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Mortality patterns of *Quercus*, *Tilia*, and *Fraxinus* germinants in a floodplain forest on the river Elbe, Germany

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Abstract

In a floodplain forest on the Elbe river, the effects of elevation—considered as a surrogate for drought stress—and light availability on the mortality of germinants of penduncular oak (*Quercus robur*), common linden (*Tilia cordata*), and red ash (*Fraxinus pennsylvanica*) were examined during the first growing season. For penduncular oak, elevation and light availability interacted, resulting in mortality rates on higher elevated sites depending upon light availability; on lower elevated sites mortality was rather independent of light, probably because better access to water resources compensated for decreased light availability. By contrast, the mortality patterns of common linden and red ash highly depended upon light availability on all sites. These species-specific mortality patterns are explained by different capabilities to access water resources due to different root-to-leaf biomass ratios being at least four times higher for penduncular oak as compared with the other species. This life history trait allows penduncular oak germinants to better access the water resources than common linden or red ash.

Light availability for germinants on these nutrient-rich floodplain sites is strongly reduced by competing ground vegetation. For forest management it is not recommended to create gaps for promoting natural regeneration on these sites until the end of the first growing season, in order not to enhance competition by pre-established ground vegetation.

Keywords: Floodplain forest; *Fraxinus pennsylvanica*; Light availability; Mortality; *Quercus robur*; *Tilia cordata*; Water availability

1. Introduction

Mortality of tree germinants is an important process affecting natural regeneration of forests. Mortality rates may influence the density of the seedling pool in forests (Streng et al., 1989). Since seedling sensitivity to harsh environmental conditions or to microhabitat structures which cause mortality can be species-specific (Collins, 1990; Jones et al., 1994; George and Bazzaz, 1999), mortality patterns may also alter species composition within a regeneration. The early phase of establishment of germinants is the most sensitive phase of regeneration, with mortality rates generally being highest (Collins, 1990; Jones et al., 1994). Therefore, investigations on species-specific mortality patterns can contribute to identifying relevant environmental factors which affect survival of germinants or seedlings and, by this, can alter density, tree species composition or age structure of the regeneration. These environmental factors, in the long run, can influence spatial or age structure of forests on community level (Collins, 1990) or—as large-scaled disturbances—on landscape level (Adams and Anderson, 1980; Sakio, 1997).

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In floodplain forests of the humid regions, flooding and light are considered to be the most important environmental variables for seedling establishment (Siebel, 1998). Floods can provide new habitats like gravel bars or sand on riverbanks for succession (van Splunder et al., 1995; Cordes et al., 1997) or may change the geomorphic conditions, such as elevation of sites or organic content of soils, and, by this, can modify tree species composition (Fonda, 1974; Nakamura et al., 1997). Large-scale disturbances like flooding can alter the age distribution of a riparian forest (Duncan, 1993; Sakai et al., 1999) or may alter succession on landscape level (Yin, 1998). Summer floods may lower the probability of seedling establishment to a greater extent than spring floods because of the reduced flood tolerance, especially of species from hardwood floodplain forests, during the growing season (Siebel, 1998). On the other hand, summer floods may reduce competition by flood-intolerant tall herbs and, by this, may promote seedling establishment (Siebel and Bouwma, 1998). Floods, in general, may limit seedlings of flood-sensitive species to higher elevated sites (Streng et al., 1989). Seedlings may respond species-specifically to light gradients in floodplain forests as regards to their mortality or growth. Hall and Harcombe (1998) carrying out long-term investigations on abundance of saplings in a Texas floodplain forest point out that both factors, flooding and light, may interact; this interaction may allow light demanding but flood tolerant species to survive under lower light conditions owing to competitive advantages against shade-tolerant but flood-intolerant species.

In addition to flooding or light, occasional water deficiency during the growing season may influence seedling mortality (Jones and Sharitz, 1998; Streng et al., 1989) or may cause vegetation differences (Hawk and Zobel, 1974).

The objectives of this study were: (i) to monitor mortality rates of germinants of three different tree species (*Quercus robur*, *Tilia cordata*, and the introduced tree species *Fraxinus pennsylvanica*) present in a floodplain forest on the Elbe river, Germany; (ii) to detect abiotic environmental factors relevant for mortality patterns within the first growing season. On this basis, autecological characteristics of these tree species shall be described and conclusions be drawn with respect to adequate silvicultural methods for natural regeneration of floodplain hardwood forests.

2. Material and methods

The investigations were carried out in a periodically flooded hardwood forest which is located on the Elbe river in the vicinity of Dessau in Germany (^{57}51530, ^{33}07415 Gauss–Krüger co-ordinates). Mean annual temperature in the natural area of the Elbe-Elster-Lowlands is 8.7 °C. Flooding occurs periodically in March–April (Institute of Hydrology, 2000). The forest stand is composed of six different tree species, with common linden, penduncolate oak, and red ash prevailing with 60, 30 and 5%, respectively, of the growing stock. Vegetation constituted by herbs (e.g. *Aegopodium podagraria*, *Urtica dioica*) and sedges (e.g. *Carex brizoides*) was already established when the investigations started; this understorey vegetation covered almost the whole ground. The nutrient-rich gleyic soil type is made up of alluvial loams.

