Survival time and mortality rate of regeneration in the deep shade of a primeval beech forest

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Abstract

Low mortality rates and slow growth differentiate shade-tolerant from shade-intolerant species and define the survival strategy of juvenile trees growing in deep shade. While radial stem growth has been widely used to explain mortality in juvenile trees, the leaf area ratio (LAR), known to be a key component of shade tolerance, has been neglected so far. We assessed the effects of LAR, radial stem growth and tree height on survival time and the age-specific mortality rate of juvenile *Fagus sylvatica* L. (European beech), *Acer pseudoplatanus* L. (sycamore maple) and *Acer platanoides* L. (Norway maple) in a primeval beech forest (Ukraine). Aboveground and belowground biomass and radial stem growth were analysed for 289 living and 179 dead seedlings and saplings. Compared with the other species, *F. sylvatica* featured higher LAR, slower growth and a lower mortality rate. The average survival time of *F. sylvatica* juveniles (72 years) allows it to reach the canopy more often than its competitors in forests with low canopy turnover rate. In contrast, a combination of lower LAR, higher growth rate and higher age-specific mortality rate of the two *Acer* species resulted in their shorter survival times and thus render their presence in the canopy a rare event. Overall, this study suggests that shade tolerance, commonly defined as a relationship between sapling mortality and growth, can alternatively be formulated as a relationship between survival time and the interplay of growth and LAR.

Keywords Acer · Dominance · Fagus · LAR · Mortality rate · Regeneration · Shade tolerance · Survival time

Introduction

The success of forest regeneration in reaching the canopy is related to species-specific patterns of radial and height growth, with shade-tolerant species growing better in the shade than shade-intolerant ones and vice versa (Givnish 1988; Popma and Bongers 1988). The better performance of shade-tolerant species under low-light conditions has been attributed to a more efficient use of light due to a larger leaf area per plant mass (leaf area ratio = LAR), a larger and deeper crown, and faster growth (Bazzaz 1979; Givnish 1988). The trade-off between high-light and low-light

growth, i.e. shade-tolerant species grow faster than shade-intolerant species in low-light and vice versa under high-light conditions, has been widely viewed as the general explanation of shade tolerance (Spurr and Barnes 1980; Thomas and Bazzaz 1999).

More recently, it has been argued that survival is more important than growth in determining regeneration success at low light levels (Canham et al. 1999; Kitajima 1994; Kobe et al. 1995; Veneklaas and Poorter 1998). Shade-tolerant species do not necessarily grow faster than shade-intolerant species at low-light levels, but they may have a higher survival rate (Kitajima 1994; Kobe et al. 1995; Kobe and Coates 1997). For a long time, the high survivorship of shade-tolerant species under low-light conditions has been attributed to efficient carbon allocation and storage, acting as a buffer against stress (Canham et al. 1999; Kobe 1997; Reich et al. 1998). Thus, the survival of regeneration may play a more important role than growth in determining plant success at low-light levels, and the trade-off between growth at high-light levels and survival (rather than growth) at low-light levels may be the key explanation for the shade

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tolerance of species. The two trade-offs were considered to be mutually exclusive until Lin et al. (2001, 2002) found that shade-intolerant species had a higher mortality risk under slow growth than shade-tolerant ones. In this sense, high shade tolerance can be characterised by low mortality despite slow growth.

In past studies on regeneration mortality, at most one or two tree traits were used to characterise shade tolerance, because the collected dead juvenile trees (0–5 m tall) offered limited information. Mortality was modelled as a function of the radial stem growth of dead and living juveniles, assuming that the collected samples provide a reliable estimate of the death rate at a given point in time in heterogeneous light environments (Dekker et al. 2009; Kobe et al. 1995; Kunstler et al. 2005; Petriřan et al. 2007) or in permanent plots (Kobe and Coates 1997; Pacala et al. 1996; Wyckoff and Clark 2000). Others applied survival analysis with radial stem increment and stem radius as explanatory variables, based on census data collected over more than 15 years (Lin et al. 2001, 2002). Collet and Le Moguedec (2007) used three variables, namely tree height, a competition index and radial growth, whereas Kneeshaw et al. (2006) included only tree height and radial stem growth. So far, the potential influence of other traits of shade tolerance (Valladares and Niinemets 2008), such as leaf (Valladares and Niinemets 2008) or storage traits (Piper and Fajardo 2016), on survival time has—to our knowledge—not been studied.

We define ‘regeneration survival time’ as the average number of years a young tree can grow in deep shade. A young tree is likely to die before the first canopy release if the latter occurs only rarely, e.g. every 100–200 years in forests with a low disturbance rate, such as less than 1% (Hobi et al. 2015b; Valverde and Silvertown 1997). In a companion study (Petrovska et al. 2021), the shade-tolerant *Fagus sylvatica* L. (European beech) seedlings (0–130 cm tall) and saplings (131–500 cm tall) were characterised by high LAR, low absolute growth rate and low storage compared with middle-tolerant *Acer* spp. (Norway maple, *A. platanoides* L. and sycamore maple, *A. pseudoplatanus* L.). However, it remains unclear whether LAR influences mortality and for how long juvenile trees survive on average, mainly because dead trees do not retain leaves and lose other biomass, such that LAR and biomass variables cannot be assessed in hindsight. Moreover, the mean survival time of juvenile *Acer* spp. has not been assessed in previous studies, and estimates of *F. sylvatica* survival time by means of dendrochronological analysis are highly variable (Trotsiuk et al. 2012).

With the present study, we complement existing mortality models, using LAR as a new variable based on the performance of low-vitality trees in deep shade (Petrovska et al. 2021). In the earlier study, the leaf area of low-vitality saplings was found to be, on average, half the values of high-vitality juveniles. We thus assume that trees that died in deep

shade were of low vitality prior to their death, which makes it possible to use the allometry of the low-vitality trees to model the leaf area and total biomass of dead trees. With this approach, we can overcome the problem of incomplete information on dead saplings. Hence, in this study we would like to answer the following questions for the three most abundant species, i.e. *F. sylvatica*, *A. platanoides* and *A. pseudoplatanus*, in a beech-dominated forest: (i) How do LAR, tree-ring growth and tree height affect the species-specific survival time of juvenile trees? (ii) What are the age-specific death rates and survival times of these species?

