



Growth–mortality relationships as indicators of life-history strategies: a comparison of nine tree species in unmanaged European forests

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Forest succession depends strongly on the life history strategies of individual trees. An important strategic element is the ability to survive unfavourable environmental conditions that result in strongly reduced tree growth. In this study, we investigated whether the relationship between growth and mortality differs among tree species and site conditions. We analysed 10 329 trees of nine tree species (*Picea abies*, *Taxus baccata*, *Fagus sylvatica*, *Tilia cordata*, *Carpinus betulus*, *Fraxinus excelsior*, *Quercus robur*, *Betula* spp. and *Alnus glutinosa*) from unmanaged forests of Europe: the continental Białowieża forest (Poland) and several oceanically influenced Swiss forest reserves. For each species, we calculated a set of flexible logistic regression models with the explanatory variables growth (as measured by relative basal area increment), tree size and site. We selected the species-specific model with the highest goodness-of-fit and calculated its discriminatory power (area under the receiver operating characteristic curve, AUC) and calibration measures. Most models achieved at least a good discriminatory power (AUC > 0.7) and the AUC ranged from 0.62 to 0.87; calibration curves did not indicate any overfitting. Almost all growth–mortality relationships differed among species and sites, i.e. there is no universal growth–mortality relationship. Some species such as *F. excelsior* showed reduced survival probabilities for both unfavourable and very good growth conditions. We conclude that the growth–mortality relationships presented here can contribute to the life-history classification of trees and that they should also help to improve projections of forest succession models.

Stress factors are acting permanently during every tree's life, i.e. trees generally experience suboptimal environmental conditions (Schulze et al. 2005). Depending on the duration and intensity of stress, trees show complex responses ranging from increased production of resin to the formation of callus and the compartmentalisation of invading fungi (Schweingruber 1996). As an ultimate consequence, the inability to cope with environmental stress may lead to tree death. In this context, the individual stress tolerance can be regarded as an important feature of the life-history strategies of trees (Grime 1977). To date, in many attempts to classify the life-history strategies of trees, stress tolerance has been expressed by auxiliary variables such as maximum age or shade tolerance (Brzeziecki and Kienast 1994, Loehle 2000). Thus, the problem of quantification has been deferred to auxiliary variables that have been derived from field observations rather than experimental evidence. An alternative approach for quantifying stress tolerance is to focus on the growth–mortality relationship of trees. Although numerous stress reactions interact in a complex manner (Franklin et al. 1987), in the

case of trees they often result in reduced radial growth increment due to the allocation of resources to defence and to the crown and root system (Waring and Pitman 1985). Hence, the radial growth patterns of trees can be regarded as an integrative stress response, which reveal the ability of trees to deal with different factors and intensities of stress (Fritts 1976). Consequently, the relation between growth and mortality can be described quantitatively with a growth–mortality relationship, where reduced growth generally results in a higher mortality risk (Monserud 1976).

However, the quantification of the growth–mortality relationship of trees is often poor due to the scarcity of observable mortality events (Hawkes 2000, Keane et al. 2001). This problem is further aggravated by the scarcity of unmanaged forests that represent a potential data source for growth and survival information (cf. Parviainen 2005). In practice, the analysis of tree mortality is often restricted to data sources that are relatively small regarding either the number of sample units (e.g. tree-ring data of dead trees) or the temporal resolution of the growth information (e.g. forest inventory data, Biondi 1999). Recently, comprehensive

simulation studies have demonstrated that even such restricted data sources allow for a reliable estimation of growth–mortality models (Wunder et al. 2008). In this context, simulated forest inventory data comprising three 10-year inventory intervals resulted in mortality models with a relatively high performance.

Many statistical tree mortality models assume site-independent tree mortality processes, i.e. the shape of the growth–mortality curve is affected only by the stress-induced growth reduction (Wyckoff and Clark 2002, Bigler and Bugmann 2004). However, it remains unclear whether the assumption of a universal, species-specific growth–mortality relationship holds true for a range of species from climatically and geologically different sites.

The objective of our study is thus to quantify the growth–mortality relationship of a range of tree species in unmanaged forests in Europe. To this end, we used long-term tree growth and survival information from Polish and Swiss forest inventories to estimate species-specific growth–mortality models. Our analysis focuses on two main questions:

Are the growth–mortality relationships different among nine common European tree species, or do some tree species behave similarly?

Do the species-specific growth–mortality relationships differ across biogeographical regions represented by the Białowieża forest in continental eastern Poland and Swiss forest reserves located on the oceanically influenced Swiss Plateau?

Material and methods

Study sites and forest inventory data

We used forest inventory data from two different biogeographical regions of Europe, the continental Białowieża forest in Poland and a set of oceanically-influenced forest reserves from Switzerland. The forests of both regions are influenced by a relatively weak disturbance regime, i.e. large-scale breakdowns due to storms or fire were not observed in the analysed period, but small-scale disturbances related to insect attacks have occurred in both regions. The diameter distribution of the unmanaged forests of both regions shows a negative exponential decrease of tree numbers with increasing diameter at breast height (DBH, Fig. 1). The maximum DBH for each region was recorded for *Quercus robur*, which reaches up to 159.8 cm in Białowieża and up to 83.0 cm in Switzerland.

Białowieża forest (Poland)

The forest is situated within the core area of Białowieża National Park, which is regarded as “the best preserved lowland forest in the European temperate zone” (Bobic et al. 2000). It has been strictly protected since 1929 (Bernadzki et al. 1998). The Białowieża forest is characterised by a continental climate (Köppen and Geiger 1930–1939, Table 1) and stocks on a flat post-glacial formation within an elevation range from 134 to 202 m a.s.l. (Bobic et al. 2000). The most dominant forest communities are oak–lime–hornbeam forests (Tilio-Carpinetum) and pine–spruce–oak forests (Pino-Quercetum)

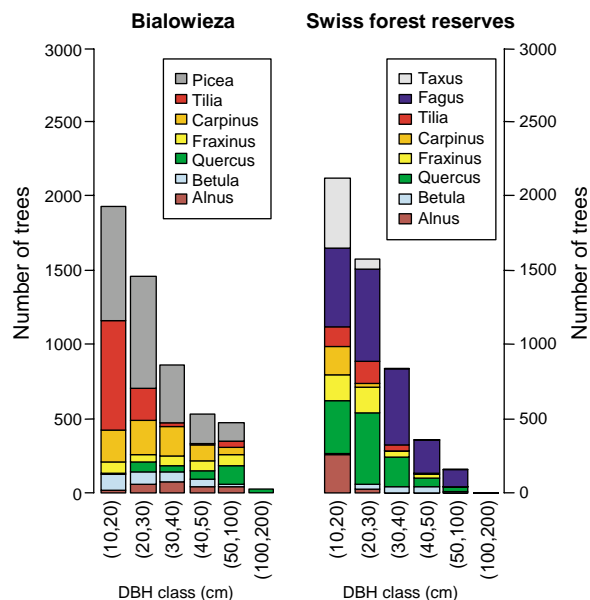


Fig. 1. Diameter distribution of the two sites Białowieża ($n = 5280$ trees, 14.8 ha) and Swiss forest reserves ($n = 5049$ trees, ca 7 ha, cf. Table 1).