In December 1998, four small-scale gaps within the stand were artificially created. Two of them were located on high-elevation sites, whereas the two other gaps were located on low-elevation sites. Within each gap 12 plots of 1 m^2 size were systematically established for characterization of ground vegetation and for monitoring tree regeneration. The ground vegetation was described in terms of the degree of area it covered and mean height for each species. Within one of both, a higher and a lower elevated gap, four additional plots were established. Within these plots ($n = 8$) the ground vegetation was manually removed during the whole growing season to allow tree regeneration free growth without competition ("free-to-grow plots"). To expand the range of environmental conditions in terms of light availability, eight additional plots were established beneath the canopy of the stand. Altogether, 64 plots differing in elevation and light availability were considered for monitoring germinants and seedlings. In this study, the term "germinant" is used for trees from germination until the beginning of the second growing season, after that being named "seedling".

Within the 64 plots, germinants of the three investigated tree species were individually tagged in June of

1999. Only vital germinants were selected which should represent the whole range of light conditions and elevation (height above sea level (a.s.l.), m) with $n = 186$ for penduncular oak, $n = 233$ for common linden and $n = 193$ for red ash. Germinants were censused in September 1999 (first observation period from June to September 1999), May 2000 (end of second observation period) and—as seedlings—in September 2000 (end of third observation period).

It was assumed that within the first 2 years after germination, intraspecific competition within the regeneration is not important for mortality patterns of the seedlings. Since light availability is considered to be one of the most important abiotic factors for seedling performance (Finzi and Canham, 2000), light resource availability was measured in July 1999 using a LiCor LAI-2000 on a single plot basis. Readings for determining the degree of available diffuse radiation (difn) were taken at two different heights above the plots: one measurement was made at a height of 1.8 m above soil surface to exclude the influence of ground vegetation on light availability, and the other one at 0.1 m within the ground vegetation. At each height two readings of difn were taken. Measurements within the forest were then related to simultaneous measurements in the open field (full light = 1) and, finally, both readings at each height were averaged to obtain a mean difn value.

Water availability could not be measured on a single plot basis. Since Richards et al. (1996) found that in floodplain forests relationships between elevation and water availability exist, the height a.s.l. (m) of each single plot was determined as a surrogate for water availability. To reveal relations not only between elevation and water availability but also between soil depth and water availability, soil water tension was permanently measured within two plots in 1999. One of the plots was located in a higher elevated gap (58.0 m a.s.l.), and the other one in a lower elevated gap (57.3 m a.s.l.). At each plot, two tensiometers (UMS, T6) were set up at different soil depths (0.1 and 0.3 m). During summer of 1999, soil water tension exceeded the device measuring range. Therefore, only tentative comparisons of soil water status between the different elevations and soil depths could be made.

Vitality of the ground vegetation was characterized by summing up the product of degree of vegetation cover of each single species within a plot multiplied by the mean height (m) of that species. The relationship between available light (difn) at 1.8 m height and the vitality of the ground vegetation (dependent variable y) was quantified by a Michaelis–Menten regression, as follows (Eq. (1)):

$$y = \frac{P_1 x}{P_1/P_2 + x} \qquad (1)$$

with x: difn at 1.8 m height, P_1 and P_2 model parameters to be estimated.

In July 1999 germinants of penduncular oak ($n = 61$), common linden ($n = 60$) and red ash ($n = 59$) were harvested outside the plots to determine biomass parameters. The germinants were dug out and kept cool in ice; in the lab the germinants were dried (24 h, 105 °C) and, afterwards, the dry weights of roots and leaves were measured. By executing a rank analysis of variance (Bortz et al., 1990), root-to-leaf biomass ratios of the three tree species proved to differ significantly ($P < 0.05$). In consequence, pairwise comparisons for all combinations of the three tree species were made using the Mann-Whitney U test (Bortz et al., 1990) where H_0 ($P < 0.05$) refers to the hypothesis that there are no differences between the mean rank of two of the three tree species concerning the root-to-leaf biomass ratio.

Mortality within the first growing season was analysed by logistic regression which estimates the probability p of an event occurring. The dependent variable y is dichotomous taking the value 1 for dead germinants with probability θ and the value 0 for live germinants with probability $1 - \theta$. For more than one independent variable the logistic regression model can be written as (Eq. (2), SPSS, 1990):

$$p = \frac{1}{1 + \mathrm{e}^{-z}} \qquad (2)$$

where z is the linear combination $z = b_0 + b_1x_1 + b_2x_2 + b_3x_1x_2$ with x_1 corresponding to height a.s.l. (m) and x_2 to difn. Predictor variables were selected by forward stepwise selection. Accuracy of regression models was diagnosed by: (i) indicators of model goodness (e.g. model significance); (ii) evaluating the proportion of correct predictions of the observations made by the model. Tests for all logistic regressions showed that the normalized residuals did not deviate from normal distribution. Finally, it has to be discussed whether the models are biologically plausible.