Materials and methods

Stud area

The Uholka-Shyrokyi Luh reserve (Ukraine) belongs to the beech-dominated primeval forests of Europe and has been listed as a UNESCO World Heritage site since 1992 (Stillhard et al. 2019; Zenner et al. 2020). We focused on the Uholka part of the reserve (centre coordinates: 48° 16' N, 23° 40' E) because it has a larger share of *Acer* species than the Shyrokyi Luh part (Commarmot et al. 2013). The Uholka area covers 4729 ha, ranging between 400 and 1300 m a.s.l. in elevation. Mean annual temperature is about 8 °C (−3 °C in January and 18 °C in July), and mean annual precipitation is 1134 mm (Commarmot et al. 2013). The almost pure beech forest (97% by basal area) was studied using a non-stratified systematic cluster sampling inventory in 2010 (314 plots) (Hobi et al. 2015a) and 2019 (238 plots). A small-scale disturbance regime dominates the forest, with a mosaic of mainly small canopy gaps (98% of gaps < 200 m²). Only a few large stand-replacing events were detected using high-resolution satellite images (Hobi et al. 2015b).

Sampling design

Six plots were selected where seed trees of *F. sylvatica*, *A. platanoides* and *A. pseudoplatanus* were present and where their regeneration (trees up to 5 m in height) was growing under low-light levels. The plots varied in size from 0.2 to 0.7 ha and covered a total area of 2.53 ha. Five plots were in the core zone of the reserve, where natural processes occur without human intervention, and one was located in the buffer zone, where limited close-to-nature management is allowed (forest management that emulates or promotes natural processes, resulting in natural stand structures; Brang et al. 2014). The distance between plots ranged from 400 to 1000 m. Nine sub-plots with areas ranging from 140 to 520 m² (total 0.26 ha) were established in the six plots. They were delineated to contain a large variety of seedlings

(0–130 cm tall) and saplings (131–500 cm tall) of the target species in different size and vitality classes.

One individual per species, vitality class (low and high) and height class (eight classes: 0–10, 11–20, 21–35, 36–60, 61–90, 91–130, 131–200 and 201–500 cm) was randomly selected and harvested in each of the six plots. This resulted in a sample of 82, 80 and 89 living individuals of *A. platanoides*, *A. pseudoplatanus* and *F. sylvatica*, respectively. Additionally, stems of dead *Acer* spp. and *F. sylvatica* trees that had died within the last 3 years (2015–2018) were randomly harvested, matching the height classes of the harvested living trees wherever possible.

Time since death was estimated based on the visual appearance of the dead trees. This method was first introduced by Kobe et al. (1995) and has been successfully applied in multiple studies (Dekker et al. 2009; Kunstler et al. 2005; Petriřan et al. 2007). Dead saplings of *F. sylvatica* from common garden experiments unrelated to this study were monitored for change in visual appearance for more than 2 years at the WSL institute (Petrovska, unpublished). Their visual appearance was tracked for this period, and juveniles were considered to have died within the last 3 years if: (i) the stem was supple, (ii) buds were still present and intact, (iii) the bark was intact, and (iv) the main branches of the crown were intact. Crown integrity was introduced as an additional variable for *F. sylvatica* because small twigs become brittle after 1 year and start to disintegrate. Visual characteristics of the dead saplings were periodically checked: after 33 months, the main twigs and stems became brittle. Dead saplings that did not match these criteria were considered to have been dead for over 3 years and discarded.

In total, 179 dead young trees (60 *A. platanoides*, 72 *A. pseudoplatanus* and 47 *F. sylvatica*) were collected. Browsing was evident in all plots, and severely browsed dead saplings were excluded. Growing conditions (light, density of regeneration and basal area of mature trees) in the plots were comparable at the time of collection. However, information on any past canopy disturbances in the six plots was not available and thus could not be ruled out.

Classification into vitality classes

The criteria for juvenile trees were developed based on the vitality assessment of adult trees, in which tree crowns are assessed visually (Eichhorn et al. 2016; Roloff 1991), whereas growth is measured (Dobbertin 2005). Crown transparency has been shown to correlate well with relative growth rate (Lorenz et al. 2004; Solberg 1999) and also with subsequent tree mortality and survival (Dobbertin and Brang 2001; Schmid-Haas 1993). Hence, seedlings and saplings were classified taking into account crown transparency (percentage of leaf loss and/or dieback of branches and crown) and the increment of the apical shoot for several years. The

branching pattern and stem condition were additionally used to differentiate between high- and low-vitality trees (Table 1; Collet et al. 2011; Roloff 1991; Roloff et al. 2016). To ensure a consistent crown transparency assessment (Dobbertin 2005), a single evaluator assessed all seedlings and saplings using site-specific reference trees. A reference tree is a tree with full foliage (defoliation 0%) that grows at a particular site, taking into account factors such as elevation, latitude, tree age, site conditions, and social status (Eichhorn et al. 2016). Trees browsed during the current season were not considered.

Measurements and calculations

Field measurements (start of May to mid-July) Diameter at root collar (DRC) and tree height (h) were measured before excavation of the living trees. The correct assignment of the dead trees to the height classes was sometimes difficult, as their tops were often damaged (twigs and entire trees fall frequently in a primeval forest). Therefore, the height of such trees was modelled based on the allometry of low-vitality living trees. The trees were excavated manually, and their roots were cleaned with water to avoid damage to the fine roots. The dead trees were cut at the level of the root collar and were not excavated, due to the high likelihood of only partial sampling of their root system. Field measurements are summarised in Table S1 and Table S2.

