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Sapling growth and survivorship as affected by light and flooding in a river floodplain forest of southeast Texas

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Abstract We investigated the effects of light and flooding on growth and survivorship of saplings in a river floodplain forest of southeast Texas. Growth responses to light were consistent with the expectation that shade-intolerant species grow faster than shade-tolerant species in high light, and vice versa. Mortality risk was not associated with shade tolerance level unless high mortality risks associated with a period of high flooding were removed. These results support the hypothesis that shade-tolerant species in floodplains may be limited by flooding as previous studies suggested. Also, compared to their performance at a nearby mesic site, common species showed little intraspecific difference in shade tolerance, especially for shade-intolerant species. Finally, the positive correlation between low-light growth and survivorship suggests that carbon allocation to continued growth may be favored as a sapling strategy in floodplains.

Keywords Shade tolerance · Flooding · Tree sapling · Radial growth · Mortality risk

Introduction

In studies of floodplain forests, predictions of regeneration success and succession are difficult because many factors influence them, including flooding, shade, herbivory, root competition, disease and occasional drought (Streng et al. 1989; Jones and McLeod 1989; Jones et al. 1989, 1994; Pacheco 2001). Among these factors, light and flooding have been identified as among the most important in both experimental manipulation and field studies (e.g. Jones et al. 1989; Hall 1993; Jones and Sharitz 1998; Harcombe et al. 1998; Battaglia et al. 2000). Contrary to expectations based on light competition, floodplain forests are often dominated by shade-intolerant species (e.g. Jones et al. 1995; Harcombe et al. 1998), possibly because frequent flooding favors fast-growing shade-intolerant species. However, few studies have addressed this issue explicitly.

One approach that can further our understanding of the role of light and flooding in dynamics of floodplain forests is to focus on demography and investigate how light and flooding affect growth and mortality of saplings. A forest dynamics model SORTIE provides a useful framework to investigate light responses of different species. In SORTIE, sapling growth and mortality are modeled as functions of light availability. Studies in northern hardwood forests using the SORTIE framework showed that species responses to light were consistent with their presumed shade tolerance: shade-intolerant species had greater growth in high light conditions than shade-tolerant species, while shade-tolerant species survived better than shade-intolerant species in low light (Pacala et al. 1994; Kobe et al. 1995). In the present study, we asked whether the above relationship between light response and shade tolerance held in a river floodplain forest, reasoning that the absence of such relationships could explain why shade-tolerant species do not replace shade-intolerant species. In a more general sense, the question to be addressed involves whether flooding effects over-ride or modify the light responses.

Modification of light responses was suggested as a possible explanation for lack of correspondence between

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position on a light gradient and species rankings of shade tolerance in a study of sapling distribution in a river floodplain forest (Hall and Harcombe 1998). In particular, shade-tolerant species were found on the high-light end of the light gradient. The disagreement between actual and predicted position on the light gradient raised the question of whether physiological shade tolerance of a species is subject to change (Hall and Harcombe 1998). In this paper, we addressed this question directly by comparing light responses of different species at a floodplain site. We also compared growth and mortality of species found both in the wet forest and in a nearby mesic forest.

Finally, in addition to addressing community-level questions, the research also allows us to pursue the issue of evolutionary tradeoffs involved in shade tolerance. Pacala et al. (1994, 1996) challenged the traditional paradigm of shade tolerance by proposing that a tradeoff between growth in high light and survivorship in low light is more important than a generally believed high-light growth vs low-light growth tradeoff (see Lin et al. 2002 and references therein). Our results in a mesic forest suggested that it may not be appropriate to think of these two tradeoffs as one opposed to another and that the importance of growth and survivorship as components of shade tolerance may be system-specific (Lin et al. 2002). Here, we extended the investigation of shade tolerance tradeoffs to a different system asking the following questions: do shade-tolerant species survive better in low light as suggested by the SORTIE researchers, or do they grow faster as suggested by our own results and those of others (Boardman 1977; Lorimer 1981; Givnish 1988)?