3. Results

3.1. Environmental factors

In 1999, precipitation amounted to 537 mm, compared to a long-term mean of 550 mm. Within the growing season (May–September), the precipitation was 269 mm in 1999, corresponding to the long-term mean of 276 mm (Institute of Hydrology, 2000). The plots' elevations ranged from 57.2 to 58.1 m height a.s.l. Measurements of soil water tension could be performed from April 20 to July 29 (Fig. 1). In July 1999 the soil water tension rose distinctly. Variation of soil water tension values was greater at 0.1 m depth than at 0.3 m depth. Furthermore, water supply was higher at lower elevation.

Monthly precipitation in July, August and September 1999 was 56, 56 and 43 mm, respectively (Institute of Hydrology, 2000). With the precipitation remaining constant over time and the demand of the vegetation for water resources rising, the soil water tension was probably drastically increasing during August and September as compared to July, by this exceeding the measuring range of the devices. It is concluded that water availability in August and September was lowest in the top soil level, and in higher elevated sites.

In 1999, the winter flood was totally drawn back from the plots around April 6. In 2000, the flood reached the experimental plots on March 14 with the maximum water level (57.7 m a.s.l.) on March 16. So, not all plots were submerged during the flood event. The flood dropped slowly from March 16 and vanished on April 7. As of that day until April 14 only stagnant water was found within some lower elevated plots where water discharge was impossible due to the microtopography around the plots.

3.2. Light–ground vegetation relations

Both the canopy of the mature stand as well as the ground vegetation cause light extinction and, therefore, decrease the degree of available light. The degree of available diffuse light at a height of 1.8 m above ground level averaged 0.14 (standard deviation (sd): ±0.06, maximum: 0.26, $n = 56$ plots). Relations between difn at 1.8 m height and the vitality of the ground vegetation could be detected, although the coefficient of determination was low (Table 1) due

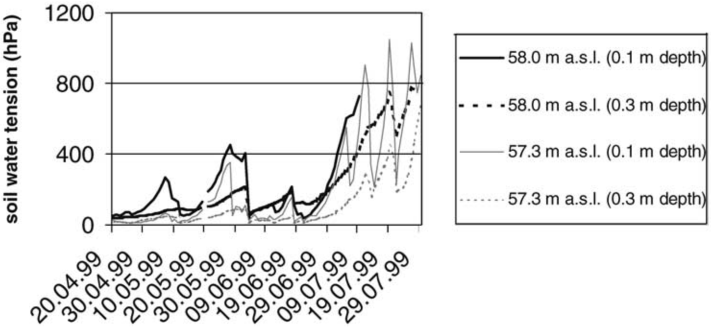

Fig. 1. Course of soil water tension (hPa) in 1999 in dependence upon height a.s.l. (m) and upon soil depth (m).

Table 1
Relation between the degree of available light at 1.8 m height (difn) and the vitality variable[a] y of ground vegetation

Parameter	Estimate	Asymptotic standard error	Asymptotic confidence interval (95%); lower–upper
P_1	0.93	0.12	0.69–1.18
P_2	22.04	8.98	3.97–40.12

[a] Vitality variable y: degree of vegetation cover × height (m) on single species basis, $y = (P_1 \times \text{difn})/(P_1/P_2 + \text{difn})$; $r^2 = 0.22$; $n = 48$.

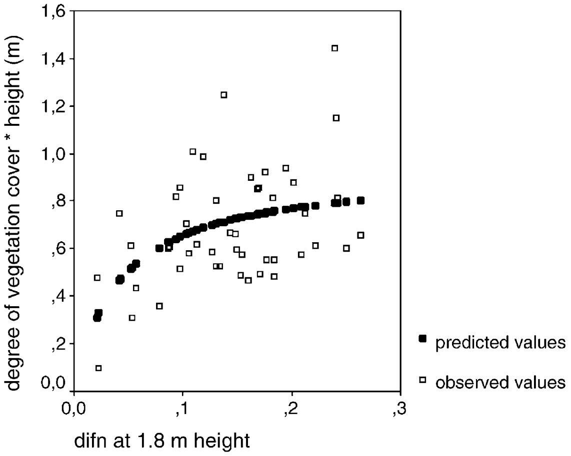

Fig. 2. Relation between vitality of ground vegetation, expressed as the summed-up product of degree of vegetation cover and the mean height of ground vegetation on species basis, and the degree of available light (difn) at 1.8 m height. Regression model from Table 1.

to high variation of observed data. The maximum value for the vitality variable reached 1.44 indicating that the whole surface of the plots was covered with ground vegetation (degree = 1) with a mean height of the single species of 1.44 m. The residuals of the regression showed no trend for heteroscedasticity.