The proportion of diffuse solar radiation at a given location relative to that in the open (indirect site factor, ISF) was assessed with hemispherical photographs (*Coolpix 4500*, Nikon, Japan) with a 183° fish-eye lens (*Nikon FC-E8*) mounted on a tripod (Thimonier et al. 2010). Photographs were taken just above the uppermost leaves of every sampled living tree (with trees > 1.3 m being bent). The hemispherical photographs were first transformed into binary black and white images by applying the algorithm of Nobis and Hunziker (2005) using Hemisfer 2.2 (© Patrick Schleppi, WSL). Five concentric rings were then superimposed on the images to partition them into zenithal sectors. In each of the five rings, the proportion of visible sky (gap fraction) was determined and the ISF was calculated for every young tree in every plot.

Lab work The sampled living trees were separated at the root collar into aboveground biomass (foliage, stem, branches) and belowground biomass (roots). All fresh leaves were scanned for leaf area with a smartphone (*Petiole version 2.0.1*, Petiole Ltd. 2019) after calibration of the camera. Tree foliage, stems, branches, and roots were dried at + 65 °C for three days until a constant weight was reached and then weighed to the nearest ± 0.01 g. Biomass of the dead trees was not assessed, as part of it was already lost (no leaves, lost branches or broken apical part of the stem).

Table 1 Criteria used to classify juvenile trees into high- and low-vitality classes: (i) crown transparency, (ii) apical shoot increment, (iii) branching pattern and (iv) stem damage (Innes 1998; Roloff 1991)

Parameter	High-vitality	Low-vitality
Crown transparency (leaf loss, crown dieback)	Leaf loss < 20%	Leaf loss > 20%
Apical shoot increment for several years	No dead branches and no crown dieback	Dead branches or crown dieback
	Long apical increments for 3–5 years	Short apical increments for 3–5 years
	Browsed in the past but recovered	Browsed in the past and not recovered

Branching pattern	Vigorous branching (see above)	Degenerative branching (see above)
Stem damage	Intact stem, no diseases	Scars, bacterial/fungi diseases

Source of images: Roloff (1991)

For each living tree, LAR was calculated according to the formula:

$$\text{LAR} = \frac{\text{LA}}{m_{\text{total}}} \quad (1)$$

where LA denotes leaf area and m_{total} is the total dry mass (aboveground and belowground) of the tree.

Dendrochronological analysis

To determine age and radial growth from each harvested living or dead tree, a stem disk at the level of the root collar was cut with a microtome. The stained disks were photographed (Canon EOS 700D, Canon Inc., Tokyo, Japan) and analysed with WinDENDRO™ (Regent Instruments Canada Inc., Quebec, Canada) under a microscope. The number and width of the rings were recorded in two to four orthogonal directions because the tree piths were acentric. Radial growth in every year was averaged across all orthogonal directions, and then, the last five rings of tree life were arithmetically averaged, excluding the last ring because it was not

known whether death had occurred at the beginning of the current or at the end of the previous growing season.

The cross-sectional increment of tree basal area (BAI) should consistently increase, at least over the early life of a tree, and is a more accurate indicator of tree growth than radial increment alone (Johnson and Abrams 2009). Therefore, ring width series were converted to BAI series based on the distance between the innermost measured ring and the pith of the tree, using the *dplR* package Bunn et al. 2021) in R (version 4.0.3; R Core Team 2019). This method assumes a circular cross-section (Biondi 1999). Because BAI at year t is equivalent to the difference between the cross-sectional area at the end of year t and that at the beginning ($t - 1$) (Biondi and Qeadan 2008); it follows that:

$$\text{BAI}_t = \pi(R_t^2 - R_{t-1}^2) \quad (2)$$

where R_t is the stem radius at the end of the annual increment and R_{t-1} is the stem radius at the beginning of the annual increment. The series of BAI for the last 5 years of tree life were then arithmetically averaged, excluding the last year.

Statistical analysis

Missing data for living juvenile trees (3% of the dataset, 6 out of 289 observations for tree age, 8 out of 289 observations for LAR) were imputed using the Multiple Imputation by Chained Equations (MICE) technique with a Random-Forest-based approach (R package *mice*, see also Van Buuren and Groothuis-Oudshoorn 2011).

Modelling missing height, leaf area and dry mass values for dead trees. In some dead trees, the apical parts of the stem were missing, and assignment to height classes was problematic. This problem was solved by modelling the height (H_{dead}) of the dead trees based on the heights of the low-vitality trees (indicated by the suffix_{low}), assuming biomass allocation to be similar in dead and low-vitality trees. Our assumption was based on several studies where dead or low-vitality juvenile trees had, on average, less height growth in the shade compared with living ones (Cleavitt et al. 2008; Collet and Le Moguedec 2007; Piper et al. 2009). Leaf area (LA_{dead}) and dry mass (m_{dead}) were also modelled using similar assumptions (Petrovska et al. 2021; Piper and Fajardo 2016; Sumida et al. 2018; Zhang et al. 2018) and variables of the low-vitality trees. In all cases, generalised linear models for the gamma distribution with logarithmic link functions (R package *rms*; Harrell 2020) were applied:

$$\ln E(H_{\text{dead}}) = \beta_0 + \beta_1 \ln(\text{DRC}_{\text{low}}) + \beta_2 \text{mean ring}_{\text{low}} + \beta_{3,1} \text{species}_1 + \beta_{3,2} \text{species}_2 + \beta_4 \text{age}_{\text{low}} \quad (3)$$

$$\ln E(LA_{\text{dead}}) = \beta_0 + \beta_1 \ln(\text{DRC}_{\text{low}}) + \beta_2 \text{mean ring}_{\text{low}} + \beta_{3,1} \text{species}_1 + \beta_{3,2} \text{species}_2 + \beta_4 \text{age}_{\text{low}} \quad (4)$$