(Faliński 1986). In five permanent plots, every tree ≥ 5 cm DBH has been tracked in several inventories (Table 1). For the present study, we aggregated the growth and survival information of all trees within the five permanent plots and refer to them as ‘Białowieża’. We focused on the most dominant tree species *Picea abies*, *Tilia cordata*, *Carpinus betulus*, *Quercus robur*, *Fraxinus excelsior*, *Alnus glutinosa* and *Betula* spp. (mostly *B. pendula* but also *B. pubescens*) (Fig. 1). For a detailed description of the Białowieża forest see Faliński (1986).

Swiss forest reserves

The Swiss forest reserve network was founded by Leibundgut (1957) and is now jointly maintained by the Swiss Federal Inst. of Technology Zurich (ETH Zurich) and the Swiss Federal Inst. for Forest, Snow and Landscape Research (WSL Birmensdorf). Since around 1920, these reserves experienced only extensive use, and since the 1960s, they are strictly protected. Four forest reserves were selected (Table 1, Supplementary material Appendix Table A2), which are influenced by a maritime west-coast climate (Köppen and Geiger 1930–1939). The forest reserves stock on hilly Tertiary material (molasse), post-glacial formations (lateral moraines) and Jurassic calcareous formations, covering an elevation range from 440 to 660 m a.s.l. (Swiss Federal Office of Topography 2004). The most dominant forest communities are mixed broadleaf beech forests such as Galio-Fagetum, Hordelymo-Fagetum and Carici-Fagetum. The four selected forest reserves represent beech-dominated forests (Fig. 1), and we refer to them as ‘Swiss forest reserves’. We focused on the same dominant tree species as in Białowieża except for *P. abies* and additionally on *Fagus sylvatica* and *Taxus baccata*. For a detailed description of the standard sampling procedure performed at the Swiss forest reserves, see Wunder et al. (2007).

Table 1. Site information of the analysed forest reserves.

Site	Białowieża (PL)	Swiss forest reserves (CH)
Elevation (m a.s.l.)	130–200	450–660
Coordinates	52°45'N, 23°50'E	*
Annual precipitation sum (mm)	592	910–1160
Mean annual temperature (°C)	6.7	8.2–8.9
Forest reserve establishment	1929	1962–1970
Forest strict reserve area (ha)	4747.17	93.52
Permanent plot area (ha)	14.80	ca 7
Inventories (mean of calendar years)	1970	1973
	1982	1985
	1992	1995
Number of living trees (2nd inventory) (in brackets: trees that died between the 2nd and 3rd inventory)	5280 (1081)	5049 (629)
<i>P. abies</i>	2253 (672)	–
<i>T. baccata</i>	–	548 (28)
<i>F. sylvatica</i>	–	1999 (243)
<i>T. cordata</i>	1024 (123)	321 (24)
<i>C. betulus</i>	802 (74)	219 (52)
<i>F. excelsior</i>	320 (23)	404 (83)
<i>Q. robur</i>	322 (52)	1149 (141)
<i>A. glutinosa</i>	227 (26)	278 (24)
<i>Betula</i> spp.	332 (111)	131 (34)

Notes: annual precipitation sum and mean annual temperature were derived from the Atlas of Switzerland 2004 (Swiss Federal Office of Topography 2004) and from the climate station Białystok (148 m a.s.l.), ca 65 km northwest of Białowieża. Sampled trees: from all trees at the two sites, we selected those that (1) were alive and not shrinking between the first and second inventory campaign and (2) exceeded 10 cm DBH at the first inventory campaign. PL and CH (Confoederatio Helvetica) are the official country codes for Poland and Switzerland. * see Supplementary material Appendix Table A2.

Processing of growth and survival information

We used the last three forest inventories from the Swiss forest reserves and those three inventories from the Białowieża forest that showed the largest temporal overlap with them (Table 1). Tree growth was calculated between the first and second inventory and was used to predict whether a tree survived between the second and third inventory. Tree growth was quantified as relative basal area increment (relbai), i.e. the percentage of newly created stem cross-sectional area of each individual tree (Bigler and Bugmann 2004, Wunder et al. 2007). We calculated relbai by dividing the basal area increment (BAI) of tree *i* between the first inventory (t_1) and the second inventory (t_2) by its basal area (BA) at t_2 :

$$\text{relbai}(i, t_1, t_2) = \frac{\text{BAI}(i, t_1, t_2)}{\text{BA}(i, t_2)} \text{ with}$$

$$\text{BAI}(i, t_1, t_2) = \text{BA}(i, t_2) - \text{BA}(i, t_1) \text{ and } t_1 < t_2.$$

Since we observed some negative BAI values for a few living trees (ca 1.4% of all living trees only) possibly due to measurement or transcription errors, we reduced our data set to those trees with non-negative increments that were alive at the first and second inventory (Table 1). The relbai values calculated between these two inventories were transformed to annual relbai values, since the length of the first inventory period was not constant for all Swiss forest reserves (Supplementary material Appendix Table A2). We excluded trees smaller than 10 cm DBH to avoid potentially different mortality processes in the regeneration phase. The selected trees were further tracked during the last inventory period and it was noted whether they were still alive at the third and last inventory.

Model development

For each species that occurred at both sites (Białowieża/Swiss forest reserves), we calculated logistic regression models of increasing complexity (Table 2): three 'simple' models (S1, S2, S3) contained the explanatory variables relbai (model S1), relbai and site (S2) or relbai, site and the interaction between them (S3). The indicator variable site summarises differences between the two biogeographical regions. Furthermore, we calculated three 'complex' models (C1, C2, C3) that exhibited the same structure as the simple models, but additionally contained the variable DBH, which can be considered as a rough proxy of tree age (Table 2). For those species that occurred only at one site (*P. abies*, *T. baccata*, *F. sylvatica*), we calculated two models that either contained the variable relbai (S1) or the variables relbai and DBH (C1). To avoid overfitting due to too many predictors, all presented models contained comparatively few fitted coefficients.

Table 2. Description of the six structural types of species-specific mortality models.

Predictors	Simple models			Complex models		
	S1	S2	S3	C1	C2	C3
relbai	×	×	×	×	×	×
site		×			×	×
relbai:site			×			×
DBH				×	×	×

Note: relbai was log-transformed and additionally transformed using restricted cubic splines with three knots; DBH was log-transformed. S1, S2, S3 and C1, C2, C3 are the shorthand names of the 'simple' and 'complex' models, respectively, which are used in the text.

The log-transformed variable *relbai* was additionally transformed using restricted cubic splines with three knots (Hastie and Tibshirani 1990). Restricted cubic splines are composed of piecewise third-order polynomials within intervals determined by the knots. The connections between the polynomials are forced to be smooth and the composite function is constrained to be linear in the tails (Harrell 2001). Applying restricted cubic splines allows for a nonlinear relationship to be fitted between *relbai* and the logits of the survival probabilities (Wunder et al. 2007). The variable DBH was log-transformed to decrease the weight of the relatively few trees with large DBH values.

Model performance

Model performance was assessed using the Akaike information criterion (AIC, Burnham and Anderson 2002). For each species, we identified the model with the lowest AIC value, i.e. the best goodness-of-fit. For that model, we calculated both discriminatory power and calibration measures using bootstrap techniques (Harrell 2001, Wunder et al. 2007).