As is evident from Fig. 2, the vitality of the ground vegetation stays almost constant at light levels >0.1, apparently only decreasing when difn drops below 0.1. Effects of ground vegetation on light availability can be seen from the degree of available diffuse light (difn) at a height of 0.1 m: within the ground vegetation difn averaged 0.03 (sd: ±0.02, maximum: 0.09, $n = 56$ plots). When ground vegetation was manually removed mean difn values amounted to 0.12 (sd: ±0.04, maximum: 0.16, $n = 8$ plots).

3.3. Root-to-leaf biomass ratio of germinants

Table 2

Root dry weight (mg) and root-to-leaf biomass ratio for penduculate oak, common linden and red ash germinants

	Roots (mg) ± sd	Root-to-leaf biomass ratio[a] ± sd	n
Penduculate oak	364 ± 225	2.8 a ± 2.0	61
Common linden	12 ± 8	0.7 b ± 0.3	60
Red ash	8 ± 4	0.5 c ± 0.3	59

[a] Different letters indicate significant differences (Mann-Whitney U test, $P < 0.05$).

The root dry weight of penduculate oak germinants reached a mean value of 364 mg and differed distinctly from the mean values of common linden (12 mg) and red ash (8 mg, Table 2). Penduculate oak germinants possessed root weights which exceeded leaf weights by a factor of 2.8. The root-to-leaf biomass ratio of penduculate oak was four times higher than that of common linden and more than five times as high as red ash, with the differences between all tree species being significant.

3.4. Mortality patterns of seedlings in a floodplain forest

3.4.1. Mortality during the entire observation period

At the end of the entire observation period, cumulative mortality rates showed pronounced differences between penduculate oak germinants on one hand (55%) and common linden (76%) and red ash (72%) on the other (Fig. 3). The first period of observation (June–September 1999) proved to be most decisive in terms of seedling mortality with red ash (63% mortality) and common linden (59% mortality) being the most sensitive species followed by penduculate oak (34% mortality).

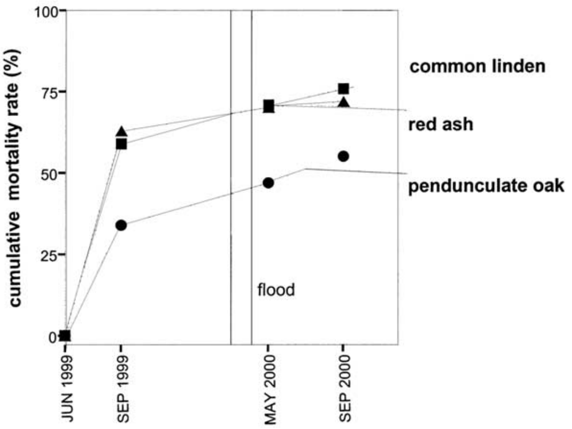

Fig. 3. Cumulative mortality rates for penduculate oak, common linden and red ash during the period from June 1999 to September 2000 derived from four census dates (sample size in June 1999: $n = 186$ for penduculate oak, $n = 233$ for common linden, $n = 193$ for red ash).

Table 3
Logistic regression model for mortality of penduncilate oak germinants ($n = 186$) during the first observation period (June—September 1999)[a]

Variables	Parameter estimate	Standard error	df	Sign
Constant	−240.6	87.7	1	0.006
x_1[b]	4.19	1.52	1	0.006
x_2[c]	2638.2	1328.2	1	0.047
x_1x_2	−46.2	23.1	1	0.046

[a] −2LL: 201.3, model chi-square: 38.2, r^2: 0.19, model df: 3, model significance: $P < 0.001$. The degrees of freedom (df) for the model chi-square are the difference between the df for the two models (models including all terms and including the constant only, respectively) being compared.

[b] x_1: height a.s.l. (m).

[c] x_2: difn.

3.5. Penduncilate oak mortality

During June–September 1999 height a.s.l., difn and their interaction (x_1x_2) significantly affected the survival of penduncilate oak germinants (Table 3). Mortality probability was highest when penduncilate oaks germinate on upper elevated sites and suffer from competition for light (Fig. 4). On these sites, survival of seedlings is improved when light availability increases. For instance, given an elevation of 58 m a.s.l., the critical value (mortality probability $p = 0.5$) for germinant survival is achieved when light availability at 0.1 m drops to <0.06. In contrast to that, on lower elevated sites the increase in mortality with decreasing light availability is far less pronounced. This is due to the interaction of the two variables height a.s.l. and difn, indicating that penduncilate oak germinants on lower elevated sites could stand competition for light better than did germinants on higher elevated sites. The mortality probability for germinants growing at an elevation of 57.2 m a.s.l. with no light available is as low as 0.28.