$$\ln E(m_{\text{dead}}) = \beta_0 + \beta_1 \ln(\text{DRC}_{\text{low}}) + \beta_{2,1} \text{species}_1 + \beta_{2,2} \text{species}_2 + \beta_3 \text{age}_{\text{low}} \sqrt{b^2 - 4ac} \quad (5)$$

where E denotes expectation, β_0 = intercept, β_i = coefficients of the covariates, DRC_{low} = root collar diameter of low-vitality trees, $\text{mean ring}_{\text{low}}$ = mean ring width, age_{low} = age of low-vitality trees, and species_1 and species_2 are two indicator (dummy) variables for the three tree species. These three equations (Eqs. 3–5) were fitted for low-vitality juveniles and then used to predict H, LA and m for the dead juveniles. For this, the *rms* function ‘predict’ was applied with a dataset for dead juveniles (DRC, ring width and age). These models assume a linear relationship between the predictors and the link function. Statistical significance of the model coefficients was tested with the Wald Chi-squared test ($p < 0.01$) and additionally checked by means of bootstrapping (1000 iterations). The models satisfied the assumptions of linearity between the predictors and the link function and

showed no multicollinearity (variance inflation factor VIF cut-off set at 5).

Survival model The goal of this analysis was to assess the survival time and age-specific death rate (instantaneous hazard rate) for young trees with the covariates mentioned below. Since there is no general consensus about which timescale (time-of-study or age) is most appropriate in survival analysis (Hurley 2015; Korn et al. 1997), chronological age was used. This approach has already been applied in many studies (Ingram et al. 1997; Lamarca et al. 1998; Thiébaud and Bénichou 2004), directly taking into account the age effect on the probability of survival. In our case, trees enter the study at random because they are born at a random point in time and exit at their death/censoring age (random, type I censoring); thus, the timescale is the age of a tree (in years) and the event of interest is its death. Three variables were thus defined: T_i (age at death), c_i (random censoring time) and δ_i (an indicator variable), which equals one if T_i is observed and zero if T_i is censored. The response variable is $\min(T_i, c_i)$, i.e. the age of the tree at death if it died before sampling (in 2018) or its age at the time when the study was completed if the tree was still alive at that point.

The parametric accelerated failure time model (AFT) with a log-normal distribution (R package *rms*; Harrell 2020) is an alternative to the semi-parametric Cox proportional hazard (PH) model if the assumptions of the latter are violated, as in our case (Online Resource S1.1). AFT is widely used in medicine and failure tests of industrial products (Wei 1992). In our case, this model was used to explore the direct effect of the explanatory variables LAR, mean ring width, species and height class on the acceleration/deceleration of survival time with the method of full maximum likelihood:

$$\begin{aligned} \log(T) = & \beta_0 + \beta_1 \ln(\text{LAR}) + \beta_2 \ln(\text{ring}) \\ & + \beta_{3,1} \text{species}_1 + \beta_{3,2} \text{species}_2 \\ & + \beta_4 \text{height class} + \sigma \varepsilon \end{aligned} \quad (6)$$

where T = age at sampling, β_0 = intercept, β_i = coefficients of the covariates, σ = scale parameter, and ε = random error term assumed to follow a standard normal distribution (Fig. S7). The model estimators were unaffected by our sampling design because they are (asymptotically) unbiased if censoring takes place at random (Leung et al. 1997; Little and Rubin 2002). In the current context, this refers to the assumption that trees enter the study at random, i.e. they are born at random times. The model with the ring width covariate (Eq. 6) was compared with a model with BAI as a covariate, using the Akaike information criterion (AIC). The model with ring width had the lower AIC and was thus selected for further analysis. A model with the interaction term height class $\times$ species was also fitted, but it had a higher AIC than the model without the interaction term and

additionally showed very high multicollinearity ($VIF > 10$). The interaction term therefore was not included in the final model.

The survival function is the probability $S(t)$ that a tree survives beyond time t , so that if F denotes the distribution function for age T , then $S(t) = P(T \geq t) = 1 - F(t)$. The first derivative of $F(t)$, denoted by $f(t)$, is the event density, and the instantaneous hazard rate is defined as $h(t) = f(t)/S(t)$, which is the instantaneous intensity of tree death at time t , provided that it has survived until time t . X denotes the vector whose elements are unity and the values of the covariates $\ln(\text{LAR})$, $\ln(\text{ring width})$, species_1 , species_2 and height class, whereas $\beta_i = (\beta_0, \beta_1, \beta_2, \beta_{3,1}, \beta_{3,2}, \beta_4)$ denotes the corresponding vector of regression coefficients. The survival probability at time t for the covariate level X is then equal to:

$$\Phi^{-1}[S(t|X)] = \mu_0 + \mu_1 \ln(\text{LAR}) + \mu_2 \ln(\text{ring}) + \mu_{3,1} \text{species}_1 + \mu_{3,2} \text{species}_2 + \mu_4 h.\text{class} - \alpha \log(t) \quad (7)$$

where $S(t|X)$ is the survival function at time t and covariate X , Φ denotes the cumulative distribution function of the standard normal distribution, $\alpha = 1/\sigma$ and $\mu_j = \beta_j/\sigma$ for $j=0, 1, \dots$ (Zhang 2005). Let $h(t|X)$ be the hazard function at time t and covariate X . Then, the log-hazard function can thus be expressed as:

$$\log h(t|X) = \log h_0(t \cdot e^{-X^T \beta}) - X^T \beta \quad (8)$$

where $\log h_0(t|X)$ is the hazard function given the covariates X when $\beta = 0$ (i.e. $\beta_i = 0, i = 0, 1, \dots$) (Zhang 2005).

The regression coefficients were bootstrapped (5000 iterations) and their significance tested with the Wald Chi-squared statistic ($p < 0.001$) (R package *rms*). Species

differences in survival were evaluated with the Mantel–Haenszel log-rank test ($p < 0.001$, Table S4). Overall, the model demonstrated high concordance (predictive discrimination in survival models; Therneau 2020). Finally, multicollinearity of covariates was checked with the variance inflation factor VIF (cut-off set at 5). Due to the absence of dead seedlings of *A. pseudoplatanus* in the height class 0–10 cm, this class was excluded from the analysis. Visualisations were performed using the R package *ggplot2* (Wickham et al. 2020).

