Assessment of tree mortality on the Estonian Network of Forest Research Plots

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Abstract. Assessment of tree mortality provides deeper understanding of forest structure and functioning. This enables evaluation of stand sustainability and provides information on stand productivity, diversity and health condition. Tree mortality can be assessed by spatiotemporal patterns as well as by studying the processes and causes of mortality. Tree mortality is caused by specific disturbance agents or by the complex effect of various disturbances. The purpose of this study is to examine tree mortality in Estonian forests, determine the causes of tree death, and estimate how different management regimes affect tree mortality and its causes. This study is based on 360 sample plots measured in 2003–2005 and re-measured in 2008–2010. The sample plots were divided into recently managed (RM, 146 plots) and low intensity/unmanaged (LU, 214 plots) plots based on forest management regime. In total, 53,990 trees were measured, of which 20,020 were located on RM and 33,970 on LU plots. The tree mortality for 5-year period was 3.4% on RM plots and 8.0% on LU plots. The main cause of tree mortality in RM stands was insect damage, which attributes to 29.8% of tree mortality, whereas in LU stands the main cause was tree competition, which attributes to 45.4% of tree mortality. The analysis of tree mortality indicated that an increase in relative tree diameter in both stand types contributes to an increase in mortality due to insect, wind or fungal damage and diseases. Opposite results were received with respect to competition – the smaller the tree relative diameter, the more probable it is that a tree will die because of competition with neighbouring trees. The analysis of game damage and other causes of tree mortality showed that these were not dependent on the relative diameter of trees. The analysis of the overall probability of tree mortality revealed that relatively smaller trees have a higher probability of mortality than larger trees.

Key words: tree mortality, survival probability, competition, permanent sample plots.

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Introduction

Assessment of tree mortality is important in studying forest dynamics and enables the use of individual tree models in stand growth modelling (Sims *et al.*, 2009). Research into the extent and causes of tree mortality provides a deeper understanding of forest structure and functioning.

This facilitates evaluating stand sustainability and it also provides information on forest productivity, diversity and health condition (Laarmann, 2007). It is fundamental to include a mortality function in forest growth models since tree mortality produces an open space which leads to (Franklin *et al.*, 1987): (1) an increased growth of surrounding trees through re-

duced competition, (2) opportunity for regeneration by the creation of gaps, and (3) the addition of coarse woody debris to the structure of stands.

Tree mortality is a complicated process affected by a variety of factors, such as environmental, physiological, pathological, and entomological factors, as well as some random events (Yang *et al.*, 2003). The causes behind tree mortality can be categorised in a number of ways, for example, into abiotic and biotic causes (Franklin *et al.*, 1987; Rouvinen *et al.*, 2002). Abiotic mortality causes include fire, wind, floods, etc., whereas biotic mortality causes lie in diseases, insect attacks, stand age, etc. Another possibility is to group tree mortality into density-dependent and density-independent factors (Ozolincius *et al.*, 2005). Density-dependent tree mortality occurs due to competition among individuals and density-independent mortality appears due to other causes. The main disturbances in managed stands are cuttings whereas in unmanaged forests many disturbances affect tree mortality simultaneously (Laarmann, 2007).

As tree deaths are relatively rare events, it is difficult to collect sufficient data for quantitative analyses. Long-term observations in permanent plots can provide suitable data for mortality analyses. A variety of empirical approaches have been used for describing and modelling tree mortality at different scales. Mortality models on a stand level predict stand density changes over time and therefore they often estimate mortality in terms of volume, basal area or number of trees per hectare, while individual tree mortality models predict the probability of survival or death for each individual tree involved in growth projections. Individual tree survival models, though more complicated, are often preferred from a management perspective because they provide a more detailed description of stand structure and its dynamics.

Previous studies on this topic in Estonia have been done by Sims *et al.* (2009) and

Laarmann *et al.* (2009). Sims *et al.* (2009) showed that relative height has the greatest effect on single tree survival. Laarmann *et al.* (2009) analysed the share of mortality causes (game, insects, etc.) depending on relative diameter. Datasets for those analyses are different: the first contains both dead and living trees, whereas the second contains only dead trees. Therefore, those two studies are not comparable and it needs to be analysed whether relative diameter is a more appropriate predictor than tree diameter to calculate the share of a certain mortality cause.

The aims of this study are (a) to examine tree mortality based on the permanent sample plot data of Estonian forests, (b) to analyse the causes (agents) of tree mortality, and (c) to analyse how management regimes affect tree mortality.

