SILVA FENNICA

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Models for integrating and identifying the effect of senescence on individual tree survival probability for Norway spruce

Highlights

- The effect of senescence was integrated into an individual tree survival model.
- The best model showed good fit for managed, unmanaged and old-growth stands.
- The probability for a large tree to survive decreased with increasing stand age.
- The best performed model included an interaction term between stem diameter and stand age and also stand age as a separate independent variable.

Abstract

Ageing and competition reduce trees' ability to capture resources, which predisposes them to death. In this study, the effect of senescence on the survival probability of Norway spruce (*Picea abies* (L.) Karst.) was analysed by fitting alternative survival probability models. Different model formulations were compared in the dataset, which comprised managed and unmanaged plots in long-term forest experiments in Finland and Norway, as well as old-growth stands in Finland. Stand total age ranged from 19 to 290 years. Two models were formulated without an age variable, such that the negative coefficient for the squared stem diameter described a decreasing survival probability for the largest trees. One of the models included stand age as a separate independent variable, and three models included an interaction term between stem diameter and stand age. According to the model including stand age and its interaction with stem diameter, the survival probability curves could intersect each other in stands with a similar structure but a different mean age. Models that did not include stand age underestimated the survival rate of the largest trees in the managed stands and overestimated their survival rate in the old-growth stands. Models that included stand age produced more plausible predictions, especially for the largest trees. The results supported the hypothesis that the stand age and senescence of trees decreases the survival probability of trees, and that the ageing effect improves survival probability models for Norway spruce.

1   Introduction

Tree mortality is a result of complex gradual processes involving multiple interacting biotic and abiotic factors (Manion 1991). According to Vanclay (1994), natural mortality can be divided into regular mortality and catastrophic mortality. Regular mortality includes tree death arising from ageing, competition, and normal incidences of pests, disease, drought, storms, etc. Catastrophic mortality refers to wildfires, flooding, severe storms, large-scale disease, and insect outbreaks. Regular mortality plays a key role in shaping stand dynamics, structure, and composition. Regular mortality is frequently initiated by the competition-related degradation of tree vigour, although the actual mortality event may be triggered by multiple secondary causes. Indeed, the between-tree competition has been quantified as the most common reason for tree mortality in boreal forest ecosystems (Yli-Kojola 2005; Laarmann et al. 2009; Sims et al. 2014). Understanding and predicting how between-tree competition influences mortality is therefore a key challenge in forest ecology and stand management.

Tree mortality is a natural demographic process in a forest stand, and trees of different sizes and ages tend to die for different reasons. In general, smaller trees are more likely to die because of between-tree competition, whereas increasing the relative size exposes trees to insect and wind damage (Laarmann et al. 2009; Sims et al. 2014). Large trees may also suffer from ageing or size-induced physiological limitations, which reduces their ability to acquire limited resources, including water, nutrients, and photosynthetically active radiation (Ryan and Yoder 1997; Ruiz-Benito et al. 2013; Young et al. 2017). Nilsson et al. (2003) found that about 10% of all standing trunks in European temperate and boreal old-growth forests were dead, but the proportion increased for the largest trees. Accordingly, previous studies have shown that the mortality rate increased in the largest diameter classes for several spruce species (Monserud and Sterba 1999; Yao et al. 2001; Vieilledent et al. 2009). Consequently, tree senescence has been attributed as one of the main factors in the death of larger trees. However, it remains unclear how age and size influence the mortality rates of trees.

Forest models typically perform poorly in old-growth forests, where mortality processes play a large role. This calls for better information concerning how tree size and age influence mortality rates and shape the size distribution of trees in a stand. Ideally, models should be able to represent differences of size distribution, and their development in managed and natural stands. There is evidence that diameter distributions and between-tree competition in old-growth forests differ from those in managed forests (Kuuluvainen et al. 1996; Siitonen et al. 2000; Siipilehto and Siitonen 2004). In old-growth stands, the inverse J-shaped distribution has been regarded as a stable climax state due to a constant regeneration and mortality rate (Hett and Loucks 1976; Tyrell and Crow 1994). However, in Sweden, Linder (1998) showed that diameter distribution in an old-growth stand could change from an inverse J-shaped to a bell-shaped distribution if no major disturbances occurred, apparently due to shading by the dominant canopy and the consequent poor growing conditions for seedlings. Accordingly, in a Finnish old-growth stand, the diameter distribution was wide, and trees were evenly distributed between the diameter classes (Kuuluvainen et al. 1996). In addition, the spatial distribution of trees was random, whereas in managed stands, spatial distribution was regular (Kuuluvainen et al. 1996). Understanding how diameter distributions are shaped by tree age and size is important for predicting the development of old-growth stands.

The aim of this study was to provide improved knowledge and models about the demographic variability of tree mortality, and the mechanisms involved in this process. We developed tree-level survival models for Norway spruce (*Picea abies* (L.) Karst.) for managed, unmanaged, and old-growth stands based on a large set of permanently monitored experimental stands in Finland and Norway. As the mortality rate has increased among large trees (Monserud and Sterba 1999; Yao

et al. 2001), we hypothesised that senescence promoted tree mortality especially in the largest diameter classes. As senescence is related to growth history of a tree and tree structure, senescence cannot be associated with the size of the individual trees alone. The hypothesis was tested by using mixed effects logistic models containing the effects of stand age and tree size, their interaction, and the competition status of trees.