For assessing the goodness of fit of the model, some indicators are included in Table 3. The −2 log likelihood (−2LL) is about 200, the coefficient of determination is 0.19. The model chi-square tests the null hypothesis that the coefficients for all the terms in the current model, except for the constant, are 0 (SPSS, 1990). For penduncilate oak mortality, the model including the constant and the three variable terms is significantly different from a constant-only model. 71% of the observations on mortality or survival of germinants are correctly predicted indicating a sufficient accuracy of the model.

During the period from September 1999 to May 2000 only a small proportion of penduncilate oaks died (23 out of 122). The mortality data showed no relationship to any of the two environmental factors (height a.s.l., difn) or to the interaction of either two. From the middle of March to the beginning of April 2000, just before sprouting, the forest was flooded.

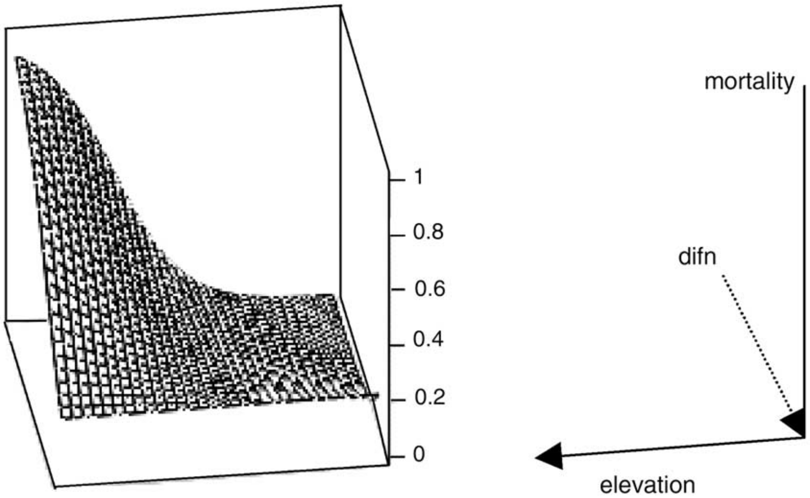

Fig. 4. Modelled mortality probabilities for penduncilate oak germinants in dependence upon elevation (m) and upon difn. Arrows indicate increasing elevation and increasing difn, respectively, with the range of scale corresponding to the measured data.

Table 4
Logistic regression model[a] for mortality of common linden germinants ($n = 233$) during the first observation period (June–September 1999)[b]

Variables	Parameter estimate	Standard error	df	Sign
Constant	2.074	0.288	1	<0.001
x_1x_2	−0.53	0.076	1	<0.001

[a] Refer to Table 3 for more explanations.
[b] −2LL: 247.1, model chi-square: 67.9, r^2: 0.25, model df: 1, model significance: $P < 0.001$.

The seedlings seemed not to be affected by this, since mortality in summer of 2000 (May–September) was very low (16 out of 99 oaks died), also indicating that either the environmental conditions were favourable for seedling survival or that the seedling vigour was high enough to withstand any potential harsh conditions.

3.5.1. Common linden mortality

Mortality of common linden germinants during the first observation period was high (59%). The significant interaction term (x_1x_2) from logistic regression analysis (Table 4) indicates that both environmental variables, height a.s.l. and difn, influenced mortality. But, as is apparent from the model presented in Fig. 5, the decisive factor for mortality is the degree of available light (difn), since this factor contributes primarily to the mortality patterns. Given an elevation of 58 m a.s.l., the critical value (mortality probability $p = 0.5$) for the survival of common linden germinants is achieved when light availability at 0.1 m height drops to <0.07. This critical value is virtually independent of height a.s.l.

The model predicts 77% of the observations correctly. The overall goodness of fit of the model, when −2LL (247.1) and the proportion of correct hits is regarded as a synopsis, is sufficient.

During September 1999 and May 2000, 30% of the remaining common linden germinants died, with the tendency of mortality probabilities to be highest on the lower elevated sites: 20 of 40 germinants growing on plots with elevations below the highest elevation of the flood in April 2000 (<57.7 m a.s.l.) died, whereas 47 out of 55 germinants growing on sites with an elevation >57.7 m a.s.l. survived. Most of the 1999 germinants still alive in May 2000 survived the second growing season (57 out of 67 seedlings).

3.5.2. Red ash mortality

The highest mortality rates during the summer of 1999 were recorded for red ash (63%). Logistic regression explained 39% of the variance of mortality patterns with the interaction term x_1x_2 of height a.s.l. and difn being significant (Table 5).