Material and Methods

This study is based on 360 sample plots (Figure 1) from the Estonian Network of Forest Research Plots (ENFRP) measured in 2003–2005 and re-measured in 2008–2010. The sample plots were divided into recently managed (RM, 146 plots) and low intensity/unmanaged (LU, 214 plots) categories according to forest cutting. Stand characteristics are presented in Table 1. Sample plots where the level of cuttings remained below 2% of the total number of trees in the last 15 years were included in LU stands. In total, 53,990 trees were measured, 20,020 of which were growing on RM plots and 33,970 on LU plots.

The ENFRP was established in 1995–2004 to provide empirical data for developing forest growth and yield models. The network follows the grid of ICP Forest level I monitoring plots. The plot locations were selected randomly and they represent the most common forest types and age groups in Estonia (Kiviste *et al.*, 2005). The plots are re-measured at five-year intervals. In general, the permanent sample plots are

Table 1. Description of stand characteristics in recently managed (RM) and low intensity / unmanaged (LU) stands.

Tabel 1. Puistute takseernäitajad hooldatud (RM) ja hooldamata (LU) puistutes.

Stand variable/ Mõõdetud puistu tunnused	Quartiles of a variable / Tunnuste kvartiilid									
	0%		25%		50%		75%		100%	
	RM	LU	RM	LU	RM	LU	RM	LU	RM	LU
Diameter, cm <i>Diameeter, cm</i>	10.3	6.8	17.2	17.4	20.3	22.6	25.2	28.2	38.7	47.4
Height, m <i>Kõrgus, m</i>	12.1	6.5	18.6	18.1	21.0	22.6	24.5	27.8	35.1	35.0
Age, years <i>Vanus, a</i>	23	20	40	47	45	63	55	80	115	240
Volume, m ³ ha ⁻¹ <i>Tagavara, m³ha⁻¹</i>	47	52	190	216	248	293	340	372	545	725
Number of trees, ha ⁻¹ <i>Puude arv, ha⁻¹</i>	219	132	527	475	728	668	975	1138	2136	4893

circular, with a radius of 15, 20, 25 or 30 m and include tree position data. The plot size depends on the forest density and age. For every fifth tree and also dominant and rare tree species, tree height to crown base was measured and the height to the first dry branch of old coniferous trees was also assessed. Second storey and undergrowth trees were measured in a smaller circle with a radius of 8 (at plot radius of 15 m) or 10 meters (at plot radius of more than 15 m) (Sims *et al.*, 2009). Measurement records are available for living trees (upper-, mid-, under-storey and shrub layer trees), dead trees (standing, downed, and broken trees) and fresh stumps (Laarmann *et al.*, 2009).

Trees that were alive during the previous measurement in 2003–2005 but had died by the given measurement in 2008–2010 were considered as dead trees. The analysis of the models explored six different groups of mortality causes both in RM and LU plots. Mortality causes were divided by visual evaluation into the following groups:

1) Game, mainly by moose peeling the bark from spruce and pine leading to the death of trees;

- 2) Insects, mainly by the bark beetle (*Ips* sp.) as the primary or secondary cause;
- 3) Fungi and disease, mainly root rot, heart rot, canker and other pathogens as primary or secondary causes;
- 4) Wind, including wind throw and stem breakage;
- 5) Density-dependent causes, mainly competition among suppressed trees;
- 6) Other, including floods, frost and unknown reasons.

Although the research by Sims *et al.* (2009) showed that tree survival best correlates with tree relative height, tree relative diameter was used to analyse tree survival probability in this study because the height of each individual tree was not measured (only the height of model trees was measured) in ENFRP. Relative tree diameter was calculated for each measured tree, where the relative diameter was defined as the ratio of an individual tree's diameter to the mean diameter of the stand.

For modelling tree survival, the logistic regression was used in R environment (R Core Team, 2014). P_i is the probability of survival of tree i , while $1-P_i$ is the probability

Figure 1. Location of sample plots in Estonia.

Joonis 1. Proovitükkide asukohad.

of death of tree i . A similar analysis was used also in studying tree mortality causes where the studied variable was the mortality cause. In dead trees data (trees that had died within 5 years), the value 1 was attributed to a certain variable (e.g. game damage) and the value 0 was attributed in the case of a different mortality cause (e.g. the wind). The logistic function (Eq. 1) was used for the mortality of individual trees with each dead tree being an observation, as

$$\text{logit}(p) = \ln\left(\frac{p}{1-p}\right), \quad (1)$$

where p is the probability of a tree mortality cause.