2 Material and methods

2.1 Datasets for old-growth, unmanaged and managed stands

The dataset for old-growth stands included 57 Norway spruce-dominated permanent plots in Southern and Central Finland (Table 1). The plot size (0.09–0.25 ha) depended on the stand density (Isomäki et al. 1998). The sites were either herb-rich (OMT) or mesic heath (MT) sites (Cajander 1925). The plots were established between 1991 and 1999 on stands that were considered unmanaged or nearly unmanaged. The stand age (the mean total age of the dominant cohort) ranged from 100 to 290 years. All the trees larger than 5 cm in diameter at breast height were measured on each plot. The second measurements of the plots were made in 2006 or 2007. The measurement period length therefore ranged from 7 to 15 years. The plots were dominated by 82% Norway spruce, but 9% Scots pine (*Pinus sylvestris* L.), 4% silver birch (*Betula pendula* Roth), 3% downy birch (*Betula pubescens* Ehrh.), and 3% aspen (*Populus tremula* L.) were present at the time of the plots' establishment. The number of surviving and dead trees was 5559 and 848 respectively. The dataset is presented in detail in Peltoniemi and Mäkipää (2011). They only included dead standing trees (646) in their analysis, but we included all dead trees, irrespective of their type, snag, or log. The proportion of dead standing and dead fallen trees from the total number of trees was 7.7% and 2.4% respectively. The number of large (dbh ≥ 40 cm) living and dead spruces was 100 and 14 respectively.

The dataset for managed forests consisted of 21 thinning experiments (stands) for Norway spruce in southern Finland (HARKAS), described in detail in Mäkinen and Isomäki (2004). The stands were even-aged almost pure-planted Norway spruce stands on mineral soil. The experimental design was a randomised block design with 1 to 3 replicates for each thinning intensity. The average area of the plots was 0.12 ha (range 0.05–0.25 ha). Treatment schedules covered unthinned control plots and thinnings from below, with intensities ranging from low intensity thinning (6–15% removal of stand basal area) up to 54% removal of stand basal area, an average of 21%. The sites were mostly herb-rich (OMT). However, some mesic heath (MT) sites were also included (Cajander 1925). The stand age ranged from 27 to 88 years (Table 1). The measurement period ranged from 3 to 14 years, and the maximum number of successive periods was nine. The proportion of tree species at the time of the experiments' establishment was 97.5%, 0.6%, 0.5%, and 1.3% for Norway spruce, Scots pine, birch, and other broadleaved species respectively. The number of surviving and dead tree observations was 84 160 and 3171 respectively.

The Norwegian dataset represented the unmanaged development of naturally regenerated almost pure spruce stands with varying initial age and density. Stands were located in the whole country. The modelling data consisted of 22 stands. Each stand included one study plot, except one stand, which included three plots. The plot size varied between 0.07–0.11 ha. About 40% of the plots were thinned at the establishment for varying initial density, which was 1670–6336 ha^{-1} after treatment. The initial density in unthinned stands ranged from 770 to 9060 trees ha^{-1}. The stand basal area had a large variation (8.3–64.7 m^2 ha^{-1}). Also age variation was large, from 19 to 148 years (Table 1). The number of successive measurements ranged between three and 13. The

Table 1. The mean tree and stand characteristics of the Norway spruce survival modelling datasets, including the Finnish old-growth stands (number of trees, n = 6407), the Finnish thinning experiment (HARKAS, n = 87331), and the Norwegian experiment (n = 48738).

Dataset	Old-growth stands			Finnish experiment			Norwegian experiment		
Variable	mean	min	max	mean	min	max	mean	min	max
diameter, cm	21.0	4.3	76.0	17.9	0.6	52.5	10.9	0.9	46.0
height, m	18.0	3.0	34.1	17.1	1.4	35.0	10.6	1.5	33.6
BAL, m^2 ha^{-1}	27.2	0.0	51.5	19.7	0.0	58.8	23.8	0.0	64.7
Age, years	159	100	290	50	27	88	42	19	148
BA, m^2 ha^{-1}	38.1	18.3	51.6	32.1	9.4	58.9	35.4	8.3	64.7
N, stems ha^{-1}	959	340	1694	1420	188	3976	4130	715	9058
DG, cm	29.1	20.1	39.6	19.5	8.9	40.3	13.3	4.7	32.7
DQ, cm	23.0	17.7	29.7	18.3	8.0	39.3	11.5	4.1	28.3
tree survival	0.868	0	1	0.964	0	1	0.894	0	1
period length, yrs	10.8	7	15	6.1	3	14	5.3	3	10
No. of periods	1.0	1	1	3.0	1	9	3.7	1	12

BAL denotes basal-area-in-larger trees; BA is total stand basal area; N is total stem number; DG is basal area weighted mean diameter; DQ is quadratic mean diameter; tree survival: 1 = surviving, 0 = death.

measurement period was typically five years but ranged from three to 10 years. The proportion of pine and broadleaved species at the time of the experiments' establishment was less than 1%. The number of surviving and dead trees was 43 559 and 5179 respectively.

The relative number of dead trees in the Norwegian dataset (10.6%) was close to that of the Finnish old-growth stands (13.2%), and almost threefold compared with the Finnish thinning experiments (3.8%). However, in the unmanaged control plots of the Finnish thinning experiments, mortality was 6.9%. The proportion of the arithmetic mean diameter and basal area weighted mean diameter (D/DG) characterises the shape of the diameter distribution (Hynynen et al. 2019; Bianchi et al. 2020). There was a continuum in the average proportion of D/DG, from 0.7 in the old-growth stands (wide and skewed distributions) to 0.8 in the Norwegian experiment (unmanaged stands), and finally 0.9 in the Finnish thinning experiments, representing relatively narrow bell-shaped distributions.

