative tree diameter (D/D1)		Continuous	Tree	31097	0.866	0.048	3.91	0.345
H	Tree height	m	Continuous	Tree	9226	16.3	2.0	37.1	7.1
HS	Relative tree height (H/H1)		Continuous	Tree	9226	0.868	0.083	1.79	0.223
KUDS	Relative tree diameter for spruce		Continuous	Tree	31097	0.154	0	3.91	0.355
HNLS	Tree height (calculated)	m	Continuous	Tree	31097	14.8	1.2	37.5	6.3
HNLSS	Relative calculated height (HNLS/H1)		Continuous	Tree	31097	0.868	0.083	1.79	0.223
HV	Height of crown base	m	Continuous	Tree	7807	8.9	0.1	30.3	5.6
SHV	Relative height of crown base (HV/H)		Continuous	Tree	7807	0.526	0.01	0.986	0.185
BAL	Basal area of larger trees	$m^2\ ha^{-1}$	Continuous	Tree	31097	17.5	0	56.0	9.7
BALS	Relative basal area of larger trees (BAL/Gtot)		Continuous	Tree	31097	0.682	0	1.000	0.276
HEG5	Competition index in 5 m radius by Hegyi		Continuous	Tree	31097	4.3	0	194.5	8.2
HEGH	Competition index in 0.4H1 radius by Hegyi		Continuous	Tree	31097	4.3	0	193.7	7.3
PKAHJ	Moose damage		Binary	Tree	31097	0.050	0	1	
RIK	Other damage		Binary	Tree	31097				
Stand Level									
KKTR	Class of forest site type		Nominal	Plot	236				
A1	Age of 1st storey	year	Continuous	Plot	236	53.6	10	230	27.4
N1	Number of trees in 1st storey	$1\ ha^{-1}$	Continuous	Plot	236	1582	143	9372	1737
G1	Basal area of 1st storey trees	$m^2\ ha^{-1}$	Continuous	Plot	236	22.2	4.2	44.5	6.9
D1	Breast height diameter of the 1st storey	cm	Continuous	Plot	236	18.2	4.1	41.1	8.3
H1	Height of the 1st storey	m	Continuous	Plot	236	18.2	3.9	35.2	7.0
M1	Volume of the 1st storey	$m^3\ ha^{-1}$	Continuous	Plot	236	210	19	745	109
T1	Relative density of the 1st storey		Continuous	Plot	236	0.61	0.08	1.53	0.27
L1	Sparseness of the 1st storey	m	Continuous	Plot	236	3.42	1.03	8.36	1.42
VG	Stand development stage		Nominal	Plot	236				
NOOR	Young stand		Binary	Plot	236	0.339	0	1	
KESK	Middle-aged stand		Binary	Plot	236	0.517	0	1	
VANA	Mature stand		Binary	Plot	236	0.144	0	1	
H100	Site index	m	Continuous	Plot	236	26.4	13.1	40.5	5.9
LTJ	Self-thinning sparseness by Tjurin	m	Continuous	Plot	236	2.59	0.76	5.45	1.05
TTJ	Relative sparseness by Tjurin		Continuous	Plot	236	0.77	0.33	1.19	0.14
PIIRT	Limit density by relative density		Binary	Plot	236	0.076	0	1	
PIIRTJ	Limit density by sparseness		Binary	Plot	236	0.064	0	1	

pines, 23.3% were spruces, 18% birches, 3.9% were aspens and 5.1% were alders.

Tree height (H) was measured on 29.7% of trees and the height to crown base (HV) on 25.1% of all trees. To estimate the height of all trees, Nilson's diameter/height relations were used (Kiviste *et al*. 2003). These relations were applied separately to every combination of tree species and storey of each plot (tree cohort). A two-parameter diameter/height regression is being used, when more than five trees per tree cohort were measured

$$\mathrm{HNLS} = \frac{H_\mathrm{C}}{1 - b\left[1 - \left(\frac{D_\mathrm{C}}{D}\right)^c\right]} \tag{2}$$

where D is the tree breast-height diameter; D_C is the mean square diameter of the respective tree cohort; b and H_C are parameters of the diameter-height regression, calculated from sample trees; c is a parameter which depends on the tree species (listed in Table 3). The variable H_C represents the mean height of the tree cohort.