The logit-transformation (Eq. 2) rendered mortality cause into a dependent variable with a normal distribution, which can be analysed with methods of regression and variance analysis:

$$\text{logit}(p) = f(x), \quad (2)$$

where $f(x)$ is a linear function of the vector x of measurement variables.

Two different analyses were carried out. The purpose of the first analysis was to find out how much management affects mortality. In this analysis a dataset with dead and living trees was used. The second analysis attempted to find out the causes of mortality (game, wind, etc.). In that analysis a dataset with only dead trees was used.

All variables in the models are tree level; therefore, R function *glm* (with a binomial family of distribution) was used for modelling. For every cause of tree mortality two different logistic regressions were used, depending on (1) tree diameter and (2) relative diameter. Model selection was based on Akaike's An Information Criterion (AIC).

Results

Between two measurements in 2003–2005 and in 2008–2010 3,485 trees died on the sample plots. In RM plots, 687 trees (3.4%) of all measured trees died, mainly Scots pine (44% of all trees), Norway spruce (41%) and silver birch (9%). In LU plots,

Figure 2. Average annual mortality rate (%) by species in RM and LU stands.

Joonis 2. Keskmise puude väljalangevus (%) aastas puuliikide kaupa hooldatud (RM) ja hooldamata (LU) puistutes.

2,798 (8.0%) of all measured trees died, mainly Scots pine (34%), silver birch (27%) and Norway spruce (25%).

The annual tree mortality rate (AMR) was, on average, 0.68% in RM and 1.60% in LU stands. The AMR for different species was between 0.40–1.59% in RM and 1.34–4.42% in LU stands (Figure 2).

The main tree mortality cause in RM stands (Table 2) was insect damage, which constituted 29.8% of mortality causes. The greatest proportion of trees that had died of insect damage was recorded in Scots pine (37.4%) and Norway spruce (30.5% of dead trees) and the lowest in grey alder (6.3%). Growth-dependent causes were the second most important mortality cause (20.8%). The greatest proportion of trees that had died of such causes was recorded in Scots pine (26.5% of dead trees) and the lowest in aspen (7.1%). The wind was the third most relevant mortality cause (18.2%). Nearly 36% of dead aspens had died due to wind breakage. Fungi and diseases as causes of mortality had almost the same proportion (18.0%).

The main mortality causes in LU stands (Table 2) were growth-dependent causes, more specifically competition, where 45.4% of dead trees had died of growth-dependent causes. Silver birch was recorded to have the greatest proportion of trees dead due to competition (62.3%), whereas common aspen had the lowest (31.7%). The second most prominent mortality cause was fungi and diseases (19.8%). The third most important cause of mortality in LU stands was insects (13.7%). 26.5% of dead pine trees were killed by insects. However, only 1.1% of dead birch trees had suffered insect damage. In both stand types, game damage as a mortality cause was the least prominent, with 0.7% in RM and 0.5% in LU stands.

The analysis of tree survival showed the model as statistically significant ($p < 0.05$), indicating that trees with a smaller relative diameter have a higher mortality probability than trees with a larger relative diameter, and survival probability is higher in RM stands compared to LU stands (Figure 3).

Table 2. Distribution of dead trees by mortality causes in RM and LU stands.

Tabel 2. Surnud puude jaotus sõltuvalt väljalangemise põhjusest hooldatud (RM) ja hooldamata (LU) puistutes.