Results

Ages and radial growth estimations

The mean age of dead trees was substantially higher for *F. sylvatica* in the height classes from 36 to 500 cm compared with *Acer* spp., i.e. *F. sylvatica* survived for a longer time (Fig. 1). Low-vitality *F. sylvatica* trees in the height classes from 61 to 500 cm were considerably older than those of the *Acer* species. High-vitality trees of the three species were, on average, similar in age up to the height class 91–130 cm, but older in *F. sylvatica* than in the two *Acer* species for taller trees. As expected, mean ISF values (i.e. relative diffuse light) were low, varying from 1.9 to 3.3% (Table S1). Browsing was apparent in all plots, with many *Acer* spp. trees showing scars but having recovered and most juvenile *Fagus* trees unaffected.

Surprisingly, we observed a higher mean radial growth rate in dead than in living trees for *F. sylvatica* and *A. pseudoplatanus* (Fig. 2a). Mean ring width was similar for dead

Fig. 1 Mean age of dead and living trees of the two vitality classes by height class: dots represent mean values and whiskers represent a standard error

F. sylvatica trees and the two *Acer* species, whereas the living *F. sylvatica* trees had a smaller mean ring width (220 and 210 μm in low- and high-vitality trees, respectively) compared with living *Acer* competitors (247 and 263 μm in low-vitality and 267 and 242 μm in high-vitality trees, respectively). Mean radial growth of the high- and low-vitality trees was quite similar on all six plots, while the mean radial growth of the dead trees was greater except in plots 1 and 5 (Fig. 2b). The radial growth of the dead trees had decreased for the last 5 years of life in plots 5 and 6 only.

Modelling of missing variables for dead trees

The explanatory variables DRC, tree age and mean ring width were significant predictors of tree height, leaf area and dry mass, while species identity was significant for leaf area only (Table 2). A low correlation between radial growth and leaf area or tree height, as well as a moderate correlation between tree age and leaf area, led to species identity being the only significant predictor of leaf area. A 1% increase in DRC corresponded to increased height growth by 1%, leaf area by 1% and dry mass by

Fig. 2 Mean ring width of tree rings in dead, low-vitality and high-vitality trees of the three species (a). Average ring width during 10 years prior to sampling or death in the plots 1–6 for dead, low-

vitality and high-vitality trees (b). Dots and thick lines=mean ring width, whiskers=standard error, thin lines=ring width data

Table 2 Summaries of generalised linear models for tree height, leaf area and dry mass. SE denotes standard error

Predictors	Tree height			Leaf area			Dry mass		
	Exp (Coef)	SE	p	Exp (Coef)	SE	p	Exp (Coef)	SE	p
(Intercept)	53.38	0.14	<0.001	115.21	0.21	<0.001	11.58	0.24	<0.001
Ln DRC (not exponentiated)	1.01	0.06	<0.001	1.06	0.09	<0.001	2.00	0.11	<0.001
Tree age	1.02	0.01	0.006	1.08	0.01	<0.001	1.07	0.01	<0.001
<i>Acer platanoides</i>				Reference					
<i>Acer pseudoplatanus</i>	1.07	0.07	0.352	0.80	0.11	0.048	0.89	0.14	0.432
<i>Fagus sylvatica</i>	0.99	0.08	0.873	1.09	0.12	0.444	0.77	0.15	0.082
Mean ring width	1.00	0.00	0.001	1.00	0.00		<0.001		
Observations	137			115			135		
(low-vitality trees)									

2%. Although age was significant, a 1% in this variable affected tree height by only 2%, leaf area by 8% and dry mass by 7%. *Acer pseudoplatanus* allocated more biomass to height (not significant) and had a significantly smaller leaf area compared with *A. platanoides* and *F. sylvatica*.

In general, the modelled height, leaf area and dry mass of dead trees matched the variation observed in low-vitality trees or remained within its lower range. For both *Acer* spp., modelled tree heights were smaller in dead than in low-vitality trees as a consequence of the smaller DRC values of the dead trees. The modelled mean leaf area and dry mass of dead trees were similar to those of the low-vitality trees except regarding *A. pseudoplatanus* (Fig. 3). As a result, the calculated LAR values based on the modelled leaf area and dry mass were close to the LAR values observed in low-vitality trees. Details on the modelled results are shown in Table S2.

Survival model

Species identity, LAR, ring width and height class significantly affected survival time (Table 3). A 1% increase in LAR prolonged survival time by 0.14%. In comparison with *A. platanoides*, survival time was 3% shorter for *A. pseudoplatanus* and 41% longer for *F. sylvatica*. Compared with

Table 3 Summary statistics of the accelerated failure time (AFT) model. SE denotes standard error

Survival model	Coef	Exp(Coef)	SE	Pr(> Z)
(Intercept)	4.189	66.009	0.388	< 0.0001
Ln LAR	0.144	0.144	0.062	0.0211
Species				< 0.0001
<i>Acer platanoides</i>	Reference			
<i>Acer pseudoplatanus</i>	−0.032	0.969	0.063	0.6153
<i>Fagus sylvatica</i>	0.342	1.407	0.074	< 0.0001
Height class				< 0.0001
H: 11–20 cm	Reference			
H: 21–35 cm	0.021	1.021	0.198	0.9152
H: 36–60 cm	0.025	1.025	0.170	0.8832
H: 61–90 cm	0.097	1.101	0.169	0.5681
H: 91–130 cm	0.366	1.442	0.175	0.0371
H: 131–200 cm	0.729	2.074	0.186	< 0.0001
H: 201–500 cm	1.136	3.116	0.213	< 0.0001
Ln (ring width)	−0.381	−0.381	0.075	< 0.0001
Likelihood ratio	$X^2(10) = 173.79$, $p < 0.0001$			
Observations	430			
Concordance	0.8

Fig. 3 Violin plots of modelled tree height, leaf area, dry mass and calculated LAR. Dot=mean, horizontal line=median, whiskers=95% confidence intervals, n =sample size per species and vital-

ity class (shown in top left panel only). The form of the violins shows the data probability density and its distribution

the height class 11–20 cm, additional tree height prolonged survival time by 2% in height class 21–35 cm and by up to 211% in height class 201–500 cm. Finally, the model estimated that a 1% increase in allocation to ring width reduces survival time by 0.38%.