When between 1 and 5 trees of each tree cohort were measured on a plot, the following one-parametric diameter-height relation was used

$$\mathrm{HNLS} = \frac{H_\mathrm{C}}{1 - \left(a - 0.0056 D_\mathrm{C}\right)\left[1 - \left(\frac{D_\mathrm{C}}{D}\right)^c\right]}$$
$$H_\mathrm{C} = \frac{1}{N}\sum_{i=1}^{N}\left(H_i\left\{1 - \left(a - 0.0056 D_\mathrm{C}\right)\left[1 - \left(\frac{D_\mathrm{C}}{D_i}\right)^c\right]\right\}\right) \tag{3}$$

where D is the tree breast height diameter; D_C is the mean square diameter of the respective tree cohort; a and c are parameters which depend on the tree species (listed in Table 3); H_i and D_i are sample tree height and diameter respectively.

The diameter/height relation (Eq. 3) was also used in the case of a tree cohort where the heights were not measured. This was the case, for example, in rare tree species which occurred on a particular plot. The mean height H_C of a tree cohort was calculated with the formula

$$H_\mathrm{C} = 1.3 + k_1\left[1 - \exp\left(-k_2 D_\mathrm{C}\right)\right]^{k_3} \tag{4}$$

where D_C is the mean square diameter of the tree cohort, and k_1, k_2 and k_3 are species-specific parameters (Table 3).

Relative tree diameter (DS), relative tree height (HS), basal area of larger trees (BAL), relative basal area of larger trees (BALS) and Hegyi competition indices (HEG5 and HEGH) were the investigated variables characterizing individual tree competitive status. Four of these (DS, HS, BAL and BALS) do not require known tree positions and it is relatively easy to calculate them. The relative tree diameter (DS) is calculated as

$$\mathrm{DS} = D/D_1 \tag{5}$$

where D is the tree diameter and D_1 is the mean square diameter of the first storey trees. The relative tree height is calculated as follows

$$\mathrm{HS} = H/H_1 \tag{6}$$

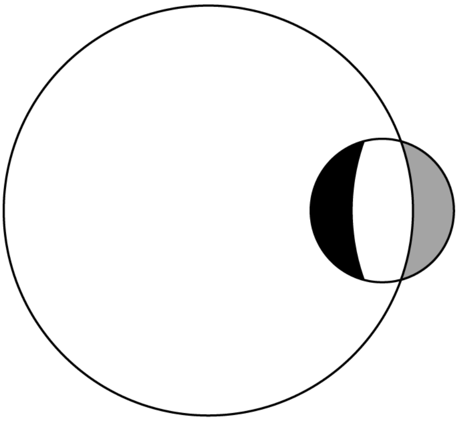
where H is the tree height and H_1 is the mean height of the first storey, weighted by the species-specific basal areas. The BAL index is calculated as basal area of trees having a diameter larger than the diameter of the reference tree. The relative basal area (BALS) is equal to the BAL index divided by the basal area of all trees in the plot.

Tree position coordinates and tree-size data are used to define a competition index which requires that the tree positions are known. An example of such a position-dependent quantity is the Hegyi (1974) competition index (HEG5), which is calculated as follows:

$$\mathrm{HEG}_5 = \sum_i \frac{D_i}{DL_i^2} \tag{7}$$

Table 3. The parameters of the diameter/height relationship for different tree species (Kiviste *et al.* 2003).