2.2 Logistic model for tree-level survival

2.2.1 Model formulation

Hamilton (1974) and Monserud (1976) introduced a logistic model for individual tree mortality. Logistic models have since been widely used, not only for tree-level mortality but for modelling stand-level mortality (Fridman and Ståhl 2001; Eid and Øyen 2003). We applied the logistic regression for the binary survival variable, in which 0 and 1 indicated dying and surviving trees between the measurement events respectively. The common structure of the logistic model is as follows (Hosmer and Lemeshow 1989):

$$F(\mathbf{X}, b) = 1/\left(1 + \exp(-\mathbf{X}'b)\right), \tag{1}$$

where $\mathbf{X}'b$ is a linear model: the transposed vector of explaining variables X and the vector of estimated parameters b. Because the length of the measurement periods varied, we applied the length of the period (L) as a power in the equation (Monserud 1976; Yao et al. 2001; Yang and Huang 2013):

$$F(\mathbf{X}, b) = \left(1/\left(1 + \exp(-\mathbf{X}'b)\right)\right)^{L}. \tag{2}$$

2.2.2 Random effect in the model

The random effect logistic regression was first presented by Jutras et al. (2003) for individual tree mortality. Accordingly, we used the stand-level random effect to describe stand-level dynamics instead of the average change over the whole dataset. In the HARKAS dataset, the stand level consisted of blocks and plots within blocks. The observed response was represented by y_{ij}, which describes the status of the i:th tree of the j:th stand at the end of the measurement period as a binary phenomenon (0 = dead, 1 = surviving). The distribution of the response variable was $y_{ij} \sim \mathrm{Bin}(\pi_{ij}, 1)$, and the two-level model with a random effect can be written as:

$$\pi_{ij} = f\left(\mathbf{X}'_{ij}b + u_j\right),$$
(3)

where π_{ij} is the expectation of the response for the i:th tree in stand j, vector $\mathbf{X}'_{ij}$ is the transposed vector of independent fixed variables, b is the vector of the estimated parameters, and u_j represents the random departure for the j:th stand with $u \sim N(0, s_u^2)$). Tree-level variance was assumed to be 1 and it was tested for over- and under-dispersion (Goldstein 1995).

The mixed effect logistic model was fitted using the NLMixed procedure and the default quasi-Newton optimisation in SAS (version 9.4, SAS Institute Inc. 2017). The NLMixed procedure enables one random effect, which was selected as a stand-level effect. The initial parameter values were selected from the preliminary results, without a random effect, using the Proc Logistic in SAS.

2.2.3 Model formulation for tree survival

Relatively simple mixed effects logistic models were fitted to ensure logical model behaviour (Jutras et al. 2003; Monserud and Sterba 2004; Monserud et al. 2005). We focused on the easily interpretable variables, namely stem diameter (d) and its derived variables (Hamilton 1986; Eid and Tuhus 2001; Jutras et al. 2003; Vieilledent et al. 2009). The transformations tested were $1/d$, $\sqrt{d}$, $\ln(d)$, and d^2. The squared diameter (d^2) enables the increasing mortality rate for the largest trees, as proposed by Monserud and Sterba (1999). The competition between trees was described with basal-area-in-larger trees (BAL) presented by Wykoff (1990). Because Peltoniemi and Mäkipää (2011) found that the BAL alone was not appropriate for explaining tree mortality in old-growth spruce stands, we tested different transformations of BAL, e.g., BAL/d, $BAL/\sqrt{d}$, and $\sqrt{BAL}$ (Pukkala et al. 2009).

We adopted the model structure suggested by Monserud and Sterba (1999) as our starting point as follows:

$$\left(\mathbf{X}'_{ij}b\right) = b_0 + b_1\left(1/d\right) + b_2 BAL + b_3 d + b_4 d^2 + b_5\, Thinning,$$
(4)

where b_0 to b_5 are parameters. Monserud and Sterba (1999) included crown ratio (CR) in their model, but this was not available in our datasets. Because CR is related to the stand management regime, we applied a thinning dummy variable ($Thinning$: 0 = unthinned, 1 = thinned). We tested two periods since thinning, i.e. 1–5 years ($Thinn5$) and 6–10 years ($Thinn6\_10$) since thinning. We also combined BAL and $1/\sqrt{d}$ as $BAL/\sqrt{d}$, because this was a superior transformation. Furthermore, this combined variable turned the untransformed diameter d into an insignificant predictor variable.

According to our hypothesis, we tested the effect of age on tree survival. Because the age of individual trees was unavailable, we instead used the average age of the dominant trees. We added stand age ($Age/100$) as a predictor, as well as its interaction with d^2. Power 2 (d^2) may not be the best option for describing the mortality rate of large trees. In an alternative model, we searched

for the power for *d* (*p1*), as well as power for stand age interaction (*p2*). The age divided by 100 (*Age*/100) was used to avoid extremely high values for the predictor variable ($d^2 \times Age$). We tried adding b_3 (*Age*/100) to Eq. 6 as in Eq. 8, but it was not significant.

The alternative structures of the fixed effects for comparisons were as follows:

$$\left(\mathbf{X}'_{ij} b \right) = b_0 + b_1 \left(BAL / \sqrt{d} \right) + b_2 d + b_3 d^2 + b_5 \, Thinning \, ; \tag{5}$$

$$\left(\mathbf{X}'_{ij} b \right) = b_0 + b_1 \left(BAL / \sqrt{d} \right) + b_3 d^2 \left(Age / 100 \right) + b_5 \, Thinning \, ; \tag{6}$$

$$\left(\mathbf{X}'_{ij} b \right) = b_0 + b_1 \left(BAL / \sqrt{d} \right) + b_3 d^{\,p1} \left(Age / 100 \right)^{p2} + b_5 \, Thinning \, ; \tag{7}$$

$$\left(\mathbf{X}'_{ij} b \right) = b_0 + b_1 \left(BAL / \sqrt{d} \right) + b_3 d^{\,p1} \left(Age / 100 \right)^{p2} + b_4 \left(Age / 100 \right) + b_5 \, Thinning \, . \tag{8}$$