According to the model, the predicted mean survival time of *F. sylvatica* was higher, with an estimated value of 72 years, compared with 47–48 years for both *Acer* spp., when adjusted for slow growth (20–100 μm) and height class 131–200 cm. These two classes were chosen as reference classes because the height class (131–200 cm) had a larger number of dead trees than the height class 201–500 cm (able S2), and the selected radial growth (20–100 μm) highlights the extremely wide range of the observed growth values. Log-rank tests indicated a significant difference in survival time between *F. sylvatica* and *Acer* spp. ($p < 0.001$, Table S4) but no difference between *A. platanoides* and *A. pseudoplatanus*. The mortality probability over 3 years increased with radial growth in all species but was significantly lower for *F. sylvatica* (10.6%) at age 25 years (mean age in height class 131–200 cm) and a radial stem growth of 210 μm , which is typical for high-vitality *F. sylvatica* in this study, than for *Acer* spp. (32.0–35.8%; Fig. 4a). In *F. sylvatica*, the age-specific mortality rate over 3 years increased slowly with age, reaching 0.036 events (i.e. a conditional probability of death of 3.6%), provided that the trees survived for 40–50 years (Fig. 4b). In contrast, the age-specific mortality rate over 3 years for *Acer* spp. increased rapidly, reaching 0.07–0.08 events at age 40–50 years.

An increase in LAR (from 10 to 40 $\text{cm}^2 \text{g}^{-1}$) slowed down the age-specific mortality rate of *F. sylvatica* from 0.03 to 0.02 events over 3 years, of *A. platanoides* from

0.07 to 0.05 and of *A. pseudoplatanus* from 0.08 to 0.05 events, given the same values of the other predictor variables as above. A reduction in radial growth (from 410 to 210 μm) decreased the mortality rate by a factor of two, i.e. from 0.04 to 0.02 for *F. sylvatica* and from 0.09 to 0.05 for *Acer* spp., given an age of 25 years, a LAR of 40 $\text{cm}^2 \text{g}^{-1}$ and the height class 131–200 cm. A change in height class from 61–90 to 201–500 cm significantly reduced the age-specific mortality rate of *F. sylvatica* from 0.1 to 0.003 and of *Acer* spp. from 0.14 to 0.02, keeping the same values of the predictor variables as above.

The model coefficients (Table 3) indicated that a reduction in growth enhances the expected survival time to a higher degree than an increase in LAR (Fig. 5). Higher LAR and less growth increased the survival time of *F. sylvatica* more strongly (i.e. steeper curves) than for *Acer* spp. An increase in LAR from 10 to 40 $\text{cm}^2 \text{g}^{-1}$ (observed minimum and mean LAR values in height class 131–200 cm) would improve the survival time of *F. sylvatica* from 35 to 43 years and of *Acer* spp. from 24 to 31 years, given a ring width of 210 μm and a height class of 131–200 cm. At the same time, a reduction in ring width from 410 to 210 μm enhances the estimated survival time of *F. sylvatica* from 33 to 43 years and of the *Acer* species from 23 to 31 years, assuming a LAR of 40 $\text{cm}^2 \text{g}^{-1}$ and height class of 131–200 cm. Further, changes in the height class from 61–90 to 201–500 cm extended the survival time of *F. sylvatica* from 23 to 64 years and that of *Acer* spp. from 15 to 46 years (Fig. 5).

Fig. 4 Probability of mortality over 3 years (a) and age-specific mortality rate over 3 years (b) adjusted to LAR = 40 $\text{cm}^2 \text{g}^{-1}$, ring width = 210 μm , age = 25 years and height class = 131–200 cm.

Shaded bands = 95% confidence intervals. Note: age-specific mortality (instantaneous hazard rate) is the intensity of tree death events at time t , provided that the tree has survived until then

Fig. 5 Effect of LAR, mean ring width and height class on survival time. Shaded bands and error bars=95% confidence intervals, adjusted to LAR=40 $\text{cm}^2 \text{g}^{-1}$, ring width=210 μm and height class=131–200 cm

Discussion

Effects of LAR, radial stem growth and height on survival time

This study represents, to our knowledge, the first estimation of survival time and age-specific mortality rate for juvenile beech and maple trees based on traits of shade tolerance (i.e. growth rate, LAR). We applied a new methodological approach by modelling LAR for the dead trees based on the difference in performance between high- and low-vitality trees and enriched existing mortality models with the new variable. LAR was introduced because several studies have demonstrated the importance of the difference between the leaf area of low- and high-vitality broadleaved trees (Petrovska et al. 2021) and between living and dying (low-vitality) conifer trees (Sumida et al. 2018). We assume that trees that died in the deep shade were of low vitality prior to their death, which makes it possible to use the allometry of the low-vitality trees to model leaf area and total biomass of dead trees. Thus, it is reasonable to assume that low-vitality saplings had a similar LAR as dead saplings. Using growth as the only dependent variable seemed unreliable because growth before death does not always decrease (Herguido et al. 2016) or show consistent patterns in broadleaved species (Cailleret et al. 2019). Moreover, individuals with more variable growth were more likely to die than trees with more constant growth (Cailleret et al. 2019; Suarez and Ghermandi 2004), as was the case in our study. Therefore, we decided to use LAR and radial growth as dependent variables for our modelling approach.