Materials and methods

Study site and species

The wet floodplain forest is on the floodplain of the Neches River, in Jasper County, Texas (30°26'N, 94°05'W), about 1 km from the main channel. The river at this location has a main channel with numerous sloughs and cutoffs forming a large system of braided sloughs, one of which bisects the study area. The climate is humid subtropical, with an average annual rainfall of 1,396 mm/year evenly distributed throughout the year (Port Arthur, Texas, NOAA 1997). Average annual temperature is 20.6°C, and mean monthly temperature exceeds 10°C for all months. The growing season is from February to November, with an average of 282 consecutive frost-free days (Port Arthur, Texas, NOAA 1997). The soil is deep and poorly drained. During winter and spring, the water table is high (Hall 1993). The understory light level ranges from 0.1% full sun to 25.5% with a mean of 4.5% ($\pm 0.4\%$). The years 1980–1988 were a period of reduced flooding, while 1989–1994 was a period of frequent and severe flooding (Hall and Harcombe 2001). In particular, the magnitude of flooding in 1989 with a peak flow of 1,342 cms greatly exceeded the 100-year flood, and the magnitude of that flow was sufficient to flood the entire study site (approximately 632 cms; Hall 1993).

The study site may have been selectively logged during the early 20th century (Streng et al. 1989), but there is no direct evidence of logging beyond stumps of cypress in sloughs dating from the early 1900s. During a 20-year period, total basal area fluctuated between 27.7 and 29.1 m²/ha (Harcombe et al. 1998). Dominant overstory species included shade-intolerant sweetgum (*Liquidambar styraciflua* L.), basket oak (*Quercus michauxii* Nutt.), and water oak

(*Quercus nigra* L.), as well as shade-tolerant red maple (*Acer rubrum* L.). The major subcanopy woody species included shade-tolerant ironwood (*Carpinus caroliniana* Walt.) and deciduous holly (*Ilex decidua* Walt.), a tall shrub. Within the sloughs, bald cypress (*Taxodium distichum* L. Rich.) and blackgum (*Nyssa sylvatica* Marsh.) were commonly found. The shade tolerance categories used were based on conventional wisdom regarding shade tolerance as summarized by Burns and Honkala (1990). These shade tolerance classifications are based largely on field observations regarding the relative abundance of different species in the forest understory.

A nearby mesic site was chosen for comparison. Species composition is typical of many mesic sites throughout the Coastal Plain of the southeastern United States (Marks and Harcombe 1981). The closed canopy of tall trees (25–40 m) is dominated by loblolly pine (*Pinus taeda* L.), water oak (*Quercus nigra* L.), white oak (*Quercus alba* L.), American beech (*Fagus grandifolia* Ehrh.) and southern magnolia (*Magnolia grandiflora* L.). Red maple (*Acer rubrum* L.), blackgum (*Nyssa sylvatica* Marsh.) and sweetgum (*Liquidambar styraciflua* L.) are abundant as small to medium stems but are infrequent as large trees. Important understory trees include American holly (*Ilex opaca* Ait.) and flowering dogwood (*Cornus florida* L.). A more detailed description can be found in Glitzenstein et al. (1986) and Lin et al. (2001, 2002).

Data collection

Sapling growth

The study site was a 4-ha area divided into 100 contiguous 20×20 m tree plots. Every 3–5 years since 1980, all stems with a diameter at breast height (DBH) ≥ 2 cm were measured with a DBH tape. In 16 randomly chosen plots, all saplings with height ≥ 140 cm and DBH ≤ 4.5 cm were measured annually. Measurements are made to the nearest 0.1 cm. Heights of the saplings used for light measurements were determined with a measuring pole to the nearest 0.01 m.

To be consistent with previous analysis that contributed to the growth subroutine of SORTIE (Kobe et al. 1995; Pacala et al. 1996), DBH increments were converted to radial increments. Annual radial growth rate was calculated as the difference in radius between year 2000 and year 1997 divided by 3. Because the sample of high-light individuals was low due to canopy closure, we used top quartile growth rate (TQGR) as an approximation of high-light growth, reasoning that within species, saplings with high growth rates are unlikely to be growing in low light. Although not all of these individuals would necessarily be growing at their maximum full-sun rate, TQGR provided a more stable estimate of the asymptote because of the larger sample size. TQGR was computed as follows: for each sapling, we calculated radial growth over 3 years after the sapling first entered the survey; we then sorted saplings in descending order of growth rates, and for the top 25% took the average of their growth rates.