Discriminatory power indicates how well the model is able to discriminate between living and dead trees, which was measured using AUC, the area under the receiver operating characteristic (ROC) curve (Fielding and Bell 1997). The ROC curve is derived by plotting all true positive values (sensitivity) against all false positive values (1-specificity). The AUC is a non-parametric and threshold-independent measure that can be interpreted as the probability that a randomly selected tree that survived between the 2nd and 3rd inventory has a higher predicted probability to survive than a randomly selected tree that died between that period (Fielding and Bell 1997).

Calibration measures express how well the predicted survival probabilities agree with the observed probabilities in the test data. In this analysis, calibration was quantified with calibration curves that relate predicted to observed probabilities. Perfect calibration, i.e. no difference between predicted and observed probabilities, is expressed by a 45° line (intercept = 0, slope = 1, Harrell 2001). Deviations from this ideal calibration curve indicate model overfitting: slope angles smaller than 45° are typical for models that are fitted too closely to the original data set, whereas slope angles larger than 45° indicate excessive regularisation, i.e. an insufficient flexibility of the model (Harrell 2001, Reineking and Schröder 2006).

All analyses were performed using R, a language and environment for statistical computing (R for Windows 2.3.1, R Development Core Team). Logistic regression models were fitted using the Design package (R-package 2.0-12, Harrell 2005). Outlier detection was performed using the car package (R-package 1.1-2, Fox 2006).

Results

Characteristics of survival and growth

During the last 10-year inventory period, approximately every fifth tree (20.5%) died in Białowieża, whereas the Swiss forest reserves exhibited a considerably lower mortal-

ity rate (12.5%, Fig. 2). However, the high average mortality rate in Białowieża was driven by *P. abies*, and without consideration of that species, the average mortality rate would decrease to 13.5%. We observed strong species-specific differences in tree survival: high mortality rates were found for *P. abies* and *Betula* spp. whereas the opposite held true for species such as *T. baccata*, *C. betulus* and *A. glutinosa* (Fig. 2).

Trees that died in the last inventory period tended to exhibit lower growth rates in the previous inventory period than surviving trees, as measured by the average *relbai* between the first and second inventory (Fig. 3). The strongest growth difference between dead and living trees was found for *T. baccata*, and the weakest for *P. abies* and *T. cordata*, where the distribution of the growth rates of dying trees was nearly identical to that of the surviving trees. However, also several fast growing trees of most tree species died during the last inventory interval (Fig. 3).

Model performance

For the species occurring in both Białowieża and the Swiss forest reserves, all models except for *Betula* spp. achieved the highest model performance (i.e. the highest goodness-of-fit) when site information was included (S3, C2, C3, Table 3). Only for *F. excelsior*, the full set of predictors was required to achieve the highest model performance (C3, Table 3). Including the additional DBH information improved the goodness-of-fit for all species but *F. sylvatica* and *C. betulus*, however, for these two species, the simpler models had only marginally lower AIC values than the complex models (S1 and C1 for *F. sylvatica*, S3 and C3 for *C. betulus*; Table 3).

The discriminatory power of the best species-specific models as measured by the bias-corrected AUC ranged between 0.62 (*P. abies*) and 0.87 (*T. baccata*) (Table 4). Thus, the selected variables *relbai*, DBH, species and site allow to differentiate well between trees that survived or died between the 2nd and 3rd inventory, least so for *P. abies*. All models were well calibrated as indicated by only

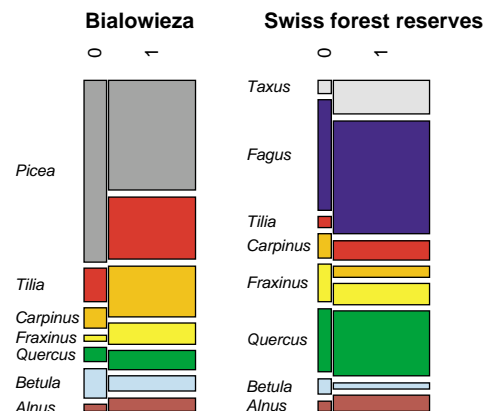


Fig. 2. Mosaic plot of the species-specific proportion of dead (0) and living (1) trees between the 2nd and 3rd inventory for Białowieża ($n = 5280$ with 20.5% dead trees) and the Swiss forest reserves ($n = 5049$ with 12.5% dead trees). Rectangle areas correspond to the proportion of the group of dead trees (left narrow column) and living trees (right wide column).

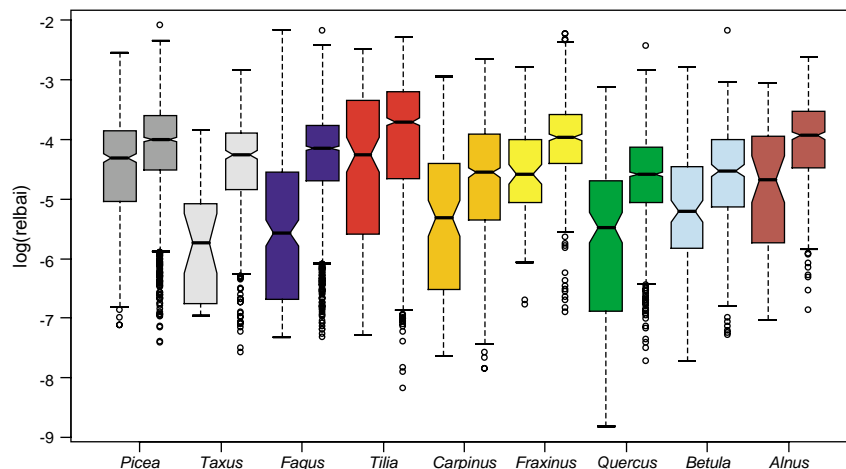


Fig. 3. Averaged annual relative basal area increment (relbai) measured between the first and second inventory, calculated for the combined data sets Białowieża and Swiss forest reserves. relbai values are shown for all dead and living trees (left box for each species = dead trees, right box = living trees). Tree numbers are given in Table 1. Box plots: the box length covers the first and third quartile of the data, the median is marked with a bold line. Notches define an approximate confidence interval of the median, “whiskers” are extended to the most extreme data point between the box and 1.5 times of the box length.

slight deviations from the perfect calibration line (intercept = 0, slope = 1, Table 4). Each species-specific model was checked for outliers. However, none of the most extreme observations could be classified as an outlier using the Bonferroni outlier test (Fox 1997).

Species-specific growth–mortality relationships

For each species and a range of growth conditions, we calculated the corresponding survival probabilities with the model that exhibited the best goodness-of-fit, i.e. the one that showed the lowest AIC value (Table 3, 5). All survival probabilities (Pr) were expressed by their logits, i.e.

$$\log\left(\frac{\text{Pr}}{1 - \text{Pr}}\right)$$

For almost all species, a reduction in growth led to a higher mortality risk (Fig. 4). Only *F. excelsior* at the Swiss forest reserves deviated from this general pattern, showing low survival probabilities under both low and high growth conditions (Fig. 4b). For many species, a larger DBH resulted in a higher survival probability (Fig. 4), i.e. the logits of the survival probabilities increased with increasing

DBH for *T. baccata*, *T. cordata*, *F. excelsior*, *Q. robur*, *Betula* spp. and *A. glutinosa*. The opposite held true for *P. abies*, even though the influence of DBH was relatively weak (Fig. 5).