Species	a	c	k_1	k_2	k_3
Pine	0.369	1.31	92.4	0.0110	1.0437
Spruce	0.394	1.47	72.7	0.0171	1.112
Birch	0.359	1.38	45.0	0.0320	1.038
Aspen	0.359	1.38	44.6	0.0387	1.290
Other	0.359	1.38	31.0	0.0529	1.144



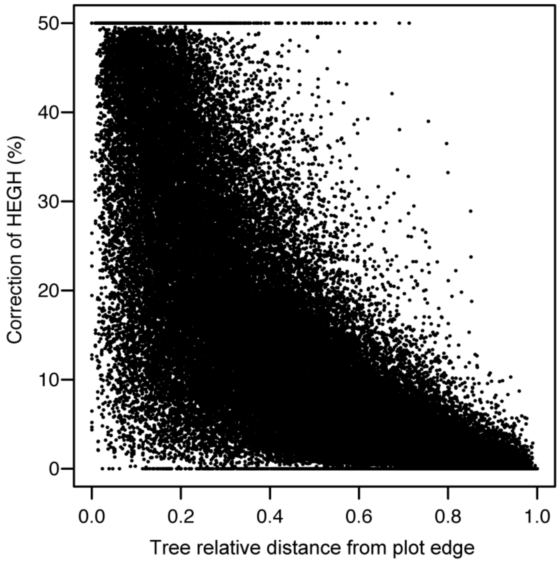


Fig. 4. Left-hand-side panel: adjustment of competition index by Hegyi. The section remaining outside the sample plot (grey) is compensated by considering the section of the same size inside the plot (black). Right-hand-side panel: correction of the edge effect of competition index by Hegyi.

where D is the diameter at breast height of the reference tree (cm); D_i is the diameter at breast height of the competitor tree (cm); L_i is the distance between the reference tree and the competitor tree ($L_i \leq 5$m).

When a tree is located near the external edge of the sample plot, Eq. 7 produces a systematic underestimate, because the influence of neighbouring trees outside the sample plot (light grey area in the Fig. 4 left) are not considered. To compensate for this lack of information, the light grey area was mirrored inside the plot (dark grey area in Fig. 4).

The relative amount of the corrections of the Hegyi index of the trees that are near the plot edges are shown in Fig. 4 (right-hand-side panel). Near the sample plot edge, the value of the competition index is increasing considerably, due to the adjustment.

The value of the Hegyi index depends on stand density and the radius of the influence zone. Thus, a fixed radius (e.g. HEG_5 = 5 m) does not always make sense. For this reason, Hegyi's competition index (HEGH) was also calculated, using an influence zone radius which was equal to 40% of the mean tree height in the first storey.

At the sample plot level, the investigated measurement variables of the first storey were stand age (A_1), density (N_1), basal area (G_1), mean square diameter (D_1), mean height (H_1), stem volume (M_1), and relative density (T_1). To calculate the stem volume of each tree, the volume equation by Ozolins (2002) was used. Stand volume (M_1) was calculated as the sum of the first storey tree stem volumes per hectare.

The site index (H_{100}, average height of dominant species at reference-age 100 years) was calculated according to the current age and height of the dominant tree species using the model developed by Nilson (1999) which is an approximation of Orlov's tables (Krigul 1969).

In the Estonian forestry practice, relative density is widely used. For tree cohorts with a mean height over 5 m, relative density (T_C) was calculated as follows

$$T_C = \frac{M_C}{a_0 + a_1 H_C + a_2 H_C^2 + a_3 H_C^3} \quad (8)$$

where M_C is the volume of the cohort trees (m^3 ha^{-1}), and H_C is the mean height of the cohort trees (m). Parameters a_0, a_1, a_2, a_3 are listed in Table 4.

In the case of the mean height being less than 5 m, the relative density (T_C) was calculated according to the National Forest Inventory Instruction (SMI 1999) based on tree cohort height (H_C) and density (N_C). In the case of pine cohorts with a height of less than 5 meters, the relative density was calculated with Eq. 9 and in the case of other tree species with Eq. 10.

$$T_C = \frac{N_C}{5610 H_C^{-0.154}} \quad (9)$$

$$T_C = \frac{N_C}{0.2966 H_C^4 - 8.9075 H_C^3 + 105.48 H_C^2 - 603.85 H_C + 3633} \quad (10)$$

The relative density for the first storey is calculated as the sum of the relative densities of the first storey tree cohorts. As indicator of high relative density, a binary variable PIIRT was used. PIIRT assumes a value of 1 if T_C is greater or equal to 1, otherwise it equals 0.