Tree species <i>Puuliik</i>	Number of dead trees <i>Surnud puude arv</i>		Proportion (%) by mortality cause from dead trees <i>Osakaal (%) surnud puudest väljalangemise põhjuste kaupa</i>											
			Game <i>Ulukid</i>		Insects <i>Putukad</i>		Fungi and diseases <i>Seened ja haigused</i>		Wind <i>Tuul</i>		Growth-dependent <i>Puude konkurents</i>		Other causes <i>Muud põhjustud</i>	
	RM	LU	RM	LU	RM	LU	RM	LU	RM	LU	RM	LU	RM	LU
Scots pine / <i>Harilik mänd</i>	302	942	–	0.4	37.4	26.5	16.6	18.4	9.9	12.5	26.5	37.4	9.6	4.8
Norway spruce / <i>Harilik kuusk</i>	282	689	1.8	1.3	30.5	15.5	12.4	11.6	25.5	14.9	16.7	41.4	13.1	15.2
Silver birch / <i>Arukask</i>	60	742	–	0.1	8.3	1.1	28.3	23.7	23.3	6.1	18.3	62.3	21.7	6.7
Common aspen / <i>Harilik haab</i>	14	63	–	–	–	–	50.0	33.3	35.7	30.2	7.1	31.7	7.1	4.8
Grey alder / <i>Hall lepp</i>	16	140	–	0.7	6.3	2.1	68.8	20.7	25.0	21.4	–	37.9	–	17.1
Black alder / <i>Sanglepp</i>	3	56	–	–	–	17.9	66.7	26.8	–	–	–	39.3	33.3	16.1
Other species / <i>Teised liigid</i>	10	166	–	–	–	3.0	20.0	35.5	–	7.2	40.0	45.2	40.0	9.0
Total / <i>Kokku</i>	687	2798	0.7	0.5	29.8	13.7	18.0	19.8	18.2	11.7	20.8	45.4	12.4	9.0

Table 3. Results of logistic regression (Eq. 2) for the probability of causes of individual tree mortality (depending on diameter or relative diameter).

Tabel 3. Logistilise regressiooni (valem 2) tulemused puude väljalangemise põhjuse tõenäosuse arvutamiseks (sõltuvalt diameetrist või suhtelisest diameetrist).

Cause / Põhjus	Intersept / Vabaliige	Diameter / Diameeter	Relative diameeter / Suhteline diameeter	Recently managed / Hooldatud puistud	p-value / Olulisuse tõenäosus	AIC
Game / <i>Ulukid</i>	-4.247 -3.939	0.721	0.032	0.622 0.547	0.081 0.049	565.43 564.87
Insects / <i>Putukad</i>	-3.504 -3.350	1.819	0.126	0.494 0.170	<0.001 <0.001	1760.98 1612.40
Fungi / <i>Seened</i>	-2.310 -1.737	1.154	0.045	-0.546 -0.644	<0.001 <0.001	2184.76 2189.97
Wind / <i>Tuul</i>	-3.618 -4.214	0.529	0.083	1.053 0.815	0.110 <0.001	809.52 765.81
Growth- dependent / <i>Konkurents</i>	2.161 2.305	-2.820	-0.274	-0.443 0.211	<0.001 <0.001	2537.20 2165.23
Other reasons / <i>Muud põhjused</i>	-2.112 -1.623	0.358	-0.014	-0.043 0.022	0.087 0.166	1733.78 1734.70

Figure 3. Tree survival probability based on relative diameter for different tree species in RM stands (A) and LU stands (B).

Joonis 3. Puude ellujäämistõenäosus suhtelisest diameetrist sõltuvana puuliikide kaupa hooldatud (A) ja hooldamata (B) puistutes.

Figure 4. Predicted probability of different causes of mortality depending on relative diameter in recently managed (RM) and low intensity/unmanaged (LU) stands.

Joonis 4. Puude suremise põhjuse esinemise tõenäosus sõltuvalt puu suhtelisest diameetrist hooldatud (RM) ja hooldamata (LU) puistutes.

Table 3 shows that mostly models with relative diameter (game, insects, wind and growth-dependent) have a lower AIC value, which means that in those cases relative diameter should be preferred instead of tree diameter. Also, the AIC values of the models for fungi and other reasons are close; therefore, relative diameter can be used for all causes.

Tree survival probability was analysed (Figure 3, Table 3) depending on relative diameter and tree species. It appeared that although in RM sample plots, relative diameter has statistical significance ($p < 0.05$), that is, tree survival probability depends on relative diameter, the tree species itself shows no statistical significance ($p > 0.05$), that is, irrespective of tree species, mortality probability is the same in all trees, and in the case of two trees with the same diameter, one of the trees does not have a higher mortality probability than the other.

The credibility of the model of mortality causes is demonstrated by the model's significance probability, which in the case of both causes was $p < 0.05$, and thus, mortality was dependent on relative diameter. The analysis of game, insects, fungi, wind and growth-dependent as mortality causes showed the models as significant. An increase in tree relative diameter raises the probability of the tree dying of insects and wind (Figures 4 A and B). However, the analysis of differences in mortality causes between RM and LU stand types revealed that the extent of insect damage is different in RM and LU stands ($p < 0.05$), that is, there is a significant difference between how insects affect the mortality of RM and LU stands. The analysis of the average mortality of both stand types indicated that in RM stands, the mortality probability due to insect damage is 36.1% higher than in LU stands. In the case of fungi and diseases,

es, no differences were recorded between the two types of stands, which means that the model had no statistical significance ($p > 0.05$) and the probability of trees dying of fungi and diseases in RM stands is 2.4% lower than in LU stands.