The synoptic comparison of all tree species emphasises the variety of growth–mortality relationships among species and between sites (Fig. 5). In general, species-specific growth–mortality relationships differed between Białowieża and the Swiss forest reserves. The only site-independent relationship was found for *Betula* spp. (Fig. 5). The species *T. cordata*, *Q. robur*, *Betula* spp. and *A. glutinosa* exhibited the same general shape of the growth–mortality curve at both sites. For *T. cordata*, *Q. robur* and *A. glutinosa*, the survival probabilities were consistently higher in the Swiss forest reserves. By contrast, the shape of the growth–mortality relationship differed strongly between the two sites for *C. betulus* and *F. excelsior* (Fig. 5). In particular, they showed a completely different reaction to low growth in the two regions: high survival probabilities at Białowieża contrasted with low survival probabilities at the Swiss forest reserves.

Comparing the relative growth ranges of an average-sized tree (Fig. 6 and 7), there are species that show relatively

Table 3. AIC values of the species-specific models of different structure. For each species, the best model with the lowest AIC value (highest goodness-of-fit) is indicated in bold.

Species	AIC (simple models)			AIC (complex models)		
	S1	S2	S3	C1	C2	C3
<i>P. abies</i>	2673.4			2663.1		
<i>T. baccata</i>	181.8			166.5		
<i>F. sylvatica</i>	1229.5			1229.8		
<i>T. cordata</i>	909.2	885.0	880.5	856.4	847.4	847.7
<i>C. betulus</i>	731.3	719.8	715.4	728.0	721.8	717.0
<i>F. excelsior</i>	546.1	518.3	513.1	513.8	507.7	501.2
<i>Q. robur</i>	1003.6	986.0	987.5	970.2	892.0	895.9
<i>Betula</i> spp.	550.4	552.1	554.5	545.0	546.9	549.6
<i>A. glutinosa</i>	299.9	301.9	303.9	300.0	299.2	302.3

Note: the structure of the simple and complex models is described in Table 2.

Table 4. Model performance indices of the models with the lowest AIC values (Table 3). Apparent R^2 and AUC were calculated from the original sample, the corresponding bias-corrected measures as well as intercept and slope of the calibration curves were based on 1500 bootstrap samples of the original data set without replacement.

Species	Best model	R^2		AUC		Calibration curve	
		apparent	bias-corr.	apparent	bias-corr.	intercept	slope
<i>P. abies</i>	C1	0.05	0.05	0.63	0.62	0.00	1.00
<i>T. baccata</i>	C1	0.24	0.22	0.88	0.87	0.09	0.95
<i>F. sylvatica</i>	S1	0.23	0.23	0.79	0.79	0.01	0.99
<i>T. cordata</i>	C2	0.13	0.12	0.73	0.72	0.06	0.97
<i>C. betulus</i>	S3	0.11	0.09	0.69	0.68	0.08	0.95
<i>F. excelsior</i>	C3	0.26	0.23	0.80	0.78	0.10	0.93
<i>Q. robur</i>	C2	0.30	0.29	0.83	0.82	0.02	0.99
<i>Betula</i> spp.	C1	0.11	0.10	0.68	0.68	0.03	0.95
<i>A. glutinosa</i>	C2	0.15	0.12	0.73	0.71	0.11	0.94

high survival probabilities over the entire growth range such as *F. excelsior* at Białowieża or *T. baccata* in the Swiss forest reserves. By contrast, there are species that consistently show relatively low survival probabilities, such as *P. abies* at Białowieża or *Betula* spp. at both sites (Fig. 6, 7).

Trees growing under low growth conditions (i.e. at 5% of the realised species-specific growth range) showed a different behaviour in the two regions. At Białowieża, relatively low survival probabilities were found for *Betula* spp., *P. abies* and *Q. robur*, and relatively high survival probabilities for *F. excelsior* and *C. betulus* (Fig. 6, 7). In the Swiss forest reserves, the lowest survival probabilities were found for *F. excelsior*, *Betula* spp. and *Q. robur*, the highest survival probabilities for *T. cordata* and *T. baccata*.

Discussion

Characteristics of survival and growth

The observed 10-year mortality rate at Białowieża (20.5%) was distinctly higher than in the Swiss forest reserves (12.5%), which can largely be attributed to a dieback of *P. abies* at Białowieża. However, both mortality rates exceeded corresponding rates measured for managed forests in Switzerland (9.1% between 1985 and 1995, Brassel and Brändli 1999) or in Austria (4.7% during a five-year period, Monsrud and Sterba 1999). This may be explained by the longer absence of human influence in the analysed regions, especially in Białowieża. Many dead trees showed reduced diameter growth prior to death, which is in line with numerous previous investigations (Suarez et al. 2004, Bigler et al. 2007).

Model performance

Mortality models with excellent discriminatory power were found for *T. baccata* and *Q. robur* (AUC > 0.8, classification scheme by Hosmer and Lemeshow 2000). Good discrimination between dead and living trees was achieved for *F. sylvatica*, *F. excelsior*, *T. cordata* and *A. glutinosa* ($0.7 < \text{AUC} < 0.8$), whereas the mortality models for *P. abies*, *C. betulus* and *Betula* spp. were rated as 'average' ($0.6 < \text{AUC} < 0.7$). The performance is in the range of AUC values calculated for single-species mortality models

of *P. pinaster* and *P. sylvestris* in Spain based on permanent plots that were re-measured every five years (AUC: 0.796 resp. 0.754 for the fitting data set, Bravo-Oviedo et al. 2006). The analysed models in this study were not overfitted as exhibited by the good calibration measures. The relatively poor performance observed for the mortality models of *P. abies* and *C. betulus* may be a result of mortality agents that do not affect tree growth or that were not included in the models. However, most models showed at least a good performance in spite of the relatively large inventory interval of more than 10 years, which is far from the optimal annual resolution (Wunder et al. 2008). Furthermore, model performance was not seriously affected by the relatively simple model structure, which is noteworthy given the known complexity of intertwined mortality agents (Manion 1981). Environmental stress as reflected by the averaged relative growth rate (relbai) and competitiveness as reflected by tree size (DBH) seem to be important variables in predicting tree mortality, which supports findings of other inventory-based studies (Monsrud and Sterba 1999, Eid and Tuhus 2001).

Ecological interpretation of growth–mortality relationships

The growth–mortality relationship of most tree species showed a pronounced site dependence, i.e. there is no universally applicable species-specific growth–mortality relationship (Fig. 5). In a recent study, Wunder et al. (2007) also found site-dependent growth–mortality relationships for *F. sylvatica* and *Abies alba* in two near-natural forests of the Jura mountains (Switzerland). This indicates that the site independence of mortality processes is more likely to be an exception than a rule. The only species with a slow-growth tolerance independent of site characteristics is *Betula* spp. This may be explained by its specialisation to early-successional sites, which may lead to similar patterns of the growth–mortality relationship irrespective of the region.

For most tree species, survival probability increases with increasing DBH, which may be explained by the increasing storage capacity and competitiveness of larger trees. These findings are in line with those from other inventory-based mortality studies in Europe, which found decreasing mortality rates with increasing tree size for forest stands in

Table 5. Parameter values of the selected mortality models with best goodness-of-fit.