Light measurement

A subset of live saplings was selected for light measurements. Five species met the sample size requirement of about 50 saplings per species: red maple, sweetgum, water oak, ironwood and Chinese tallow. Saplings were selected in a stratified random fashion by plots to obtain a broad range of light conditions. Fish-eye photographs were taken at the top of each sapling (following Rich 1989; Pacala et al. 1994) in mid summer (late June to mid July) 1999. To increase contrast, all photos were taken early in the morning before sunrise and late in the afternoon after sunset when skylight is evenly distributed. All photos were taken on Kodak TMAX ASA 400 (black and white) film and the film was underexposed by 1 f-stop to further enhance contrast. Images were scanned, digitized and analyzed using CANOPY (Rich 1989). Thresholds were set individually to minimize problems with halo effects (Anderson 1964; Becker et al. 1989; Rich 1989, 1990).

The global site factor (GSF) was estimated from each photo. GSF quantifies the total amount of light availability (both diffuse and direct) that a sapling experienced during the growing season. The GSF value was multiplied by 100 to give percent of full sun. It is important to note that GSF is an index of light availability, not an absolute value. Since no major canopy disturbances occurred during the 1997–2000 period, the light index measured in 1999 was considered to be a reasonable representation of the average light environment over the 3-year period at a given location.

Mortality

Each sapling was checked annually for survival. Survival time was calculated as the length of time a sapling was followed during the course of the study. If a sapling died, then its survival time would be the difference between the year of death and the year when it entered the study. If a sapling was alive at the end of the study, its survival time was the difference between the ending year and the year when it entered the study. Saplings that were alive at the end of the study were flagged as right censored (Lee 1992). The mortality status of an individual that survived or was lost to follow-up in a longitudinal study is defined as right censored (Lee 1992).

To model mortality as a function of recent growth, we calculated pre-mortality growth rate for dead saplings as well. Pre-mortality annual growth rate of a dead sapling was the difference in radius over the last 3 years prior to death divided by 3. All live and dead saplings recorded were included in the analysis. The final sample size for mortality analysis ranged from 33 (bald cypress) to 1,338 (ironwood) per species depending on the abundance of each species.

To examine the effects of the 1989 flooding on sapling mortality, we broke the study period into pre-flooding (1980–1988), flooding (1989–1994) and post-flooding (1995–1999) intervals following Hall and Harcombe (2001). Survival time of each sapling was recalculated and the censorship flag was recoded in correspondence to the study period. After the data set was broken down into three subsets, only red maple and ironwood met the sample size requirement for separate statistical analysis in each of the three time periods.

Growth-light analysis

In this study, we used Michaelis-Menten function to model growth as a function of light (c.f. Pacala et al. 1994; Wright et al. 1998). In our case, however, the asymptote parameter was replaced by TQGR (an approximation of high-light growth), which was treated as a constant instead of a parameter. The one-parameter model takes the following form:

$$\mu = \frac{aL}{a/S + L} \quad (1)$$

where μ is the mean growth response given light availability, a is the top quartile growth rate (TQGR), S is the slope at low light and L is the light availability (% of full sun).

Maximum likelihood estimates of parameter S (slope of growth response at low light) were found by maximizing the following likelihood function:

$$\prod_{i=1}^n \left[\frac{1}{\sqrt{2\pi C[aL/(a/S + L)]^D}} - \exp\left(-\frac{[G_i - aL/(a/S + L)]^2}{2C[aL/(a/S + L)]^D}\right) \right] \quad (2)$$

where L is the percent of full sun, G_i is the radial growth rate of sapling i (3-year average), and C and D are two parameters that account for heteroscedasticity. Confidence intervals of S were

obtained by bootstrapping. Both model fitting and bootstrapping were done using Splus 5.1 (Mathsoft. 1999). A more detailed description of the maximum likelihood estimation method can be found in Lin et al. (2002).