In addition to traditional stand variables, the stand sparsity (L_1), recommended by Nilson (2006), was also used in the present study:

$$L_1 = \frac{100}{\sqrt{N_1}} \quad (11)$$

where N_1 is the number of trees of the first storey per hectare. L_1 is an estimate of the average distance between trees, assuming a rectangular distribution of tree positions. A. Nilson (pers. comm.) calculated the self-thinning standard (LTJ), based on Tyurin's growth and yield tables of normal forest (Krigul 1969).

$$\text{LTJ} = k_4 + k_5 D_1 + k_6 D_1 H_{100} + k_7 H_{100} \quad (12)$$

where D_1 is the mean square diameter of the first storey trees (cm); H_{100} is the site index; k_4, k_5, k_6, k_7 are species-specific parameters (listed in Table 4).

Analogically to the relative density calculated by the self-thinning model (Eq. 12), the relative sparsity of a stand (TTJ) may be calculated as follows

$$\text{TTJ} = \text{LTJ}/L_1 \quad (13)$$

We assume that if the value of the relative sparsity (Eq. 13) is greater than 1, then the stand has exceeded the self-thinning line which will result in greatly increased mortality of trees. As an indicator of crossing of the self-thinning line, a binary variable PIIRTJ was used. PIIRTJ assumes a value of 1 if TTJ is greater or equal to 1, otherwise it equals 0.

According to a conceptual model of forest stand development based on the study of the Estonian long-term permanent sample plot data (Kangur *et al.* 2005), stand dynamics can be divided into four stages: stand initiation, stem exclusion, demographic transition and old multi-aged. These stages are characterised by different ecological processes. In this study, we have the data from after the stand initiation stage, thus we determined three different stand development stages (VG) according to dominant species and stand age (Table 5), which is common practice in Estonian forest management.

Methods

In the present study, the dependent variable is EJ, which defines the probability that a tree will survive during the next 5-year period. The value of EJ was set equal to 1, if the tree was still alive after five years, and 0 if it was not. Thus, the probability of tree mortality is equal to

$$\text{VL} = 1 - \text{EJ} \quad (14)$$

Table 4. The species-specific parameters of the relative density model $T_c = M_c/(a_0 + a_1H_c + a_2H_c^2 + a_3H_c^3)$ developed on the basis of Tretyakov's standard tables (Krigul 1969) and of the self thinning model LTJ = $k_4 + k_5D_1 + k_6D_1H_{100} + k_7H_{100}$ developed on the basis of Tjurin's growth and yield tables (Krigul 1969).

Species	a_0	a_1	a_2	a_3	k_4	k_5	k_6	k_7
Pine	–30.595	16.631	0.0254	0	–0.00437	0.1834	–0.00216	0.008641
Spruce	–7.988	9.279	0.3473	0	0.1807	0.1556	–0.00181	0.003598
Birch	15.344	0	0.7411	–0.0087	0.4083	0.1822	–0.00151	0.00671
Aspen	–18.758	8.385	0.3233	0	0.02032	0.1991	–0.00277	0.01046
Other	–11.713	8.474	0.2767	0	0.3867	0.1878	–0.00277	0.0000325

where EJ is the survival probability and VL is the mortality probability. One advantage of modeling the survival probability EJ is that it can be treated as a Markovian process so that the survival probability over a period of N years is given by the Nth power of the annual probability of survival (Vanclay 1994: p. 178).

Simple linear functions are not suitable for modeling survival because they may give predictions of the survival probability outside the feasible range (0, 1). For modeling a variate which follows a binomial distribution, a logistic model may be used where the dependent variable is logit-transformed as follows:

$$\text{logit(EJ)} = \ln[\text{EJ}/(1 - \text{EJ})] \quad (15)$$

Through logit-transformation the dependent variable is transformed into a variate with a normal distribution, which can be analyzed using logistic regression:

$$\text{logit(EJ)} = f(\boldsymbol{X}) \quad (16)$$

where $f(\boldsymbol{X})$ is a linear function of the vector $\boldsymbol{X}$ of measurement variables.