Trees growing in deep shade have been shown to maximise light capture through an increase in leaf area and its proper arrangement in space (Canham 1988; Givnish 1988; Poorter 1999). Survival increases with LAR in shade-tolerant species because a larger leaf area per unit of plant biomass supports the production of more photosynthates (Sanford et al. 2003; Valladares et al. 2003). However, LAR diminishes during ontogeny and can undermine species performance and persistence in the shade (Delagrange et al. 2004; Lusk 2004). Our results confirm that juvenile *F. sylvatica* trees, with their higher LAR, survive longer on average than *Acer* spp., while the age-specific mortality rate of *F. sylvatica* is half of that of its competitors. *Fagus sylvatica* saplings in the height class 131–500 cm featured a larger leaf area compared with *A. pseudoplatanus* and *A. platanoides* in two vitality classes (Table S1). In contrast, both *Acer* species minimise leaf and branch biomass by retaining petioles, even in taller height classes (Beaudet and Messier 1998), as an adaptation to frequent browsing (Modrý et al. 2004). Thus, these species clearly differ in LAR and, therefore, survival time and mortality rate.

The relationship between juvenile tree growth and mortality seems to contradict current mortality models for tree regeneration, which are often based on the finding that mortality increases with reduced radial growth under conditions of more than 5% diffuse or direct light (Dekker et al. 2009; Kneeshaw et al. 2006; Kunstler et al. 2005; Petriřan et al. 2007). For instance, Kunstler et al. (2005) demonstrated a 1.5-fold difference between mean ring width of living (332 μm) vs. dead *F. sylvatica* saplings (208 μm) under 5–100% relative irradiance, and Petriřan et al. (2007) measured declining ring width in dead *F. sylvatica* and *A.*

pseudoplatanus trees for the last 5 years along a diffuse light gradient of 3–33%.

The growth patterns of juvenile trees in our study refer to deep shade (mean range 2–3% of diffuse light) and thus may not follow the classical point of view. For example, Dekker et al. (2009) showed that average growth prior to death spanned a wide range, and for *Pseudotsuga menziesii*, *Pinus sylvestris* and *Larix kaempferi* it even encompassed the full range in growth of living individuals under conditions of no direct light. In our study, juvenile tree growth patterns followed a similar pattern. Mean radial growth of dead trees was similar to or slightly greater than in surviving individuals (Fig. 2) and did not show a decreasing trend in the last 5 years, except in two plots. A physiological explanation for less growth in small trees surviving at very low light levels is that carbon stress forces the trees to prioritise carbon allocation to respiration, maintenance and active storage instead of growth (Wiley et al. 2017; Wiley and Helliker 2012).

At low-light levels, a young tree makes adjustments to minimise CO₂ losses by slowing growth and respiration rates, an ability that causes shade-tolerant species to perform better and survive longer than shade-intolerant species (Walters and Reich 2000). In our study, we found *F. sylvatica* to be able to grow very slowly over long periods with a low mortality rate, thus increasing its survival time. The estimated mean survival time of *F. sylvatica* juveniles (72 years) is close to the average age (65 years) when they experienced the first release in Uholka (Trotsiuk et al. 2012). Moreover, juvenile *F. sylvatica* in Uholka can survive on average 65 years (varying from 21 to 177 years), due to long suppression periods until the first release (Trotsiuk et al. 2012). Since the mortality rate of older juveniles is not known (maximum observed tree age was 46 years), the similarity between average survival time and time until first release for *F. sylvatica* seems to be a coincidence, but the difference to the findings regarding the *Acer* spp. is striking. They allocate more biomass to growth at the cost of higher respiration (Walters and Reich 2000), have higher mortality rates and consequently have shorter survival times.

In other studies comparing *F. sylvatica* with other species, the relationship between the growth rate and mortality rate was different than observed here. At a light level of 3%, both *F. sylvatica* and *A. pseudoplatanus* showed slow radial and height growth but had a high mortality probability over 3 years (ca. 50 and 70%, respectively; Petriřan et al. 2007). At that same light level, the relative growth of *F. sylvatica* juveniles was similar to that of shade-intolerant downy oak (*Quercus pubescens*), but annual mortality rates were around 2% for *F. sylvatica* and 20% for *Q. pubescens* (Kunstler et al. 2005). The difference in *F. sylvatica* mortality estimation during slow growth is likely mainly due to the small sample size at a light level of 3%, as samples were collected at a wide range of light levels in both studies

(3–33% indirect light, Petriřan et al. 2007; 5–100% of full sun, Kunstler et al. 2005), in contrast to in our study. Moreover, in several studies (Kunstler et al. 2005; Lin et al. 2002) the authors concluded that European beech (*F. sylvatica*) and American beech (*Fagus grandiflora*) are more tolerant to slow growth and thus have a lower mortality rate, while less shade-tolerant species suffer high mortality when growing slowly. Our results suggest that such conclusions do not apply to growth and mortality at mean light levels of 2–3%, due to the methodological limitations mentioned above. In deep shade, slow growth is advantageous in the long term, due to low maintenance and respiration costs. Shade-tolerant species are able to decrease growth (and respiration) more efficiently than shade-intolerant ones (Rodríguez-Calcerrada et al. 2019; Valladares and Niinemets 2008). Hence, the conventional belief that shade-tolerant species can survive in spite of suppressed growth should be revised because slow growth is actually a resource-saving strategy which enables survival.

As a consequence of slow growth in deep shade, *F. sylvatica* has overall higher LAR, which decreases more slowly with increasing height (Annighöfer et al. 2017; Petrovska et al. 2021) than in the other studied species, contributing to its low mortality rate. In contrast, the LAR of the two *Acer* spp. studied here is lower and decreases faster with height (Annighöfer et al. 2017; Petrovska et al. 2021), which increases the mortality rate and decreases survival time of these species (Figs. 4 and 5). This difference in strategy is likely to be even more striking if high-vitality vs. dead trees were studied because our survival model was built on average LAR values.