Survival analysis

Mortality risk (annual death rate) as a function of growth

A negative exponential function was used to model mortality risk as a function of growth and size:

$$\lambda = e^{-\beta_0 - \beta_1 X_1 - \beta_2 X_2} \times \theta \quad (3)$$

where X_1 is the radial growth rate (mm/year), X_2 is the initial size (radius in mm), λ is the species-specific parameter of mortality risk, and θ is the error term. Estimates of parameters β_0 , β_1 and β_2 were found by maximizing the following likelihood function:

$$\prod_{i=1}^r \lambda e^{-\lambda T_i} \prod_{i=1}^{n-r} e^{-\lambda t_i} \quad (4)$$

where r is the number of saplings that died during the study and $n-r$ is the number of saplings that are right-censored. T_i and t_i are lifetimes of a non-censored and right-censored sapling i , respectively; λ is the parameter of mortality risk.

Mortality risk as a function of light

By combining Eqs. 1 and 3, mortality risk can be predicted directly from light:

$$\lambda = \exp[-\beta_0 - \beta_1 aL/(a/S + L)] \quad (5)$$

where λ is mortality risk, L is light availability (% full sun), a is the top quartile growth rate, and S and β_s are parameters obtained from the model fitting above.

An index of low-light survivorship, probability of survival at 1% full sun within 3 years was computed as:

$$P3 = \exp(-\lambda \times 3) \quad (6)$$

where $\lambda = \exp[-\beta_0 - \beta_1 \times a/(a/S + 1)]$. a , S , and β_s are the same in Eq. 5.

Maximum likelihood estimation of annual death rate

We also examined whether overall mortality risk (annual death rate) exhibited temporal variation caused by flooding by comparing annual death rates (λ) for the periods of 1980–1988, 1989–1994 and 1995–1999. The maximum likelihood estimator of annual death rate is:

$$\hat{\lambda} = \frac{D}{\sum_{i=1}^D T_i + \sum_{i=1}^{N-D} t_i} \quad (7)$$

where D is the number of deaths during the time interval, T_i is the lifetime of dead sapling i , and t_i is the lifetime of censored sapling i .

The 95% confidence interval of λ is:

$$\hat{\lambda} \pm \frac{\hat{\lambda} \times 1.96}{\sqrt{D-1}} \quad (8)$$

Results

Growth in response to light

Top quartile growth rate (TQGR, the index of high-light growth) was highest for shade-intolerant Chinese tallow, and lowest for shade-tolerant ironwood (Table 1). Chinese tallow and sweetgum grew significantly faster than the four shade-tolerant species, ironwood, blackgum, deciduous holly and red maple (ANOVA followed by Tukey's multiple comparison test, $p < 0.05$). The pattern was consistent with expectation: shade-intolerant species showed higher maximum growth than shade-tolerant species. The low-light growth index, slope at low light, was highest for ironwood followed by water oak, red maple, Chinese tallow and sweetgum (Table 1). These results indicate that low-light performance was also consistent with shade tolerance expectation.

Mortality as a function of growth

Growth was a significant predictor of mortality for 7 out of 8 species, but size was significant for only 2 species (results not shown). To keep the number of predictor variables consistent among species and also consistent with previous work (Lin et al. 2001, 2002), we dropped size as a predictor variable. At zero growth, the order of mortality risks did not correspond to shade tolerance expectation (Table 2, Fig. 1, entire period). For example, ironwood, a very shade-tolerant species, had the highest risk of mortality; red maple, a shade-tolerant species, ranked the second highest in mortality. Why did mortality risks of red maple and ironwood rank unexpectedly high? Annual death rate during the flooding period (1989–1994) was significantly higher than during the other two periods for both red maple and ironwood saplings (Table 3) suggesting that flooding might play a role.