2.2.4 Model evaluation

The models were compared with each other by fit statistics, –2 log-likelihood, Akaikes's information criteria (AIC), and Bayesian information criteria (BIC). The smaller the criterion, the better the model fit and the smaller the model rank (rank 1 for the best). The models' behaviour were also evaluated with survival curves predicted for the following 5-year period. Stand characteristics for this evaluation were taken as the averages of the old-growth forest (number of stems 1010 ha^{-1}, stand basal area 38 m^2 ha^{-1}, and basal area weighted mean diameter 30 cm). The Weibull diameter distribution (Siipilehto and Mehtätalo 2013) was recovered based on these average characteristics. Thereafter, trees were systematically sampled for the 5-cm diameter classes, and *BAL* was calculated for them (Fig. 1). When evaluating model behaviour (Figs. 2 and 3), we used the same sample trees (*d* and *BAL*) but a varying stand age (100, 150, 200, and 250 years).
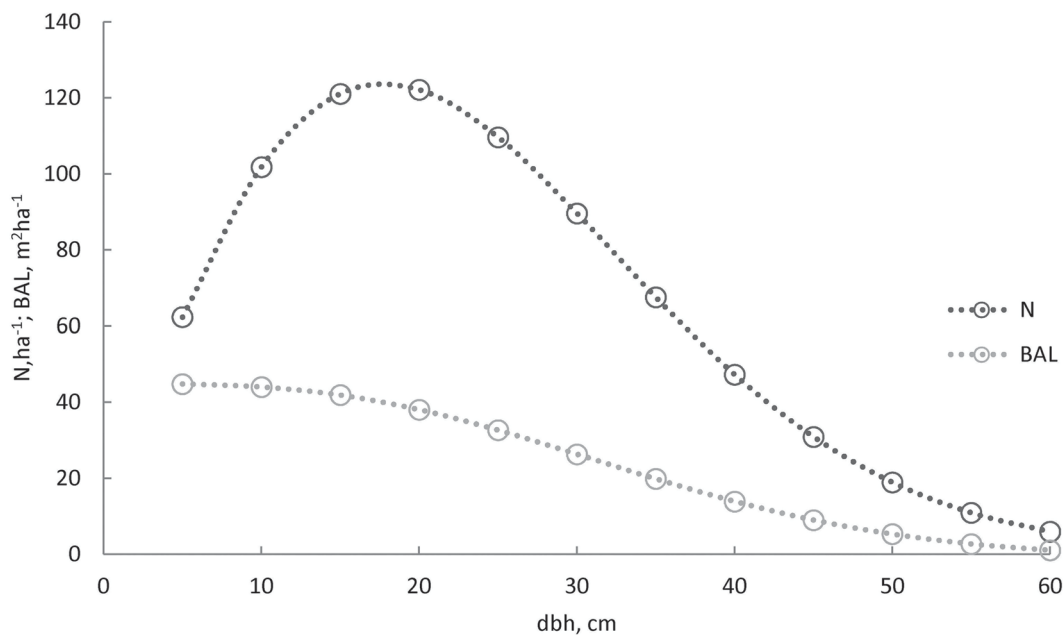

Fig. 1. The diameter distribution for the Norway spruce survival model evaluation was calculated using the model by Siipilehto and Mehtätalo (2013), based on the average characteristics of the old-growth stand (stand basal area 38 m^2 ha^{-1}, number of stems 1010 ha^{-1}, basal area weighted mean diameter 30 cm, and age 150 years). Trees (○) were sampled for 5-cm classes, and basal-area-in-larger trees (*BAL*) was calculated for the sampled trees.

The model differences were illustrated using bar plots for the observed and predicted survival rates with respect to stem diameter (Monserud and Sterba 1999). Eq. 5 without stand age and the best performing alternative model with age variable were additionally evaluated using the datasets for the managed (HARKAS) and unmanaged old-growth stands (old-growth dataset). The latter evaluation was made to test the hypothesis that senescence promoted tree mortality especially in the largest diameter classes.

3 Results

3.1 Alternative individual tree survival models

The initial forms of the alternative models for tree survival are given in Eqs. 4–8. All the variables shown in Tables 2 and 3 were statistically highly significant. The best performing powers $p1$ and $p2$ differed between Eqs. 7 and 8. In Eq. 7, powers $p1$ and $p2$ were 1.8 and 0.8, while in Eq. 8, they were 1.4 and 0.9 respectively (Table 3). The dummy variable for the thinnings carried out six to 10 years ago (*Thinn6_10*) was statistically significant, but the dummy variable for the first five years following thinnings (*Thinn5*) was not.

Models without stand age (Eqs. 4 and 5) had considerably poorer fit statistics (i.e. higher –2 log-likelihood, AIC, and BIC), and they therefore had a lower rank (ranks 5 and 4 respectively) (Table 2) compared with the models that included the stand age (Table 3). Eq. 6 (rank 3) and Eq. 7 (rank 2) had almost the same fit statistics (Table 3). Eq. 8, which included the interaction term between d and *Age*, and the independent effect *Age* in addition to the powers $p1$ and $p2$, was ranked the best model (Table 3). All the estimated variances (s^2u 0.69–0.76) showed slight under-dispersion.

We also tested dummy variables separating the different subsets of the data, such as *Naturalness* for the Finnish old-growth forests and *Norway* dummy for the Norwegian experiments. They were not statistically significant (P=0.65 and 0.98 respectively), denoting that survival behaved similarly in terms of the stand age and competition status of trees in the different datasets.

Table 2. The estimated logistic models for Norway spruce survival without stand age (Eq. 4, Eq. 5).

Variable	Eq. 4 estimate	Eq. 4 std	Eq. 4 t value	Eq. 5 estimate	Eq. 5 std	Eq. 5 t value
Intercept	5.4896	0.1413	38.8	7.1545	0.139	51.5
$1/d$	–2.1721	0.2199	–9.88			
BAL	–0.09364	0.0014	–66.4			
BAL/√(d)				–0.2844	0.0042	–67.2
d	0.2693	0.0080	33.8	0.03613	0.0075	4.84
d^2	–0.00673	0.0002	–36.6	–0.00206	0.0002	–10.6
Thinn6_10	0.3231	0.0826	3.91	0.2927	0.0826	3.54
Variance	0.6908	0.1173	5.89	0.7403	0.1238	5.98
–2 log-likelihood	39 794			39 384		
AIC	39 808			39 396		
BIC	39 825			39 410		
Rank	5			4		

d; breast height diameter (cm) of a tree; *BAL*; basal area (m^2 ha^{-1}) of trees larger than the subject tree; *Thinn6_10*; dummy for thinnings carried out between 6 and 10 years ago (0 = unthinned, 1 = thinned). Rank; the order of fit statistics from the smallest (1 = the best fit) to the highest (5 = the worst fit) for all models.