Our findings highlight that tree height is more important for extending survival time than LAR and radial growth. However, the absolute number of years of acceleration resulting from our models should be interpreted with caution, as we evaluated the effect of height by keeping the other covariates fixed. Biomass allocation to tree height greatly improved survival in the shade, probably because light conditions improve with size (Collet and Le Moguedec 2007; Eerikäinen et al. 2014). In contrast, survival in North American hard- and softwood species did not differ significantly between small and large saplings at radial growth of < 200 µm across light gradients between gap and non-gap environments (Kneeshaw et al. 2006). In the same study, mortality increased with height in shade-tolerant species at radial growth of 500 µm. In our case, radial growth of 500 µm seems disadvantageous (Fig. 2), and the probability of survival diminished (Fig. 5) with height due to increased maintenance costs and reduced LAR. However, at radial growth of 200 µm, typical for our data set, height growth was positively related to survival probability and extended survival time.

Other biotic and abiotic factors, such as browsing, pests, low temperature and drought, may affect mortality as well. In this study, the influence of past browsing of dead juveniles cannot be ruled out and may partly contribute to the mortality rates, particularly of *Acer* spp. A high frequency of shoot leader removal, especially in the height classes from 50 to 130 cm (Szwagrzyk et al. 2020), increases the mortality rate of saplings (Sipe and Bazzaz 2001). In deep shade, browsed saplings cannot usually recover the height loss and thus lag behind in size compared to unbrowsed saplings (Kupferschmid et al. 2008). *Acer pseudoplatanus* is browsed more frequently than *F. sylvatica* (Szwagrzyk et al. 2020), but a 60% probability of mortality in both species was found at a 70–80% decrease in height increment (Eiberle and Nigg 1987). Regarding pathogenic fungi, these were not studied in detail here, but we did not find conspicuous traces suggesting an important role of this mortality agent. Lastly, while frost and drought have the potential to reduce growth and induce mortality, this is not likely in our case because living juveniles had similar or slower radial growth rates as the dead trees (Fig. 2). Moreover, living and dead juveniles were sampled close to each other in the same plots; if weather factors played a role in the death of juveniles, it would remain difficult to explain why some juveniles were affected but others not.

Evaluation of annual mortality

Data on the annual mortality of juvenile trees, although scarce in Europe, are important for comparison with the model results presented here. Annual mortality in young *F. sylvatica* (3.3%) and *A. pseudoplatanus* (7.3%) was observed on long-term plots in the UK (Kerr and Mackintosh 2012). Similar results for *F. sylvatica* saplings (4.2–4.9%) were reported by Collet and Le Moguedec (2007) along a light gradient from closed canopy to large gaps in north-eastern France. Kunstler et al. (2005) observed an annual mortality rate of 2% in *F. sylvatica* saplings in a transect featuring a 5–100% light gradient in a sub-Mediterranean forest in France. In Austria, the mean annual mortality rate of juvenile *F. sylvatica* reached 2.6% in the diameter at breast height class 2.6–7.5 cm (Platter 2008). Our age-specific mortality rate (although estimated over 3 years) in *F. sylvatica* (3.6% conditional probability) and in *A. pseudoplatanus* (7–8% conditional probability) is close to the values listed above. It seems that the annual mortality of juvenile *F. sylvatica* usually varies between 2 and 3.3%, with the highest reported value (4.9%) occurring after windthrow (Collet and Le Moguedec 2007). Such low variation in the observed annual mortality of *F. sylvatica* across Europe suggests that its survival strategy varies only slightly within the temperate zone. Wang et al. (2020) have recently confirmed that *F. sylvatica* seedlings of different geographic

provenances show similar trait responses in shade, drought or combined stress conditions. Given the low variability in observed annual mortality of *F. sylvatica* across Europe, we hypothesise that the responses of this species to shade (i.e. ontogenetic changes in LAR and growth) are likely similar across the temperate zone.

In contrast to the observed annual mortality rate, the modelled probability of mortality varies strongly depending on (1) light conditions, (2) other variables included in the mortality models (cf. *Introduction*) and (3) regional differences that cannot be explained by the environment. In our study, the probability of *F. sylvatica* mortality (10.6%) over 3 years was much lower than values observed by Petriřan et al. (2007)—approximately 19% over 3 years at a radial growth rate of 210 μm . In our study, the probability of mortality of *A. pseudoplatanus* over 3 years (35.8%) was much lower than the almost 50% over 3 years reported by Petriřan et al. (2007) at a radial growth rate of 210 μm . Finally, Kobe et al. (1995) suggested that there was little variation in modelled mortality for the same species sampled in different forests and climate zones in the USA, but our comparison of the variability in modelled probability of mortality for European forests demonstrates the contrary.

Conclusions

Our study shows that shade tolerance, which is commonly defined as a relationship between sapling mortality and growth, can alternatively be formulated as a relationship between survival time and the interplay of growth and LAR, leading to a more general explanation for the survival of shade-tolerant trees in deep shade. *Fagus sylvatica*'s marked ability to sustain slow growth and a high LAR, leading to low mortality over extended periods, makes it more independent of long canopy turnover time and more likely to reach the canopy once a gap is formed. Its *Acer* competitors, in contrast, grow faster and invest less in leaf area, but exhibit a higher age-specific mortality rate, rendering their upgrowth to the canopy a rare event in a dark forest with a small-scale disturbance regime.

A species' survival time and mortality rate can be better explained by a combination of different traits (leaf, growth and storage) than with just one or two variables capturing growth traits. Our approach extends the variables used in mortality models while focusing on very-low-light levels. Ideally, one method, one model and a fixed set of variables from the traits mentioned above would be used for studying the mortality of juveniles in a tree species, with a sample covering low-, moderate- and high-light levels across environmental gradients within the species' range. A standardisation of the variables used in survival/mortality models

would make it possible to minimise unexplained variability and achieve comparable results.

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