The inverse of the logit-transformation (Eq. 15) is the model that we are using to predict tree survival probability:

$$\text{EJ} = e^{f(X)}/[1 + e^{f(X)}] \quad (17)$$

where $f(X)$ is the equation of a logistic regression.

In logistic regression analysis, the *deviance* (also called as *log-likelihood statistic*) is used to characterize goodness of fit, calculated by logarithmic likelihood. The *likelihood-ratio test* helps to estimate the influence of new arguments, added into the model. The likelihood ratio follows a χ^2 distribution $\chi^2(p)$; where p is the number of parameters, which allows estimation of the statistical significance of added arguments (Dobson 2002). To select the best subset of variables the score statistic was calculated for every single tree variable for ranking single tree influence on survival using PROC LOGISTIC (Freund & Littell 2000) in SAS. The *score statistic* is asymptotically equivalent to the likelihood-ratio test statistic but avoids the need to compute maximum-likelihood estimates (Schaid *et al* 2002).

In the case of the traditional linear regression analysis (with the assumption of a normal distribution of residuals) to characterize the goodness of fit of a model, the root mean square error or coefficient of determination (R^2) are being used (Dobson 2002). By analogy with R^2 for ordinary regression, the generalized R^2 was used which represent the proportional improvement in the log-likelihood function due to the terms in the model of interest as compared with the minimal model (Dobson 2002, Shtatland *et al*. 2002).

$$R^2 = 1 - \frac{\log L(M) - p - 1}{\log L(0) - 1} \quad (18)$$

where $\log L(M)$ is the maximized log-likelihood for the fitted model with number of parameters p; $\log L(0)$ is the "null" model containing only the intercept term.

The SAS LOGISTIC procedure presents two different definitions of generalized coefficients of determination. One has been developed by Cox and Snell (1989: pp. 208–209), the other is an adjusted one by Nagelkerke (1991). In this study the coefficient of determination defined by Eq. 18 was used because Shtatland *et al* (2002) has shown that it has a number of important

Table 5. Age criteria by dominant tree species for stand development stages (VG).

Species	Young stands (NOOR)	Middle-age and maturing stands (KESK)	Mature and over-mature stands (VANA)
Pine	< 50	50–99	≥ 100
Spruce	< 40	40–79	≥ 80
Birch, black alder	< 35	35–69	≥ 70
Aspen	< 25	25–49	≥ 50
Grey alder	< 15	15–29	≥ 30

Table 6. Characteristics of survival probability by storey.

Layer	Number of trees	Number of sample plots	Proportion of spruce (%)	Number of surviving trees	Survival probability (%)	95% CL of survival probability		Survival probability at DS = 0.5 (%)	95% CL of survival probability (DS = 0.5)	
						Lower	Upper		Lower	Upper
1st storey	25477	236	13.5	23654	92.8	92.5	93.2	79.2	78.1	80.3
2nd storey	5380	154	68.3	4927	91.6	90.8	92.3	91.9	91.1	92.5
Regeneration	178	14	74.7	160	89.9	84.5	93.5	92.3	85.3	96.1
Shrub layer	62	5	27.4	37	59.7	47.1	71.0	60.5	45.3	73.9

advantages over the coefficients of determination of Cox and Snell (1989) and Nagelkerke (1991).

For the logistic ANOVA, the procedure GENMOD of the SAS software (Littell *et al* 2002) was used for analysing the tree cohort influence. For multilevel analysis of tree and stand variable influences the generalized linear methods (SAS procedure GLIMMIX) (Schabenberger 2005) and the R function **lmer** (Crawley 2007) were used. The SAS procedure GLIMMIX fits statistical models to data with correlations or non-constant variability and where the response is not necessarily normally distributed. Function **lmer** is used for fitting mixed-effects models in R (package lme4). Both allow analysing a a response variable with a binomial distribution and logit transformation. However, the SAS procedure GLIMMIX implements a restricted pseudo-likelihood (RPL) method whereas a restricted maximum likelihood (RML) method is used in the R function **lmer**.

Results and discussion

Tree survival probability dependence on tree storey

In the present study, four storeys were separately identified on the analyzed sample plots — the first storey (1), the second storey (2), the regeneration (J) and shrub layer trees (A). The results show that the survival probability of the trees which belong to the first storey is higher than that of trees in other storeys (*see* Table 6). The difference in survival probabilities is statistically significant between the first and the second storeys and between the first storey and the regeneration.