Table 3. The estimated logistic models for Norway spruce survival with stand age (Eq. 6, Eq. 7, and Eq. 8).

variable	Eq. 6			Eq. 7			Eq. 8		
	estimate	std	t value	estimate	std	t value	estimate	std	t value
intercept	7.4445	0.1092	68.2	7.5515	0.1121	67.4	7.327	0.146	50.2
$BAL/\sqrt{(d)}$	–0.2856	0.0031	–91.2	–0.2898	0.0032	–89.1	–0.294	0.0034	–86.1
$d^2(Age/100)$	–0.00098	0.00006	–16.7						
$d^{1.8}(Age/100)^{0.8}$				–0.00234	0.0001	–16.2			
$d^{1.4}(Age/100)^{0.9}$							–0.01079	0.0007	–15.5
$Age/100$							0.4124	0.1158	3.56
$Thinn6\_10$	0.2812	0.0826	3.41	0.2755	0.0826	3.34	0.2796	0.0826	3.38
Variance	0.7543	0.1263	5.97	0.7621	0.1275	5.98	0.7154	0.12	5.96
–2 log-likelihood	39346			39342			39335		
AIC	39356			39352			39347		
BIC	39368			39364			39362		
Rank	3			2			1		

d; breast height diameter (cm) of a tree; BAL; basal area (m^2 ha^{-1}) of trees larger than the subject tree; $Thinn6\_10$; dummy for thinnings carried out between 6 and 10 years ago (0 = unthinned, 1 = thinned). Rank; the order of fit statistics from the smallest (1 = the best fit) to the highest (5 = the worst fit) for all models.

3.2 Evaluation results

For a wide variety of diameters, the survival probability was quite similar, despite the model (Figs. 2 and 3). Differences between models were visible in large trees. The survival probability of the largest trees (d = 55 cm) was 2% when using Eq. 4, but as high as 75% when using Eq. 5 (Fig. 2). For models including stand age, the survival probability was also very low (3%) according to Eq. 6 (Fig. 3), but considerably higher (19%) according to Eq. 7. The squared stem diameter (d^2) in Eq. 6 resulted in a more rapid decrease in the survival probability for large trees than $d^{1.8}$ in Eq. 7 (Fig. 3). The most plausible behaviour was provided by Eqs. 7 and 8 (Fig. 3). The difference
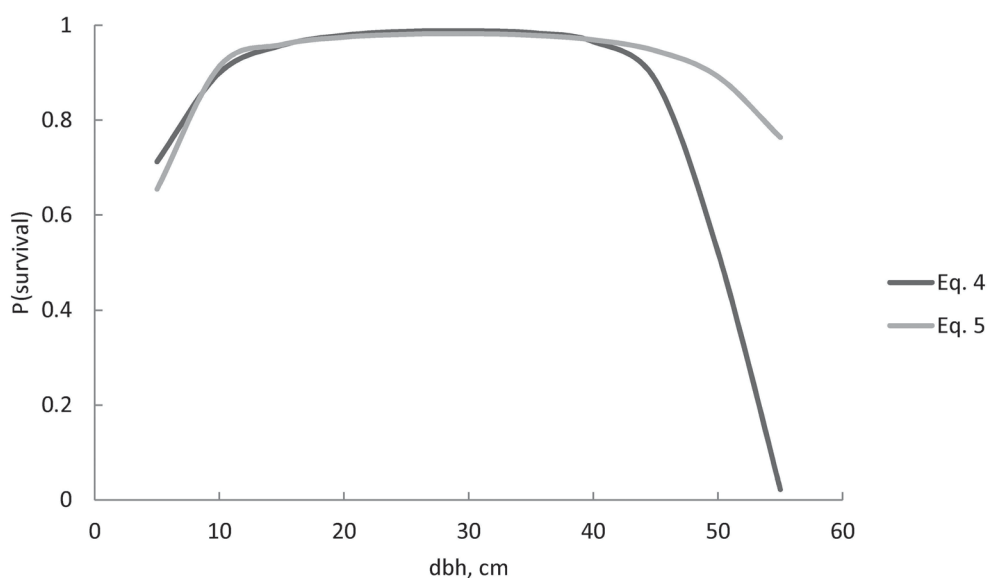