The model from Table 5 being presented in Fig. 6 makes clear that, again, the degree of available difn limited survival of red ash germinants during summer of 1999 more than height a.s.l. does. The critical light

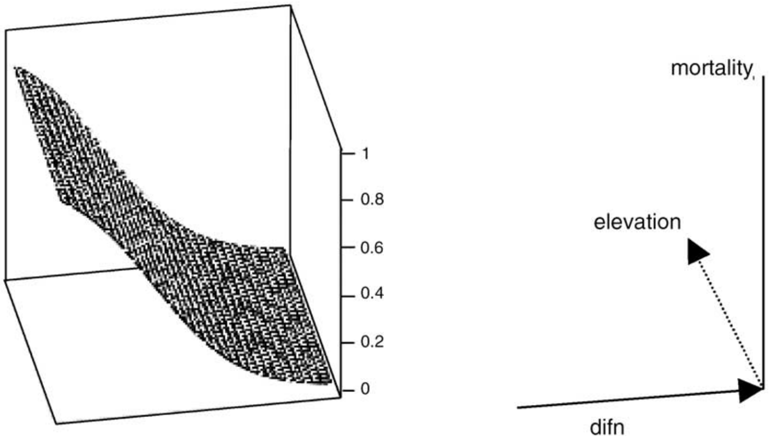

Fig. 5. Modelled mortality probabilities for common linden germinants in dependence upon height a.s.l. (m) and upon difn. Arrows indicate increasing elevation and increasing difn, respectively, with the range of scale corresponding to the measured data.

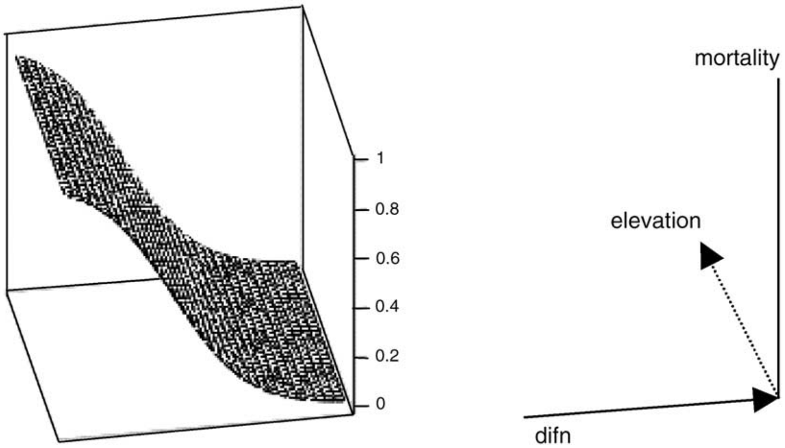

Fig. 6. Modelled mortality probabilities for red ash germinants in dependence upon height a.s.l. (m) and upon difn. Arrows indicate increasing elevation and increasing difn, respectively, with the range of scale corresponding to the measured data.

Table 5
Logistic regression model[a] for mortality of red ash germinants ($n = 193$) during the first observation period (June–September 1999)[b]

Variables	Parameter estimate	Standard error	df	Sign
Constant	2.877	0.372	1	<0.001
x_1x_2	−0.648	0.087	1	<0.001

[a] Refer to Table 3 for more explanations.

[b] −2LL: 159.0, model chi-square: 96.0, r^2: 0.39, model df: 1, model significance: $P < 0.001$.

level (difn at 0.1 m height) for a mortality probability p of germinants of 0.5—assuming an elevation of 58.0 m a.s.l.—is 0.08.

The regression model is significant (Table 5), with −2LL being the lowest of the three species-specific models. Most of the observations are predicted correctly by the model (83%).

During the second observation period (September 1999–May 2000), every fifth germinant (21%) died. Almost all seedlings (96%) survived the second growing season (May–September 2000).

4. Discussion

The climatic conditions of 1999, when the mortality of germinants of the three considered tree species was analysed, corresponded to the long-term average. Under these normal conditions two of the three species (common linden, red ash) showed high initial mortality rates, whereas penduncule oak germinants to a major degree survived the first growing season. Two environmental factors were related to mortality rates of the three species within the first growing season: height a.s.l., which served as a surrogate for water availability, and the degree of available diffuse light (difn) at 0.1 m height. While difn could be measured on a single plot basis, it was not possible to completely relate site characteristics (elevation, soil depth of the tensiometer location) to water availability. This was due to a restricted measuring range of the devices. But, from the measurements taken some general tendencies could be shown for site-water availability relations. Higher elevated sites showed lower water availability than lower elevated sites. Water availability is again lower on a short-term basis at the top level soil as compared to deeper soil due to higher variation of water tension values. These findings are confirmed by data reported by Richards et al. (1996), showing that soil water status of sites on the Isère river (France) in summer decreased with increasing elevation; also, recorded data showed increasing water availability with greater soil depth.