We assume that the difference of the survival probability in the storeys in the stand is largely caused by the differences in the relative diameter. To evaluate that assumption, a model of logistic covariance analysis was applied using the procedure GENMOD of SAS

$$\text{logit}(\text{EJ}_{ij}) = \mu + \tau_i + (\beta + \delta_i)\text{DS}, \qquad (19)$$

where EJ_{ij} is the survival probability of a tree in the *i*th storey and the *j*th relative diameter; logit() is the logit-transformation (15); μ is the model intercept; τ_i is the influence of the storey to the intercept; β is the slope of the regression line between the logit-transformation and the relative tree diameter DS; δ_i is the influence of *i*th storey on the slope of the regression line; DS is the ratio between the tree diameter and the first storey mean squared diameter.

Table 6 presents survival probabilities, calculated with Eq. 19 and their confidence limits for different storeys. These results are interesting because of the differences in the viability of the suppressed trees in the different layers. The value of the relative diameter DS was set to 0.5 at each layer. In the case of the suppressed trees in the second storey and regeneration layer, the tree survival was found to be substantially higher than the viability of the trees in the first storey (where DS was also equal 0.5). Much less viable were the shrub layer trees. The relatively high viability of the regeneration and second storey trees is probably due to the fact that spruce, a shade-tolerant tree species, is very prominent in these storeys, and is found here in greater proportions than in the first storey and in the shrub layer.

In many sample plots the smaller understorey trees (trees of the second storey, and of the regeneration and shrub layer) were either not present at all, were measured within a smaller circle, or were not measured at all. Therefore, only the trees from the first storey are considered in the following analysis.

Tree survival probability depending on a single variable

At first, the influence of each variable on tree survival was investigated individually without considering the influence of other variables. The influences were assessed separately for the entire data set as well as for the data sets of the three stand development stages (young, middle-aged, mature).

Table 7 presents the score statistics on different data sets, characterizing the influence of the measurement variable X in the logistic regression formula

$$\text{logit(EJ)} = \mu + \beta X, \qquad (20)$$

where EJ is the survival probability; logit() is the logit-transformation; X is the measurement observation; μ, β are parameters of the regression equation.

The results in Table 7 show that for the entire dataset and also on separate data sets of all stand development stages, the tree survival probability EJ depended most on the relative height of a tree HNLSS. As mentioned before, the tree heights which were not measured were calculated using a specific diameter/height relationship. For the total database, the second most important variable was the tree relative diameter DS. But in middle-aged and older stands this variable was not in the first triple. The third most important variable in the total data set was BALS (the ratio between the relative basal area of larger trees and the stand basal area).

Table 7. Variables, influencing tree survival probability the most. The numbers in the table represent score statistics of differences between intercept only and intercept with variable.

Variable	All data	Young stands	Middle-aged and maturing stands	Mature and overmature stands
HNLSS	1881	640	1166	109
DS	1300	435	810	73
BALS	1099	403	620	70
HEGH	907	247	920	85
D	859	188	800	88
HEG5	776	187	932	82
BAL	725	435	249	74
HNLS	606	88	610	60

Considering the total data set, effective variables were also both Hegyi competition indices (HEGH and HEG5) and then the tree height *H*, the tree diameter *D* and the basal area of larger trees BAL. Stand variables (both versions of relative density and quality class) and tree species were clearly less important than the measured variables which characterize the relative state of a tree. From the practical viewpoint, the tree diameter *D* and the tree relative diameter DS are explanatory variables which can be used in distance-independent forest-growth models. Therefore, these variables are often preferred to competition indices which require known tree positions.

The influence of the height to crown base and of the relative height of crown base on the tree survival probability was analyzed for sample tree data sets where the height to crown base was measured and the spruce trees were left out. The results show that in young and middle-aged stands, the influence of the height to crown base on the tree survival probability was less than the influence of the other variables listed in Table 7. Old stands were an exception; there, the influence of relative and absolute height to crown base on mortality was clearly higher than the influence of other variables.