Figure 4 (C) describes the relationship between growth-dependent causes (mainly tree competition) and tree relative diameter in RM and LU types. As shown in the figure, the smaller the tree relative diameter, the more likely that the tree will die of competition. The credibility of the model is indicated by the model's significance probability. By analysing the model, it may be suggested that competition affects mortality in a significantly different manner in RM and LU stands. In RM stands, the mortality probability based on relative diameter 1.0 is 17.4%, whereas in LU stands it is 39.2%.

Discussion

Tree mortality is a complex process, which is difficult to predict and which is determined by many external factors. These factors may be divided into primary and secondary factors; the primary factors are capable of destroying a completely healthy tree, whereas the other factors attack already weakened trees (Lännenpää *et al.*, 2008). Stand ageing may expose a tree to becoming less resistant to insect damage, diseases and the wind, ultimately resulting in death. The resistance of trees to disturbances depend on stand structure, age of trees, location of damaged trees in a stand, and tree species. Depending on disturbance factors (storms, increase in insect population, etc.), they may cause the death of trees or the physiological weakening of trees (Aakala, 2010). The process of dying is usually slow in the beginning and the weakening of a tree may take years, but after the tree has been populated by secondary pests, pest groups start varying quickly, thus accelerating the process of dying (Laarmann *et al.*, 2009).

The AMR of various tree species in Europe remains between 0.1–1% (Ozolincius *et al.*, 2005; Lõhmus & Kraut, 2010). According to some studies (Monserud & Sterba, 1999; Rouvinen *et al.*, 2002), Scots pine has a higher mortality rate than Norway spruce. However, Scandinavian (Jönsson & Jonsson, 2007; Eid & Tuhus, 2001) and Lithuanian (Ozolincius *et al.*, 2005) studies present contrasting results. The analysis of data collected in this research showed that in RM sample plots, the AMR of Scots pine is 0.7% and that of Norway spruce is 0.8%. The somewhat higher mortality rate of Norway spruce in RM plots may be caused by the spruce's low drought tolerance and, since its roots are not deep in the soil, the spruce is also not very storm-resistant. In LU plots, the AMR of Scots pine was 1.4% and that of Norway spruce was 1.3%. Conifer mortality within a stand was even, whereas the AMR was two times higher in LU stands compared to RM stands. This phenomenon may occur due to differences between the competition situation in natural and cultivated stands, which is why Scots pine and Norway spruce vary in resistance and mortality, and this is supported by studies from the Swedish National Forest Inventory (Jonsson *et al.*, 2005). The annual average mortality rate of Silver birch in RM stands was 0.5% and in LU stands it was 2%.

Natural forests usually contain various species of different age and for this reason, more tree species that have a shorter lifespan than other species tend to grow in them, which may lead to higher mortality rates in unmanaged stands. In addition, the flow of deadwood characterises natural processes within a natural forest ecosystem (Laarmann, 2013).

In RM stands, the primary mortality cause was insect damage (30%). In RM stands, natural diversity is not as rich as in LU stands and since RM stands have been turned more homogeneous, trees have a higher risk of dying of extensive insect attacks than in LU stands. Insects are a source

of considerable disturbances. They may kill trees or lower their resistance which may result in death and eventually, the trees fall on the ground. In LU stands, however, growth-dependent causes, that is, competition and old age (45%), are the main sources of mortality. Determining competition or old age as mortality causes may be done when by visual observation no causes as to why the tree has died are found or if a tree has fallen behind in growth (compared to other trees in the stand). In this case, competition is usually indicated as the main mortality cause (Laarmann, 2007). As this research explores LU plots where no signs of human activity have been detected in the last 10-15 years, the large proportion of competition as a mortality cause is expected, which shows that timely improvement cuttings have not been done in the sample plots.

The analysis of data by Laarmann *et al.* (2009) showed that as the tree relative diameter increases, the probability of a tree dying due to wind, insect or fungal damage also increases. This research also received similar findings which showed that an increase in trees' age and diameter leads to an increase in the probability of the trees dying of various fungi, insects and wind (Figure 4).