Model formula

$$\log\left(\frac{\text{Pr}}{1 - \text{Pr}}\right) = \beta_0 + \beta_1 x_1 + \sum_{j=2}^4 \beta_j (x_1 + \kappa_{j-1})_+^3 + \beta_5 x_2 + \beta_6 x_3 + x_3 [\beta_7 x_1 + \sum_{k=8}^{10} \beta_k (x_1 + \kappa_{k-7})_+^3] \text{ with } (z)_+ = z \text{ if } z > 0, 0 \text{ otherwise and } \text{Pr} = 10\text{-year survival probability, } x_1 = \log(\text{relbai} + c^*), x_2 = \log(\text{DBH}) \text{ and } x_3 = \text{site (PL} = 1, \text{CH} = 0)$$

Species	Model parameterisation													
	Parameter values β and knots κ of the restricted cubic spline transformation													
	β_0	β_1	β_2	β_3	β_4	β_5	β_6	β_7	β_8	β_9	β_{10}	κ_1	κ_2	κ_3
<i>P. abies</i>	4.647	0.440	0.071	-0.196	0.125	-0.384	0	0	0	0	0	-5.615	-4.078	-3.361
<i>T. baccata</i>	-10.095	1.382	0.431	-1.305	0.873	3.833	0	0	0	0	0	-6.040	-4.296	-3.629
<i>F. sylvatica</i>	10.009	1.743	-0.113	0.328	-0.215	0	0	0	0	0	0	-6.068	-4.233	-3.490
<i>T. cordata</i>	-0.847	1.022	-0.095	0.289	-0.194	1.591	-0.940	0	0	0	0	-5.852	-3.746	-2.917
<i>C. betulus</i>	1.827	0.207	0.626	-1.373	0.747	0	3.454	0.436	-0.682	1.496	-0.814	-6.566	-4.593	-3.472
<i>F. excelsior</i>	5.413	2.418	-0.786	1.444	-0.658	1.171	-8.713	-2.085	1.496	-2.749	1.253	-4.961	-4.056	-3.098
<i>Q. robur</i>	-0.465	1.801	-0.157	0.382	-0.225	2.075	-2.320	0	0	0	0	-5.959	-4.255	-3.328
<i>Betula</i> spp.	1.073	0.813	-0.031	0.073	-0.042	0	0.623	0	0	0	0	-6.613	-4.702	-3.750
<i>A. glutinosa</i>	1.918	1.217	-0.092	0.220	-0.128	1.105	-0.960	0	0	0	0	-5.235	-3.996	-3.228

Notes: *c was introduced to deal with 0 values (Stahel 2000), $c = (25\text{-quantile})^2 / 75\text{-quantile} = 0.002531$ where the quantiles are calculated for the relbai values excluding 0 values. relbai = averaged (annual) relbai between the first and second inventory, DBH = DBH (mm) at the second inventory. Factor coding for site [PL (Białowieża) = 1, CH (Swiss forest reserves) = 0], knots of the restricted cubic spline transformation are located at the 10%-, 50%- and 90%-quantiles of the observed log(relbai). For detailed information on standard errors and p-values of the coefficients, see Appendix Table A1.

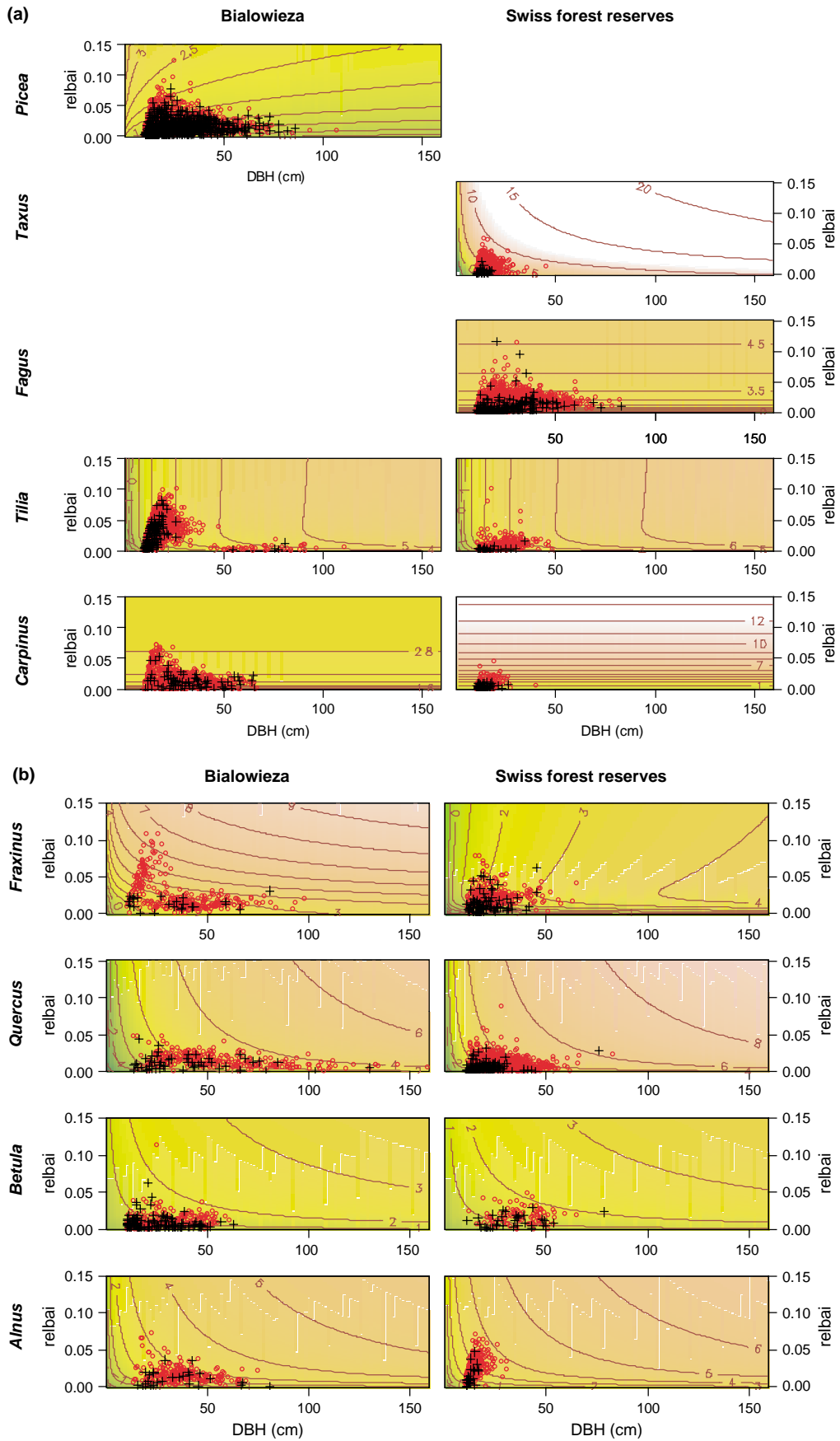


Fig. 4.