Tree survival probability dependence on several variables

Tree survival probability EJ was modeled with the two-level mixed model

$$\begin{aligned}\operatorname{logit}\left(\mathrm{EJ}_{ij}\right) &= \beta_{0j} + \beta_1 X_{1ij} + \beta_2 X_{2ij} + \ldots \\ &\quad + \beta_m X_{mj} + \beta_{m+1} X_{m+1j} + \ldots\end{aligned} \tag{21}$$

where EJ_{ij} is the tree survival probability; logit() is the logit transformation (Eq. 15), β_{0j} is the random intercept ($\beta_{0j} = \beta_0 + u_j$:$u_j \sim \mathrm{N}(0, \sigma_u^2)$, i is the tree number; j is the plot number; X_{1ij}, X_{2ij} are tree level variables; X_{mj}, X_{m+1j} are stand level variables; $\beta_0, \beta_1, \beta_2, \beta_m, \beta_{m+1}$, ... are model parameters.

Taking a great number of arguments into the model may be justified in the case of a random sample, such as a forest inventory, where all elements of a population have the same probability to be part of the sample. Unfortunately, the selection of stands in the Estonian forest research plot network was not entirely random, which is also revealed in the distribution histograms in Figs 2 and 3. That is why the principle of developing a model which is as parsimonious as possible (Burkhart 2003) was followed in this study.

The selected variables (Table 2) were divided into three groups: vertical size variables (HNLS, HNLSS, H_1, etc.), horizontal size variables (*D*, DS, D_1, etc.) and competition variables (BALS, BAL, HEG5, HEGH, etc.). Variables of relative size (relative diameter, relative height) could be handled as size group variables as well as competition group variables. However, in this study relative size variables were handled as size group variables, because we assume that they are indicative of the amount of resources needed for tree survival. For selecting variables into the multiple model, an ordered list of score statistics was calculated for all variable combinations using the LOGISTIC procedure. However, not all variable combinations on top of the list of score statistics were biologically interpretable and with statistically significant parameter estimates. For multilevel logistic modeling with a random intercept (Eq. 21) we selected one tree level variable from each group, a stand level competition variable, and the tree species as regressors (HNLSS, DS, BALS, TTJ, KUDS, PL). The results of this multilevel logistic modelling on different data sets are presented in Table 8.

Table 8 presents two sets of results of multilevel logistic modelling, one obtained with the SAS procedure GLIMMIX and the other with the R function **lmer**. Both procedures use different methods for parameter estimation. Nevertheless, both methods established the same set of significant variables and produced similar parameter estimates which is somewhat reassuring. All terms in the model are biologically sound: tree survival (EJ) is increasing with increasing relative height (HNLSS) and decreasing with increasing competition status (BALS, TTJ). Considering the effect of different tree species, spruce survival was significantly higher and grey alder survival significantly lower than other tree species for all development stages. This can be explained by the shade tolerance of spruce and the short life of grey alder. Significance of variable KUDS for old stands indicates a relatively lower survival of bigger spruces because of wind- and fungi damages (Laarmann 2007).

Conclusions

Tree mortality is a key factor in the understanding of forest dynamics. The accuracy and relevance of a growth model depends on the accuracy of predicting tree survival. The present study has shown which tree and stand variables affect tree survival probability most in Estonian forests.

Tree survival was analyzed using a data set which includes 31 097 trees from 236 research plots, measured twice during 1995–2004. During the 5-year period between measurements, altogether 2319 trees (or 7.5%) had died (dead standing, broken or fallen).

The survival probabilities, presented in Table 6 are interesting because of the differences in the viability of the suppressed trees in the different layers. In the case of the suppressed trees in the

Table 8. Results of generalized linear mixed modeling with PROC GLIMMIX (SAS) and function lmer (R) for Eq. 21.