Ground vegetation responded to a decrease of available light at 1.8 m height by a reduction of the vitality parameter used in this study. Siebel and Bouwma (1998) found that the probability of the occurrence of herbs in a floodplain along the Rhine was related to the degree of light transmitted through the canopy. Tall herb species, like *U. dioica*, also present in the floodplain forest studied here, were only absent (probability of occurrence <0.5) when the degree of transmitted light was less than approximately 4%. It has to be considered that the variation of the vitality parameter was high; this may, among others, reflect the differing composition of ground vegetation: with sedges prevailing within a plot, the vitality parameter will be lower by way of calculation due to lower mean height of sedges as compared to tall herbs.

As found in other forests (Streng et al., 1989; Collins, 1990; Jones et al., 1994), mortality was highest during the first growing season. The mortality pattern of pendunculate oak germinants found in this study presented a complex species-specific response to environmental factors. Pendunculate oak germinants showed only a slight dependence of mortality rates upon light availability at lower elevated sites during the first growing season. This was explained by high root-to-leaf biomass ratios which enabled oak germinants to better access the water resources as compared to common linden and red ash. Light availability seemed to be of minor importance under these environmental conditions. On higher elevated sites, water availability in summer time of 1999 was generally lower. Here, with the possibility of compensating for low light levels with high water availability being distinctly less, even pendunculate oak germinants were suffering from water deficiency resulting in mortality rates mainly dependent upon light availability. During investigations in a floodplain forest in eastern Texas, Streng et al. (1989) found that water oak (*Quercus nigra*) germinants better survived drought stress than other tree species; they assumed that these differences among species may have been caused by the significantly longer roots of water oak as compared to other species. The relatively high shade tolerance of *Quercus rubra* germinants was demonstrated in investigations on survivorship on terrestrial sites (George and Bazzaz, 1999). Survivorship of *Q. rubra* within the first growing season was even distinctly higher (∼80%) as compared to the survivorship of *Q. robur* in this study presumably because of generally better water availability during the growing season.

Hall and Harcombe (1998) analysed mean abundance of saplings in a Texas floodplain forest over 10 years; they found evidence that flooding and shade tolerance interacted species-specifically, leading to the persistence of some flood tolerant species under lower light conditions than expected. Likewise, it was found in the study presented here, that pendunculate oak germinants can stand extremely low light levels if a sufficient water resource availability during the growing season was provided.

The level of common linden germinants' mortality in summer 1999 was high when compared to that of pendunculate oak. The mortality rate was negatively correlated to the degree of available light. No distinct influence of height a.s.l. on mortality was detected, although this variable was statistically significant. The high mortality rate being virtually independent of elevation may be explained by insufficient access of common linden germinants to water resources due to an unfavourable root-to-leaf biomass ratio. Despite height a.s.l. not being important for germinant survival during the first growing season, this factor seemed to influence mortality during the second observation period (September 1999–May 2000), since most of the germinants within lower elevated plots died. Reasons for that could not be revealed. It remains unclear whether water that stayed within lower elevated plots after flooding in March/April 2000 had affected germinants vitality and, thus enhanced mortality (damping-off effect).

Red ash germinants responded almost in the same way to the environmental conditions in 1999 as did common linden germinants. Again, it is assumed that the limited access to water resources due to low root-to-leaf biomass ratios made germinants sensitive to decreased light availability. Similar results concerning the light dependence of mortality patterns were found for *Fraxinus americana* germinants on terrestrial sites (George and Bazzaz, 1999).

The goodness of fit of the regression models has to be interpreted with the help of a synopsis of several statistic criteria. All models were highly significant. Regarding −2LL and the coefficient of determination, the mortality patterns of red ash germinants could be modelled best, followed by common linden germinants and pendunculate oak germinants. Anyhow, coefficients of determination were lower than 0.4, which might indicate that other factors like pathogens or herbivores (mice, snails) affected germinant survival. However, the proportion of correct predictions made by the models was fairly good. Moreover, in addition to the discussion about statistic criteria assessment is needed on whether the models are biologically plausible. To evaluate the models as regards biological plausibility the following two aspects shall be examined: (1) How can species-specific responses to environmental factors be biologically explained? (2) Is the use of a multiplicative model for the interaction of environmental factors supported by ecological theory?

Life history traits like shade tolerance or seed size have been used as explanations for mortality patterns in a lot of studies. In some studies the survival of species was explained by seed size, e.g. with oak germinants showing high survival rates as compared to species with small-seed size (George and Bazzaz, 1999), whereas others did not find significant correlations (Streng et al., 1989; Jones et al., 1994). In this study, seed size may explain high root-to-leaf biomass ratio of pendunculate oak and, thus, have contributed to a higher survivorship in general as compared to small-seeded common linden or red ash. Studies of tree seedling recruitment in an Appalachian forest (Beckage et al., 2000) indicate that large-seeded *Q. rubra* germinants survived the first year equally, in small-scale gaps as well as beneath a closed canopy. Contrary to this, survival patterns of small-seeded *Acer rubrum* germinants reflected environmental light conditions in the first year. The authors explain the species-specific response by high first year energy reserves for *Q. rubra* germinants allowing them to survive even under low light conditions. Seedling densities of older *Q. rubra*, with the energy reserves being already depleted (Long and Jones, 1996), however, reflected more strongly the environmental light conditions, with mortality beneath the canopy being higher as compared to gaps.