This suggestion is supported by temporal fluctuation in mortality risk. For ironwood, the mortality-growth function during 1980–1988 had the shape typical of shade-tolerant species (Fig. 2a): low mortality risk at zero growth and shallow slope (Kobe et al. 1995; Lin et al. 2001). In 1989–1994, mortality risk increased dramatically, especially for saplings with low growth rates. For red maple, the pre-flooding mortality-growth curve was also typical of shade-tolerant species (Fig. 2b), but during the flooding

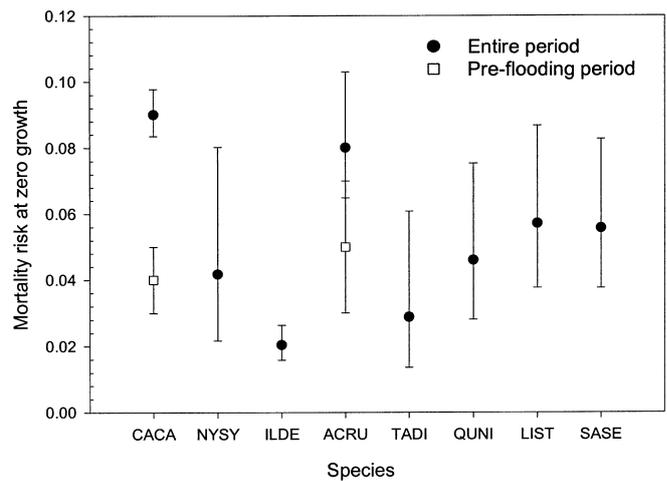


Fig. 1 Mortality risk (λ) at zero growth with 95% confidence intervals for different species. For ironwood (*CACA*) and red maple (*ACRU*), estimation of λ is based on data from the pre-flooding period (1980–1988) and entire study period (1980–1999), respectively. For other species, estimation of λ is based on the entire study period (1980–1999) only. Species are arranged in descending order of shade tolerance from left to right: *NYSY* *Nyssa sylvatica* (blackgum), *CACA* *Carpinus caroliniana* (ironwood), *ILDE* *Ilex decidua* (deciduous holly), *TADI* *Taxodium distichum* (bald cypress), *ACRU* *Acer rubrum* (red maple), *QUNI* *Quercus nigra* (water oak), *LIST* *Liquidambar styraciflua* (sweetgum), *SASE* *Sapium sebiferum* (Chinese tallow)

period, it too experienced increased mortality risk. Unlike ironwood, the post-flooding mortality stayed high for slow-growing individuals (Fig. 2b).

To investigate why post-flooding mortality stayed high for slow-growing red maple saplings, we examined the association between spatial distribution and mortality status of red maple saplings. During the post-flooding period (1995–1999), slough plots contained 70.4% of dead saplings (19 out of 27) but only 21.8% of live saplings (54 out of 248) and 26.5% of all saplings (73 out of 275). The chi-square test showed that mortality status of saplings was significantly associated with location ($\chi^2=29.49$, $p < 0.001$) indicating that probability of death was significantly higher in slough plots than in flat plots. That is, location was important to mortality; death rate was high in the slough where flooding occurs. Thus, one possible explanation for the shade-intolerant-like curve is that post-flooding mortality was biased because most dead saplings occurred in flood-prone areas where flooding is presumably severe and long lasting.

Table 1 Top quartile growth rates (TQGR) and slope at low light with 95% confidence intervals. Values not sharing the same letter are significantly different (ANOVA followed by Tukey's multiple comparison adjustment, $p < 0.05$). NA Not available. The first N value is for TQGR; the second is for slope

Species	Shade tolerance	N	TQGR	CI of TQGR	Slope	CI of slope
Chinese tallow	Intolerant	197/53	5.171 a	5.015–5.327	0.401	0.301–0.563
Sweetgum	Intolerant	248/52	3.217 b	3.078–3.356	0.138	0.087–0.213
Water oak	Intolerant	91/54	2.358 c	2.128–2.587	0.771	0.622–0.972
Red maple	Tolerant	67/45	1.918 cd	1.650–2.186	0.509	0.407–0.621
Bald cypress	Intermediate	6/NA	1.736 cde	0.915–2.557	NA	NA
Deciduous holly	Tolerant	/189/NA	1.650 d	1.503–1.796	NA	NA
Black gum	Tolerant	13/NA	0.696 e	0.138–1.253	NA	NA
Ironwood	Very tolerant	157/48	1.634 d	1.459–1.809	0.917	0.515–1.429