Regressor		All data		Young stands		Middle-aged and maturing stands		Mature and overmature stands	
Coefficients of model with GLIMMIX									
		Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
Intercept		2.1624	0.4232	4.8111	0.9713	–1.2635	0.4227	10.2931	2.2789
HNLSS		4.3433	0.2559	4.5473	0.6140	4.6567	0.5607	3.4531	1.1361
DS				–1.7344	0.7159	1.7057	0.3859		
BALS		–1.8928	0.2319	–4.1013	0.7873			–2.3698	0.8679
TTJ		–2.1976	0.2510	–1.7800	0.3975	–1.8281	0.3929	–9.9323	1.8795
KUDS								–3.8111	1.7460
PL	Aspen	–1.3529	0.1125	–1.3610	0.1885	–1.4853	0.1609	–1.1760	0.5093
	Birch	0.0796	0.0871	0.0317	0.1583	0.0179	0.1261	–0.1850	0.4064
	Spruce	0.2272	0.1032	0.2561	0.1470	0.3762	0.1732	1.7442	1.7761
	B. alder	–0.1938	0.2058	–0.6747	0.2605	1.0037	0.5192	–1.6863	0.9211
	G. alder	–1.9203	0.1083	–1.5491	0.2054	–2.2703	0.1403	–2.6151	0.4481
Type III Tests of Fixed Effects									
		F	Den df	*F*	Den df	*F*	Den df	*F*	Den df
HNLSS		288.06	24906	54.85	8718	68.99	14203	9.24	1969
DS				5.87	8718	19.53	14203		
BALS		66.63	24906	27.14	8718			7.46	1969
TTJ		76.66	234	20.05	78	120	21.65	27.93	32
KUDS								4.76	1969
PL		94.40	374	25.95	138	173	71.49	7.42	53
Coefficients of model with lmer									
		Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
Intercept		1.9623	0.6442	4.7740	1.2959	–0.7766	0.7268	8.9933	2.3692
HNLSS		5.3326	0.3016	4.8669	0.8782	4.8496	0.6391	3.5957	1.0692
DS				–1.0344	0.9549	1.8207	0.4109		
BALS		–1.6489	0.2420	–3.8207	0.8970			–2.2355	0.8047
TTJ		–2.8763	0.6070	–2.8202	1.0808	–2.4132	0.7999	–8.4635	2.1181
KUDS								–3.5764	1.6793
PL	Aspen	–0.8172	0.1998	–0.6762	0.3882	–0.9910	0.2642	–1.1893	0.5332
	Birch	0.1714	0.1479	0.4230	0.2951	0.1042	0.1910	–0.3125	0.4440
	Spruce	0.4109	0.1701	0.7031	0.2699	0.3845	0.2434	1.6453	1.7147
	B. alder	–0.2659	0.2540	–0.6531	0.3643	1.0362	0.5261	–2.0163	0.8827
	G. alder	–2.0647	0.1924	–1.5209	0.3300	–2.6542	0.2577	–2.5840	0.5444
Fit statistics									
logLik		–4856		–1692		–2752		–363.1	
Deviance		9712		3384		5505		726	
R^2		0.168		0.189		0.168		0.084	

second storey and regeneration layer, the tree survival was found to be substantially higher than the viability of the trees in the first storey (for a given value of DS = 0.5).

The logistic form was used for modeling tree survival probability. The influence of 35 tree and stand measurement variables (Table 2) to tree survival probability was estimated using the score statistics of a logistic regression.

The research of separate single variables revealed that the mortality of trees is mostly influenced by tree measurement variables (presented in decreasing order of score statistic, Table 7): tree calculated relative height HNLSS, tree relative diameter DS, relative basal area of larger trees BALS, Hegyi competition index HEGH in a circle with radius $0.4H_1$, tree diameter *D*, Hegyi competition index HEG5 in a circle with a 5-m radius, basal area of larger trees BAL and tree height *H*. The study revealed that it is useful to divide the total data set into three development stages defined by dominant tree species and age: young, middle-aged and maturing, mature and very old stands. In each of these categories, different influencing factors turned out to be dominant.

The obtained results improve our knowledge of Estonian forest stand dynamics. It is possible to apply the proposed models in forest simulation studies as a preliminary approximation of a tree mortality component. The development of flexible simulators, which complement existing yield-tables, will significantly improve decision-making in practical forest management.

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