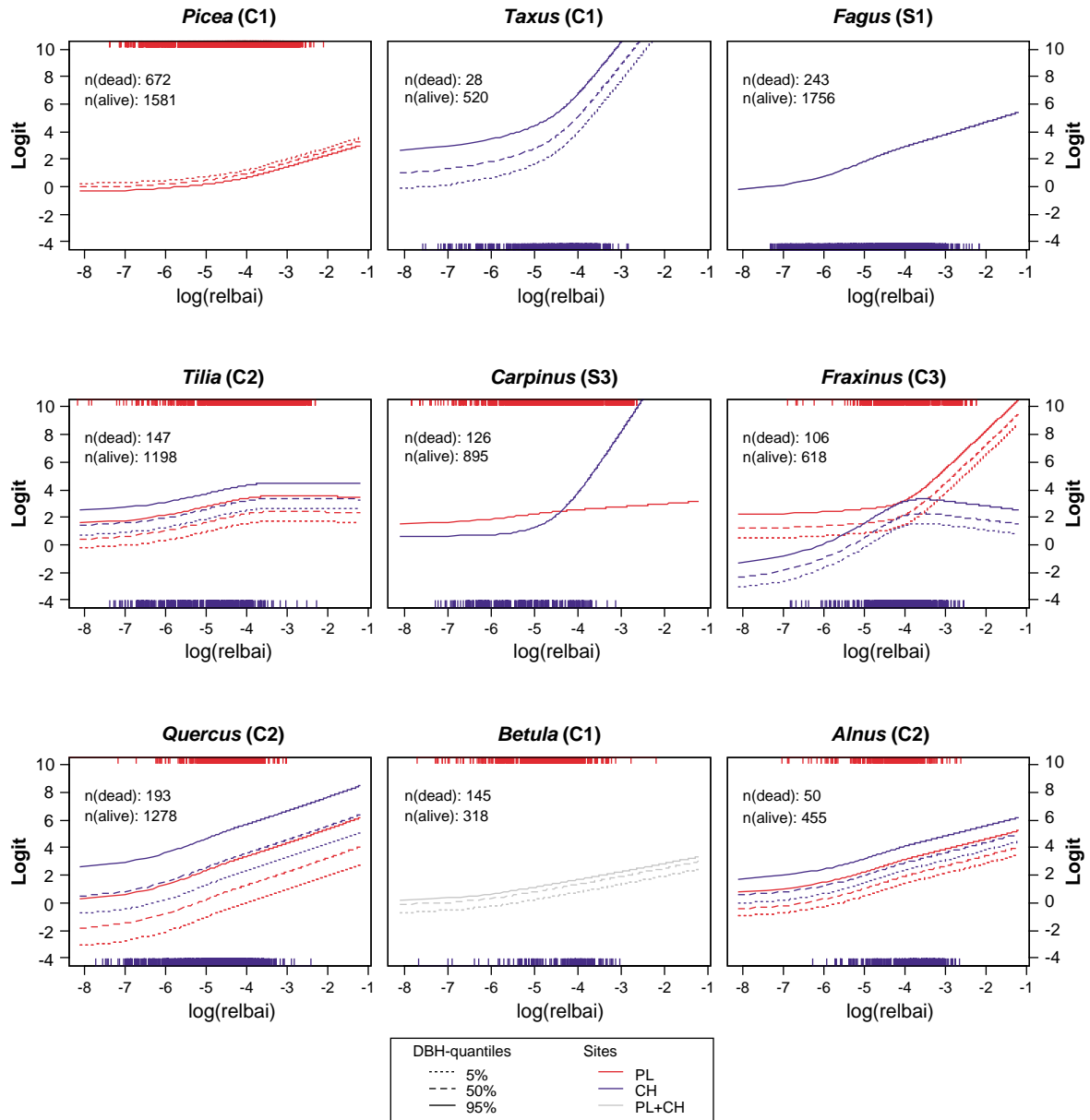


Fig. 5. Growth–mortality relationships shown as estimated logits (i.e. the logarithm of the ratio of the survival probabilities and the mortality probabilities) for a range of growth (log-transformed relbai) values. For tree species with a significant size (DBH) effect, logits are shown for the 5%, 50% and 95% quantiles of DBH (no significant size effect was found for *F. sylvatica* and *C. betulus*; Table 2, 3). Codes in brackets indicate the model structure with the highest goodness-of-fit (Table 2 and 3). Red lines show logits for Białowieża (PL = Poland), blue lines for the Swiss forest reserves (CH = Switzerland), and grey lines for site-independent models (i.e. same model for Białowieża and Swiss forest reserves; PL + CH). For each species, the distribution of the averaged annual relbai values is indicated with a rug plot (1-d plot, red: Białowieża, blue: Swiss forest reserves).

Austria (Monserud and Sterba 1999) and increasing survival probabilities with increasing diameter for forest stands in Norway (Eid and Tuhus 2001). However, a study from Sweden reported significant size effects only for one tree species (*Pinus sylvestris*); the lack of significance for other

tree species was probably due to the restricted size distribution with all trees having a DBH > 10 cm and most trees having a DBH < 35 cm (Fridman and Ståhl 2001). Due to the allometric relationship between tree height and DBH, taller trees (i.e. trees with a large DBH)

Fig. 4. Predictive map of survival probabilities for a range of growth (relbai) and size (DBH) values for (a) *P. abies*, *T. baccata*, *F. sylvatica*, *T. cordata*, *C. betulus* and (b) *F. excelsior*, *Q. robur*, *Betula* spp., *A. glutinosa*. Survival probabilities are expressed as logits, i.e. the logarithm of the ratio of the survival probabilities and the mortality probabilities. The logit values are displayed with hues ranging from dark green (logit = -2) to white (logit ≥ 12). Contour lines represent equal logits, and the values printed on the contour lines denote the corresponding logits. For example, logits of -2, 0, 2, and 5 correspond to survival probabilities of 0.12, 0.50, 0.88, and 0.99. Observed data are represented by red circles (living trees) and black crosses (dead trees).

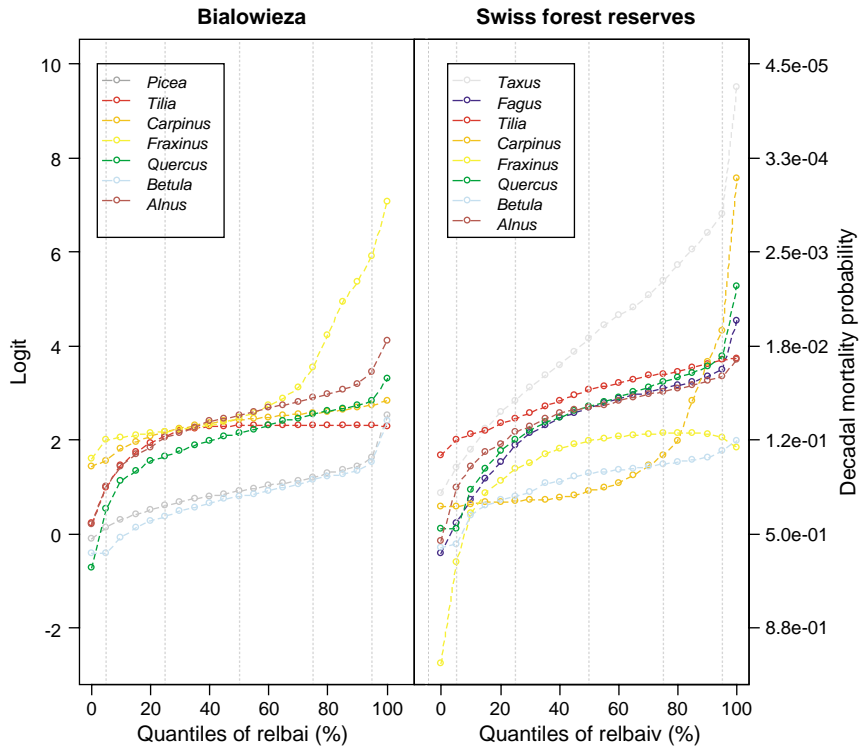


Fig. 6. Growth–mortality relationships of an average-sized tree (median of the DBH) for the range of relative growth values of each species (Białowieża and Swiss forest reserves). Quantiles of the species-specific growth values range from 0% to 100%, with one dot at each 5%-quantile. The logit (i.e. the logarithm of the ratio of the survival probabilities and the mortality probabilities) on the left y axis in the left panel corresponds to the decadal mortality probability on the right y axis in the right panel (note: values increase from top to bottom).