Table 2 Parameter estimates of the negative exponential model. b_0 and b_1 are estimates of β_s of the model in Eq. 3. Species-specific mortality risk (λ) at zero growth is calculated as $\exp(-b_0) \cdot N$ is the sample size

Species	Shade tolerance	N	b_0	b_1	95%CI of b_0	95%CI of b_1	λ	95% CI of λ
Water oak	Intolerant	261	3.080	1.169	2.587–3.573	0.357–1.981	0.046	0.028–0.075
sweetgum	Intolerant	695	2.863	2.102	2.445–3.280	1.269–2.935	0.057	0.038–0.087
Chinese tallow	Intolerant	378	2.887	1.238	2.493–3.281	0.570–1.905	0.056	0.038–0.083
Bald cypress	Intermediate	33	3.548	0.304	2.800–4.296	0–1.682	0.029	0.014–0.061
Red maple	Tolerant	386	2.492	1.481	2.278–2.706	1.029–1.934	0.083	0.067–0.103
Deciduous holly	Tolerant	1,020	3.891	2.263	3.636–4.147	1.526–3.001	0.020	0.016–0.026
Blackgum	Tolerant	64	3.178	2.310	2.523–3.833	0.594–4.026	0.042	0.022–0.080
Ironwood	Very tolerant	1,338	2.464	1.364	2.369–2.560	1.141–1.588	0.085	0.078–0.094

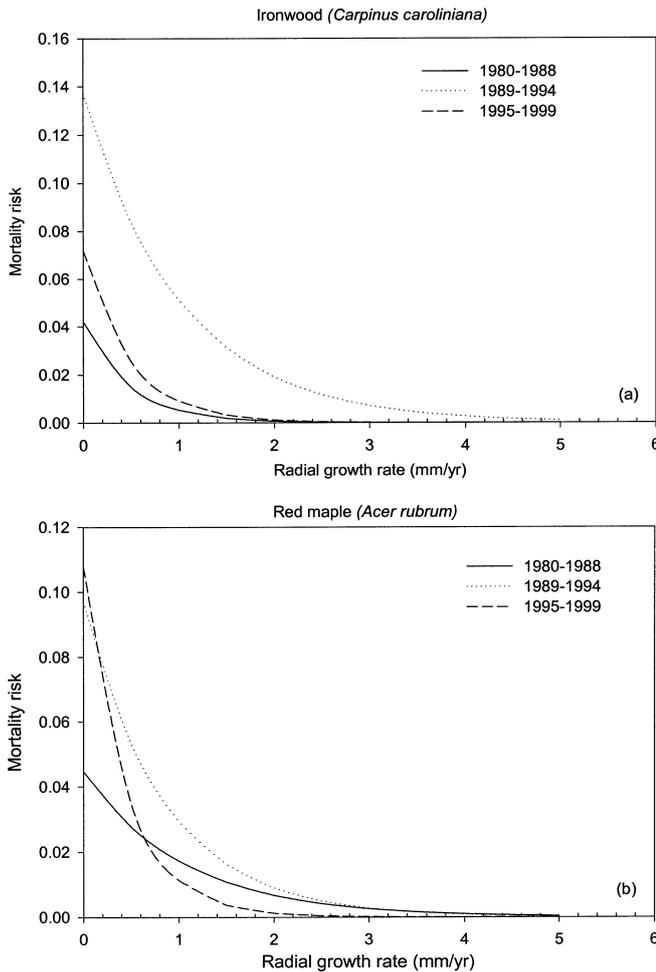


Fig. 2 Mortality risk (λ) as a function of radial growth for ironwood (a) and red maple (b) during pre-flooding (1980–1988), flooding (1989–1994) and post-flooding (1995–1999) periods

After accounting for the effect of flooding on mortality for two species (white boxes, Fig. 1), the correspondence between mortality and shade tolerance is no longer contradictory to expectation, and there is an indication that shade-tolerant species may have lower risk of mortality at low growth.