Streng et al. (1989) observed that mortality rates of three species (*Liquidambar styraciflua*, *Carpinus caroliniana*, *A. rubrum*) in a Texas floodplain forest deduced from weekly censuses of germinants were positively correlated to leaf water potential used as an indicator of drought stress. As mentioned above, in contrast to this, the survival of water oak (*Quercus nigra*) germinants in their investigations were almost unaffected by drought stress, with the authors explaining this phenomenon by better water access of water oaks due to longer roots.

In the long-term study of abundance of saplings in a floodplain forest in Texas (Hall and Harcombe, 1998), it was found that sapling distribution responded primarily to flooding and light. It was shown that life history traits like flood and shade tolerance interacted as regards species distribution.

These findings support our hypothesis that the root-to-leaf biomass ratio—which, in turn, may be attributed to seed size—is an important life history trait explaining the species-specific responses to environmental factors.

The multiplicative approach of testing the influence of elevation (as a surrogate for water availability) and available light revealed that penduncculate oak germinants responded independent upon light availability in terms of mortality. With the water stress getting worse even for pendunculate oak on higher elevated sites, the mortality patterns of pendunculate oak germinants were highly dependent upon light availability. If these findings are referred to Tilman's (1982) resource competition theory, the results can be interpreted as follows: if water resource availability remains under a certain level (e.g. on medium to higher elevated sites), light and water are substitutable resources, i.e. that under these site conditions one resource can be substituted for the other to maintain a certain level of survival. Since even on the higher elevated sites water availability was restricted but not absolutely absent during the whole observation period, conclusions with respect to the question whether or to what extent water is an essential resource cannot be drawn. Similar results concerning the multiplicative interaction of environmental factors were found by Reed et al. (1983); they postulate that Douglas-fir seedlings compensated for decreased nitrogen availability with high light levels. Compared with the findings related to higher elevated sites, light is not a limiting resource anymore, when water availability exceeds a certain level (e.g. on lower elevated sites). On the contrary, the mortality patterns of common linden and red ash were almost exclusively dependent upon light availability due to generally limited water access; i.e. that generally limited water access prevented the possibility of testing the influence of water availability on mortality patterns on a broad-scaled gradient. Generally limited water access for these two species was explained by low root-to-leaf biomass ratios.

For practical considerations of forest management it is worthwhile having an idea of potential regeneration niches (Grubb, 1977). Regeneration niches as regards light availability of the three investigated tree species can be defined by an upper threshold which is deduced from the competitors' light response, and from a lower threshold which corresponds to the critical value of minimum light availability needed for germinant survival. The vitality of competing ground vegetation is clearly reduced, once the degree of available light drops below 0.1. The minimum threshold of the regeneration niche—except for penduncülate oak germinants on lower elevated sites—was 0.06 for oaks on higher elevated sites, 0.07 for common linden, and 0.08 for red ash, on all sites.

Normally, such low light conditions for potential regeneration of these tree species with competing vegetation being suppressed, can only be found if species with highly shading crowns like common linden or *Ulmus minor* are present in the canopy. Siebel and Bouwma (1998), who conducted investigations in a floodplain forest along the Rhine river, state that woody juveniles were mostly found below a 5% light transmission. The difference in assessing regeneration niches concerning light availability for woody seedlings to the study presented here might be explained by a different flood regime, with summer floods occurring in the Rhine riparian zone. Resulting from summer floods, lower water stress may occur in the floodplain forests along the Rhine river which, in turn, might result in either higher shade tolerance of seedlings due to better water resource availability; or, secondly, summer floods might cause higher light availability for woody regeneration after the flooding due to physical damage to herbs during floods.

The potential regeneration niches for successful survival of germinants of these tree species cannot be provided by creating gaps right after seedfall; this would strengthen competition for light between the germinants and the pre-established ground vegetation. For forest management of hardwood floodplain forests on these sites with drought stress occurring during summer, it is therefore recommended to create gaps at the end of the first growing season at the earliest. Such a procedure would take into account the increasing light requirement of seedlings with time (Siebel, 1998), and has the advantage that the survival of germinants can be judged at the end of the first growing season. Only if high survival rates after the first growing season occurred, gap creation would be sensible with the intention that the older juveniles—generally showing higher survival rates (Streng et al., 1989)—may better withstand the increasing competition by ground vegetation after gap creation.

Microenvironmental factors like soil moisture or light availability exert a species-specific influence on mortality patterns of germinants and, thereby, determine spatial distribution of the seedling bank. By this, the seedling bank of this floodplain forest is formed right at the very beginning of a process which, in the long run, may replace the canopy of the old-growth.

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