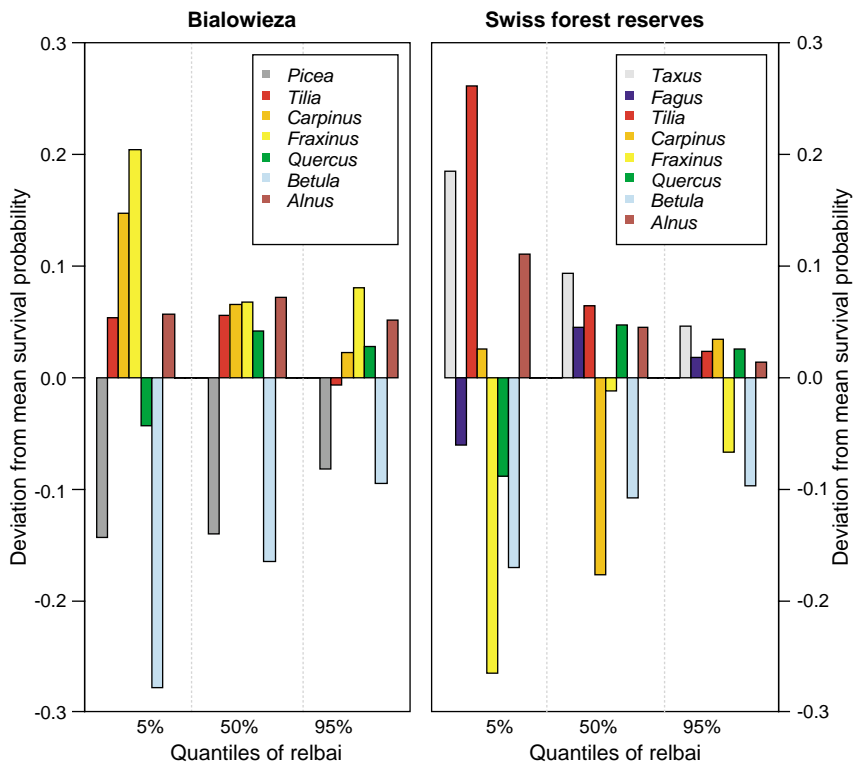


Fig. 7. Deviations of the survival probabilities of each species from the corresponding mean survival probability across all species at the 5%-, 50%- and 95%-growth quantiles (see vertical dotted lines in Fig. 6).

usually experience less competition than smaller trees. For these trees, negative effects of size such as an increased susceptibility to storm damage or lightning seem to be small relative to the benefits of size. The increasing mortality risk of *P. abies* trees with increasing DBH is likely related to the high susceptibility of spruce to bark beetle *Ips typographus* infestations of larger trees. The storm-caused death of tall trees may provide an additional explanation, which seems plausible for *P. abies* in Białowieża because its maximum height (55 metres) exceeds that of all other species by more than 10 metres (Faliński 1977). Increased mortality rates have been observed for large, old-growth *P. abies* in Austria as well, which were probably related to a loss of vigour (Monserud and Sterba 1999). The same study describes decreasing mortality rates with increasing size for *F. sylvatica*, which does not agree with the observed lack of a size effect in our study (cf. Table 3, Fig. 4). However, the two models (i.e. without and with DBH) show a similar goodness-of-fit (S1 and C1; Table 3). For *C. betulus*, size did not show a significant effect either (Table 3), which might be related to the low frequency of large trees, particularly in the Swiss forest reserves (Fig. 1). In general, there are potentially confounding effects of tree size and tree age, which are often not related linearly. However, tree size (DBH) often has to be used as a reasonable proxy for age (Harcombe 1987), because forest inventories generally do not provide tree-specific age data for uneven-aged stands (Monserud and Sterba 1999). If age data were available, the performance of the mortality models might be improved considerably. However, even without including age data in the models, we were able to show that the models achieve a high discriminatory power for many tree species.

The observed growth–mortality relationships cannot be used to conclusively test theoretical frameworks of plant defence (cf. Stamp 2004). Still, the empirically quantified stress tolerance may be used as an indicator for or against certain plant defence hypotheses. Most tree species showed increased survival probabilities with increased growth, as hypothesized by Waring and Pitman (1985). However, the reduction of the survival probabilities for fast growing *F. excelsior* (Swiss forest reserves) and to a smaller extent for *T. cordata* (Białowieża) deviates from this general pattern (Fig. 4, 6). Thus, the strategies of the latter two species support the growth-differentiation hypothesis (Herms and Mattson 1992, Stamp 2003), which states – inter alia – that very stressed and very vigorous plants are most vulnerable to any stressors. The reduced survival probabilities of vigorous trees may be explained by the increased allocation of resources to growth at the cost of defence under very favourable conditions (Fig. 6). In addition, tree herbivores often favour large plant modules (Price 1991). For example, the ash bud moth *Prays fraxinella* is an important herbivore for *F. excelsior* that is known to prefer large buds, typically found on vigorous trees (Foggo and Speight 1993).

Below, we will discuss separately the growth–mortality relationship of each tree species, i.e. their general shape and differences between the two regions (Białowieża and the Swiss forest reserves). There are some species-specific patterns in the growth–mortality relationships that are not congruent with current ecological knowledge, and there are also some strong region-specific differences of the growth–mortality relationships for *C. betulus* and *F. excelsior*

(Fig. 5, 6), which are difficult to explain given the data at hand. Some of these inconsistencies may be explained if more detailed information on abiotic site effects related to topography, elevation, temperature, soil moisture and soil characteristics as well as biotic effects related to stand density, diseases and insect attacks could be provided for each tree. However, this would require a completely different sampling regime, and possibly also additional data from other sites covering different soil and climatic conditions.

Picea abies

The relation between growth and mortality probability is relatively weak. This may be explained by the widespread occurrence of mortality agents such as bark beetles (*I. typographus*) and windstorms that often cause sudden tree death and thus mask a possible species-specific growth–mortality relationship.

Taxus baccata

The relatively high survival probabilities at reduced growth rates indicate a high stress tolerance, which agrees with the high shade tolerance and maximum lifespan (> 1000 years, Thomas and Polwart 2003).