Mortality as a function of light

Mortality as a function of light can be obtained by combining the equations of mortality vs growth with the equations of growth vs light. Within species, mortality risk decreased with light availability (Fig. 3). At extremely low light (e.g. 0.1% full sun), shade-intolerant species (e.g. sweetgum, tallow, water oak) tended to have higher probability of death than tolerant species (e.g. ironwood). As light level increased, mortality risk decreased rapidly for most species, particularly for sweetgum and Chinese tallow. Mortality risk of ironwood remained the lowest below 10% full sun. (Because the mortality-growth relationships of red maple and ironwood were highly influenced by flooding, we used the pre-flooding mortality-growth equation for this analysis.)

Cross-site comparisons

To investigate possible growth and mortality response differences between sites, we compared the wet site with a nearby mesic site. Growth functions for the shade-intolerant water oak and sweetgum did not show significant differences between the wet site and the mesic site (Fig. 4a, b). The 95% confidence intervals (not shown) overlapped. The 95% confidence intervals of red maple overlapped below 20% full sun but differed significantly above that (Fig. 4c).

Table 3 Mortality risks (annual death rates) over time for red maple and ironwood with 95% confidence interval. See Eqs. 7 and 8 for calculation

Species	Year 1980–1988	Year 1989–1994	Year 1995–1999
Ironwood	0.029 (0.025–0.033)	0.092 (0.083–0.101)	0.027 (0.020–0.034)
Red maple	0.032 (0.022–0.042)	0.059 (0.045–0.073)	0.033 (0.020–0.045)

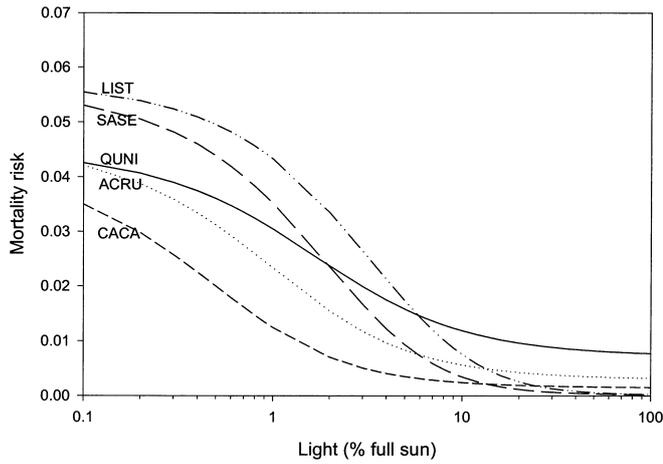


Fig. 3 Mortality risk (λ) as a function of light (see Eq. 5 in text for calculation) for different species. Species are coded as in Fig. 1