Fig. 2. Predicted Norway spruce survival probability (P) for the following 5-year period, using Eq. 4 and Eq. 5. Neither model included stand age as a predictor variable.
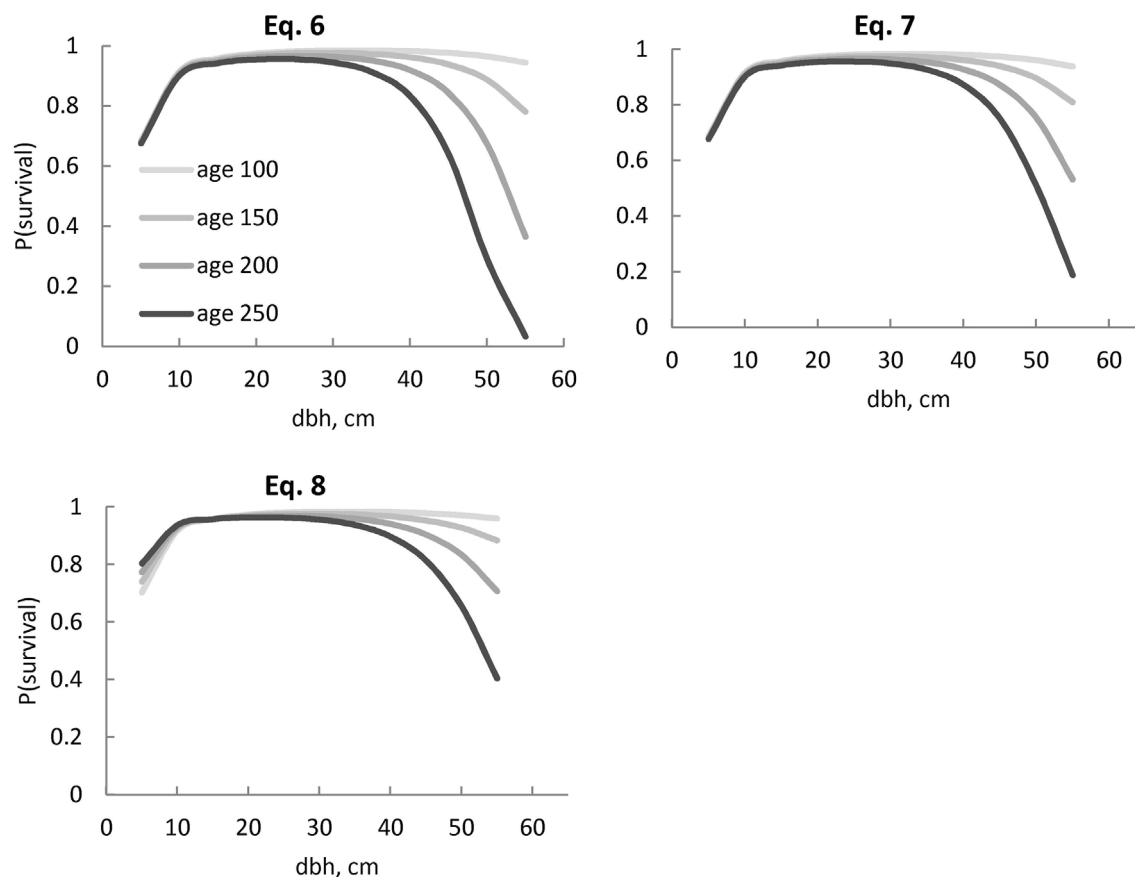
Fig. 3. Predicted Norway spruce survival probability (P) for the following 5-year period with the models (Eqs. 6–8), including interaction between age and stem diameter. The stand age ranged from 100 years (age 100) to 250 years (age 250). Eq. 8 also included stand age per se as a predictor variable, allowing intersecting curves.

between these two models was that the increasing age always decreased the survival probability for all size classes in Eq. 7, but in Eq. 8, the survival probability for the smaller trees was higher in an older stand compared with a younger stand with a similar diameter distribution, i.e. the survival probability curves of different stand ages crossed each other (Fig. 3). In a 100-year-old stand, the largest trees had a high survival probability (94–96%) according to Eqs. 7 and 8 (Fig. 3), but the probability decreased with increasing stand age. In a 250-year-old stand, the survival probability for a 55-cm tree increased from 19% to 40% for the following 5-year period, using Eq. 7 or 8 respectively. The powers $p1 = 1.4$ and $p2 = 0.9$ in Eq. 8 therefore reduced the effect of increasing stem diameter and age on the survival probability more than powers $p1 = 1.8$ and $p2 = 0.8$ in Eq. 7.

All the models predicted the survival probability well for small and middle-sized trees, but they tended to underestimate survival probability for the largest trees (Fig. 4). This was partly because the survival probability in the 45–49 cm diameter class was significantly higher than in the previous 40–44 cm class. However, the number of observations was low in diameter classes above 40 cm. The differences between the survival probabilities in Eqs. 6 and 7 were small in different diameter classes (Fig. 4), as were the differences in their fit statistics (Table 3). The least underestimation was provided by Eq. 8 (Fig. 4), as well as the best statistical fit (Table 3).

Eq. 5 without an age variable provided a reasonable fit in the whole dataset (Fig. 4). However, due to the formulation of Eq. 5, it could provide only an average decrease in the survival probability for large trees without a senescence effect. It was therefore not surprising that Eq. 8 fitted the subsets of the data which had a large difference in stand age much better (Fig. 5). On the
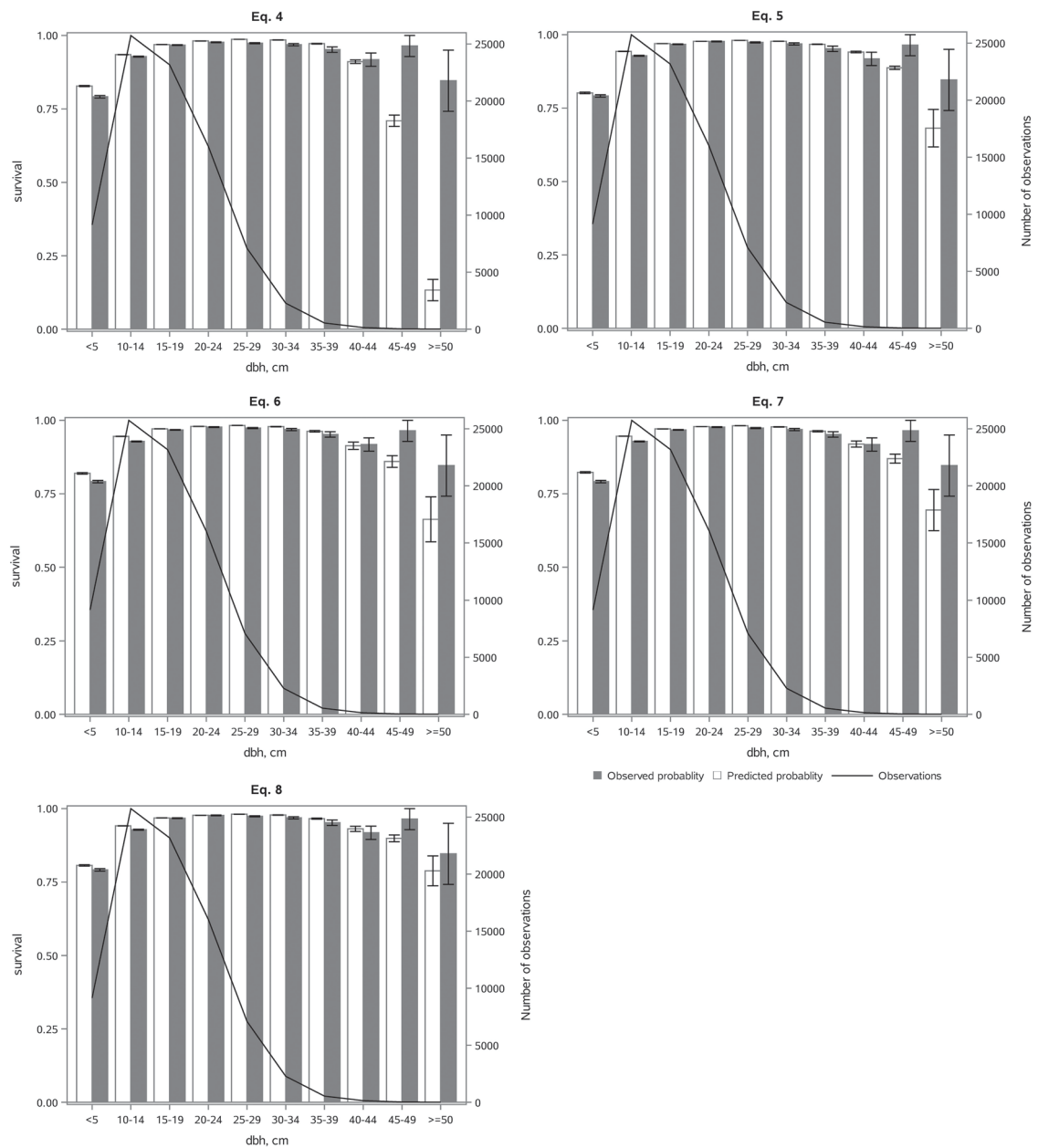
Fig. 4. The observed and predicted Norway spruce survival rate (with standard errors) by diameter classes (*dbh*), and the number of observations by diameter class, using the alternative models (Eqs. 4–8) in the whole dataset.