Fagus sylvatica

This species, which is known to be quite shade tolerant (Leibundgut 1984, Ellenberg 1996), shows only intermediate survival probabilities. Thus, its smaller stress tolerance as compared to *T. baccata* and also to *T. cordata* may be related to its relatively low lifespan (up to 350 years, Piovesan et al. 2005).

Tilia cordata

In the Swiss forest reserves, the intermediate to high survival probabilities of *T. cordata* under low growth (Fig. 6, 7) are in line with its intermediate shade tolerance and high longevity (maximum age 1000 years, Pigott 1989). However, the fairly high number of small trees (low DBH; Fig. 1, 2) dying in Białowieża at relatively high growth rates deviates from this observation (high relbai; Fig. 4a). At this site, we have observed that many *T. cordata* trees had regenerated in form of distinctive clusters, and the high mortality of small trees might be a result of the intense between-tree competition and increasing overcrowding.

Carpinus betulus

Low survival probabilities at intermediate growth of this species in the Swiss forest reserves are congruent with its intermediate shade tolerance and relatively short lifetime (150 years, Bartels 1993). The growth–mortality relationship identified in the Swiss forest reserves shows a ‘bowl form’ (Fig. 7), i.e. under intermediate growth conditions, *C. betulus* shows the lowest relative survival probabilities of all tree species in the Swiss forest reserves. One possible explanation for this effect is that *C. betulus* grows relatively close to its upper elevational limit in central Europe (Ellenberg 1996). However, the switch of the described slow growth tolerance behaviour of *C. betulus* into its

opposite at Białowieża results in very high survival probabilities exceeding those of *T. cordata*, which may be a result of different environmental conditions (particularly elevation and topography), successional stages, competition or even genotypes.

Fraxinus excelsior

Similar to *C. betulus*, *F. excelsior* shows a completely different growth–mortality relationship at the two sites: low survival probabilities in the Swiss forest reserves are in line with the intermediate shade tolerance of that species (Tapper 1996), which decreases with increasing age (Prentice and Helmsaari 1991). However, at Białowieża, *F. excelsior* is among the species with the highest slow growth tolerance and its life expectancy may exceed 400 years (Faliński 1986).

Quercus robur

The low survival probabilities under low growth conditions agree with the low shade tolerance of this tree species (Bartels 1993, Ellenberg 1996). The species shows a strong increase in survival probabilities with increasing growth rates. Thus, at good growth conditions, *Q. robur* is found within a group of tree species with the highest survival probabilities in both regions. Intermediate to low mortality rates found for *Quercus* spp. in Austria (Monserud and Sterba 1999) support our findings.

***Betula* spp.**

The consistently low survival probabilities in both regions are in line with the tree's behaviour as a pioneer species characterised by low shade tolerance and low maximum age (Ellenberg 1996). Even if the observed relatively low growth rates (relbai, Fig. 3, 4b) are considerably lower than would be expected for fast-growing pioneer species (Bartels 1993), the distribution of relbai is quite similar to that of *Q. robur*, which has the same low shade tolerance as *Betula* spp. (Ellenberg 1996).

Alnus glutinosa

The intermediate to high positive deviations of the mean survival probabilities in both regions (Fig. 7) indicate a high stress tolerance caused by specific adaptations to wet micro-sites such as the symbiosis with the nitrogen-fixing bacteria *Frankia* spp. (Bond 1976). It seems that the relatively low maximum age (up to 200 years, Tallantire 1974) contrasts with the mortality behaviour of this species, which shows features that are typical of long-lived tree species. However, the estimated intermediate survival probabilities (Fig. 6) are consistent with the intermediate shade tolerance of this species (Ellenberg 1996).

Perspectives and limitations

It may be possible to group the tree species analysed here into functional groups that are characterised by similar growth–mortality relationships (Grime 1977, Brzeziecki and Kienast 1994). As an update to the life-history classification by Brzeziecki and Kienast (1994), the present

analysis suggests that some species such as *A. glutinosa* and *C. betulus* would have to be placed closer to the 'stress tolerator' corner, and *F. excelsior* further away from the 'competitor' corner of Grime's triangle (Brzeziecki and Kienast 1994).

Because growth patterns are influenced by a range of different environmental variables, there is a potential confounding effect of variables that are not considered in the models. For example, slow growth may be explained by site effects such as shallow soils (e.g. low soil moisture holding capacity) or low temperature, but just as well also by the incidence of diseases or high stand density. Lorimer et al. (2001), for example, found changes in mortality–size trends with stand age for mature and old-growth forests. However, the models in our study only contain a general 'site' variable (Table 2), which implicitly integrates different environmental effects such as the climate regime, soil depth, stand density or disturbance regimes. To separate these potentially confounding effects and to further evaluate the observed differences in the growth–mortality relationships across the two biogeographical regions, micro-site information at the tree level and at the level of permanent plots (e.g. soil type, soil moisture, degree of competition, forest community type; cf. Caspersen and Kobe 2001, Getzin et al. 2006) would have to be included in the models. Additional tree species and inventory data from different biogeographical regions could be used for the estimation of a new generation of species- and site-specific mortality models. The high spatial variability of growth–mortality relationships between two climatically different regions also raises the question about the temporal variability within sites that could be driven for example by climate variations. Additional investigations of long-term research networks could help to elucidate the behaviour of species-specific growth–mortality relationships with time.

The aggregation of the five permanent plots of Białowieża and the four Swiss forest reserves may have led to a bias, because heterogeneity within the two sites is not reflected. Further analyses could focus on this heterogeneity, but they would have to be restricted to those species that are present at each permanent plot. Furthermore, our species-specific models do not incorporate variations caused by different genotypes. Genetic analyses of tree species at both sites could highlight potential differences due to environmental conditions or herbivory pressure (Pritinen et al. 2006) that may help to better understand the site dependence of the growth–mortality relationship.

The growth–mortality relationships that have been quantified in our study may help forest managers to identify trees that are prone to die. For example, a random sampling of trees in even-aged unmanaged forests and a record of the growth information for each selected tree (e.g. DBH records every five years) would allow for an estimation of the expected mortality probabilities in the entire stand. In regions with a high proportion of even-aged unmanaged stands that are typical of many current protection forests in the European Alps, such estimations could identify sites with the highest overall mortality risk. Regarding basic research, species-specific growth–mortality relationships could be implemented into forest succession models, e.g. gap models (Shugart 1984), and replace their mortality submodels, which are often based on theoretical

assumptions rather than field data (cf. Keane et al. 2001, Wunder et al. 2006). Ideally, improved gap models would project structural and compositional features of tomorrow's forests in a more reliable manner, which in turn would help today's forest managers.

In conclusion, the application of mortality models to forest inventory data from different biogeographical regions shows the absence of a simple universal growth–mortality relationship: most mortality models differed among species and between the two regions. Thus, the observed variability of mortality phenomena might hinder a grouping of species into functional groups. However, the flexible models identified in this study were able to pinpoint changes of the growth–mortality relationship of one species, e.g. reduced survival probabilities at low and high growth rates. Hence, they could also be used to analyse ecological phenomena of forest dynamics beyond the specific context of tree mortality.

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Supplementary material (available online as Appendix O16371 at www.oikos.ekol.lu.se/appendix). Table A1: Parameter values of the mortality models with the best goodness-of-fit for each species. Table A2: Detailed site information of the analysed Swiss forest reserves.