Differences between mortality causes in RM and LU stand types were also analysed, which revealed that in RM stands, the mortality probability due to insect attacks is 16.1 percentage points higher than in LU stands, whereas no difference was recorded between the stands when fungi and other diseases as mortality causes were compared. As insects are a natural part of a forest ecosystem, each forest type (Voolma, 2000) has its own pathogens of various species and numbers. In natural mixed forests, the collection of pathogens is richer and more balanced, whereas in managed pure stands, the number of pathogen species is smaller but their numbers are less balanced. This means that in favourable conditions the pathogens are

prone to massive spreading. Stands poor in species are always more endangered by pathogens compared to mixed stands (Laarmann, 2007).

Conclusions

The average annual tree mortality rate was 0.68% in recently managed and 1.60% in low intensity/unmanaged stands. The highest mortality rate was observed in grey alder (1.6% in managed and 4.4% in unmanaged stands) and the lowest mortality rates in aspen (0.4% in recently managed stands) and in black alder (1.3% in low intensity/unmanaged stands).

The main cause of tree mortality in recently managed stands was insect damage, which attributed to 29.8% of causes of death. The greatest proportion of trees that had died because of insect damage was expressed by Scots pine and Norway spruce (37.4% and 30.5% of dead trees, respectively) and the lowest in grey alder (6.3%). In low intensity/unmanaged stands the main cause of death was tree competition, which attributed to 45.4% of tree mortality. Birch was recorded to have the greatest proportion of trees dead because of growth-dependent causes (62%), whereas common aspen had the lowest share (31.7%).

The analysis of tree mortality indicated that an increase in relative tree diameter contributes to an increase in mortality due to insect, wind or fungal damage and diseases. Contrary results were received with respect to growth-dependent causes – the smaller the tree relative diameter, the more probable it is that a tree will die because of competition with neighbouring trees. The analysis of game damage and other causes of tree mortality showed that these were not dependent on the relative diameter of trees.

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Puude väljalangevuse hindamine metsa kasvukäigu püsiproovitükkidel

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Kokkuvõte

Puude väljalangevus on tähtis komponent puistute dünaamika uurimisel ja kasvukäigu modelleerimisel. Puude suremise ulatuse ja põhjuste uurimine annab parema arusaamise metsa struktuurist ja funktsioneerimisest. Saadud andmete alusel on võimalik hinnata puistu tootlikkust, mitmekesisust ja tervislikku seisukorda.

Käesoleva töö eesmärgiks oli uurida Eesti metsade kasvukäigu püsiproovitükkide põhjal puude väljalangevust, välja tuua puude suremise põhjused ning uurida, kas majandamisrežiim mõjutab puude suremise põhjuseid ja sagedust. Töös on kasutatud 2008–2010. aasta kevadel ja suvel mõõdetud 360 proovitüki andmeid. Kasutati ainult neid proovitükke, mida on mõõdetud nii aastatel 2003–2005 kui ka 2008–2010. Proovitükid jagati majandusrežiimi järgi hooldatud ja hooldamata proovitükkideks. Uurimustöös kasutati 360 püsiproovitükki, neist 146 asusid hooldatud ja 214 hooldamata puistutes.

Puude väljalangevus 5-aastase perioodi jooksul oli 3,4% hooldatud ja 8,0% hoolda-

mata puistutes. Analüüsides puude väljalangevuse seoseid puu dimensioonidega selgus, et suhteliselt väiksema diameetriga puude väljalangemise tõenäosus on suurem kui suhteliselt suurema diameetriga puudel. Hooldatud puistutes on puude ellujäämistõenäosus suhteliselt väiksema diameetri puhul suurem kui hooldamata puistutes. Peamiseks puude suremise põhjuseks hooldatud puistutes on putukate poolt põhjustatud puude suremine, mis moodustab 29,8% puude suremise põhjustest ning hooldamata puistutes on selleks puudevaheline konkurents, mis leiti olevat põhjuseks 45,4% surnud puudel. Puu suremise põhjuste mudelist selgus, et suhtelise diameetri suurenedes suureneb puul tõenäosus surra putukakahjustuse, tuule või seente ja haiguste tõttu. Samas, mida väiksem on puu suhteline diameeter, seda tõenäolisem on, et puu sureb puudevahelise konkurentsi tõttu.

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