managed HARKAS plots, there was hardly any mortality in the largest diameter classes. On the other hand, the survival rate in the smallest diameter classes was higher in the old-growth stands than on the managed HARKAS plots. Eq. 8 performed well in both subsets of the data (Fig. 5). However, no significant differences between the performance of Eqs. 5 and 8 were found in the Norwegian dataset, which had a maximum age of 148 years.
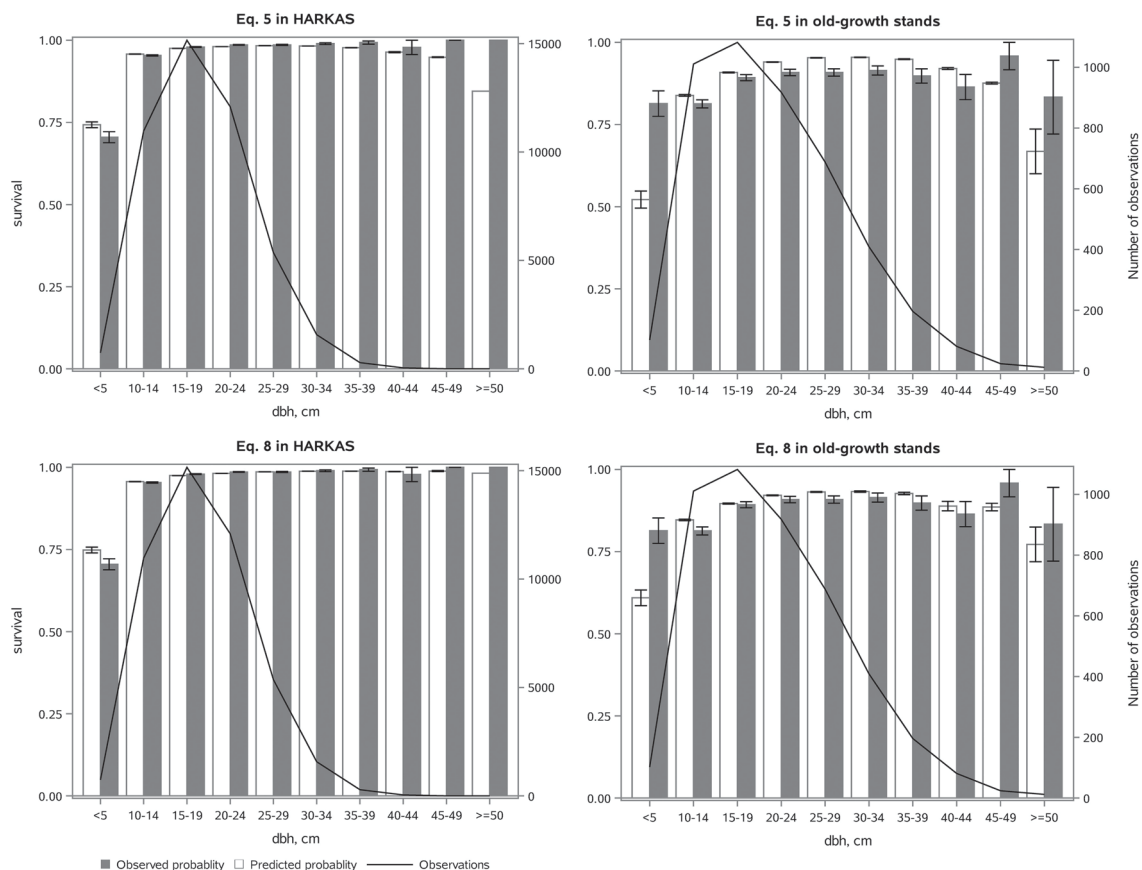
Fig. 5. The observed and predicted Norway spruce survival rate (with standard errors) by diameter class (*dbh*) estimated with Eq. 5, without stand age, and Eq. 8, which included the effect of age interaction with stem diameter on the tree survival, as well as the number of observations in each diameter class. The subfigures represent the HARKAS dataset, comprising both managed and unmanaged plots, and the old-growth forest stand dataset.

4   Discussion

The results of this study show that the senescence effect should be taken into account when modelling tree mortality for Norway spruce. The senescence effect is especially important when dealing with a combination of managed and unmanaged stands, in which trees of a certain size may differ greatly in age, depending on the past development of a stand (Henttonen et al. 2019). Indeed, the largest trees may be vigorous if their large diameter is the result of intensive thinnings, not old age.

In most datasets, the age of individual trees is typically unknown. However, stand age as the average age of dominant trees provides an effective way to account for the effect of senescence on tree survival. Although the study's forests have been unmanaged for a long period, it is likely that the dominant individuals were regenerated after a severe natural disturbance or human activity (e.g. a slash-and-burn cultivation harvest). We therefore do not believe the use of stand age characterising tree ages to be a problem, especially as the models focus on depicting the mortality of the largest and oldest trees. Smaller trees in unmanaged stands, on the other hand, are less affected by stand age, which is a less relevant variable for them in the model.

Monserud and Sterba (1999) used a squared diameter (d^2) in their model for Norway spruce in Austria, as did Yao et al. (2001) and Vieilledent et al. (2009) in their models for conifer and broadleaved species in Canada and Switzerland. Actually, the original model by Monserud and

Sterba (1999) did not predict such a sudden decrease in survival rate for the largest trees as Eq. 4 in our data. Due to the large variation in the mean age in our dataset, we used the interaction of stem diameter and stand age to account for the age-dependent increasing mortality rate of the largest trees. During model development, the interaction $d^2 \times (Age/100)$ proved to have a marked effect on predicted survival rates. We therefore looked for alternative powers to improve model fit and behaviour (d^{p1} and $(Age/100)^{p2}$). This resulted in the exponents 1.8 and 1.4 for stem diameter, and 0.8 and 0.9 for age, i.e. as $d^2 \times (Age/100)$, $d^{1.8} \times (Age/100)^{0.8}$, and finally, $d^{1.4} \times (Age/100)^{0.9}$. Because the exponents, $p1$ and $p2$, were lower than the corresponding powers in Eq. 6, they enabled higher survival rates for the largest trees in the old stands when using Eq. 7, and especially when using Eq. 8.

In Eq. 8, which had the best fit, the survival probability curves intersected each other. The survival probability of the smaller and intermediate trees was slightly higher in the older stands than younger stands with the same stand structure. This may be the result of increasing spacing between trees and declining resource use efficiency later in stand development (Binkley 2004). Decreasing the water and nutrient use efficiency of the largest trees (Ryan and Yoder 1997; Tyree 2003) may reduce their level of dominance in an older stand, and they may not suppress smaller trees as much as more vigorous trees of a similar size in younger stands. It is also likely that these stands have mortality events that create space for smaller trees.

The stand development classes in our dataset range from young stand some years after canopy closure to old-growth forests. The average and maximum ages of the Finnish old-growth stands were 159 and 290 years respectively. Kuuluvainen et al. (2002) found that in an old-growth forest in Russian Karelia close to Finland the oldest Norway spruce was 286 years old, while the oldest pine was as much as 525 years old. Slightly older 325-year-old spruce trees have been found in old-growth forests in Sweden (Steijlen and Zackrisson 1986; Hofgaard 1993). Norway spruce larger than 50 cm are rarely found in boreal old-growth forests in the Nordic countries (Linder 1998; Siitonen et al. 2000; Kuuluvainen et al. 2002; Rouvinen and Kuuluvainen 2005). This study's dataset can therefore be regarded as covering the whole age and diameter range from young to old-growth stands (Henttonen et al. 2020), but not necessarily as a representative sample, because the locations of the experiments and plots were subjectively selected. We found that tree survival did not differ between the used datasets (HARKAS, the Norwegian dataset, and old-growth stands). We are therefore confident that the best fitting models are capable of predicting the survival probability for a wide range of management regimes (old-growth, unmanaged, and managed Norway spruce-dominated stands) and geographical locations.

Thinning plays a contradictory role in tree survival. On the one hand, thinning decreases between-tree competition, thereby increasing survival probability. Moreover, diameter distribution changes due to thinning, which results in changes in the basal area of larger trees (BAL). The effect of thinning on tree survival is therefore partly accounted for by using the BAL variable. On the other hand, before adapting to new conditions after thinning, trees are exposed to wind and snow damage (Valinger and Pettersson 1996; Nykänen et al. 1997; Suvanto et al. 2019). Probably due to this two-sided effect, the first five years following thinning showed no significance, whereas six to 10 years since the last thinning significantly increased survival probability. The additional effect of thinning accounts for the removal of the weakest trees with supressed tree crowns.

In the initial model adopted from Monserud and Sterba (1999), crown ratio was used to indicate tree vigour, i.e. survival probability. Unfortunately, crown size was not available in our datasets. However, it is probable that the variables for thinnings at least partly account for the relationship between the crown ratio and stand management regime. Moreover, tree vigour can be characterised by its growth rate (Monserud 1976; Yao et al. 2001; Yang and Huang 2013). However, it is laborious to measure, and the growth rate is therefore rarely available when applying the

models, especially in datasets from temporary plots. Instead, we used other tree-level characteristics such as tree dbh and *BAL* to describe tree vigour and between-tree competition within a stand.

In conclusion, stand age appeared to play a role in the tree-level regular mortality of Norway spruce. Senescence should therefore be considered when modelling tree survival. Although our study was restricted to Norway spruce, the effect of senescence probably exists in other tree species too (Yao et al. 2001). In future studies, our intention is therefore to test if the relationship between senescence and survival probability is similar for less shade-tolerant tree species such as Scots pine and birch. Because the best model (Eq. 8) seems to perform well regarding longer rotations, we recommend it to be implemented in the decision-support tools in the Nordic countries.

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