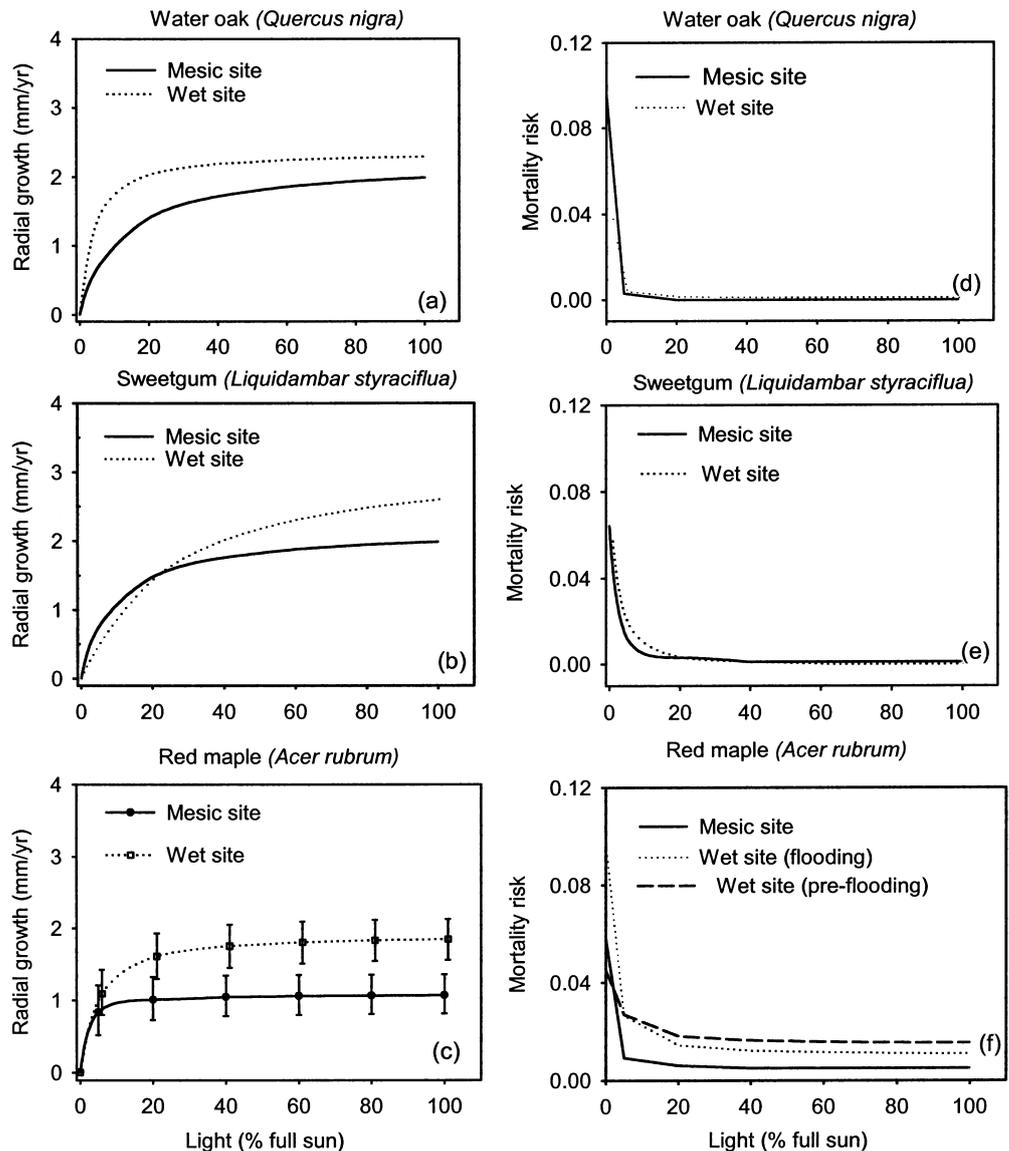
Mortality functions for water oak and sweetgum were similar between sites (Fig. 4d, e). For red maple, mortality risk was consistently higher at the wet site during flooding, although confidence intervals (not shown) overlapped (Fig. 4f). During the pre-flooding period, however, mortality risk was higher at the mesic site than at the wet site at very low light levels (Fig. 4f). The large increase in mortality for low-light saplings at the wet site during the flooding period may indicate an interaction of light and flooding (see Discussion).

Overall, species showed little intraspecific variation in shade tolerance parameters across the two sites, especially shade-intolerant water oak and sweetgum.

Interspecific tradeoffs

To look for tradeoffs involved in shade tolerance, species-specific parameters representing growth and survival in high and low light were plotted. (Note we used the pre-

Fig. 4 Radial growth as a function of light for water oak (a), sweetgum (b) and red maple (c) at the mesic site and wet site; mortality risk as a function of light for water oak (d), sweetgum (e), and red maple (f) at the mesic site and wet site



flooding values for red maple and ironwood.) The correlation between high-light growth and low-light growth (slope at low light) was negative, but it was not statistically significant ($R_s = -0.8, p > 0.05$). The negative correlation between high-light growth and low-light survivorship was not significant either ($R_s = -0.8, p > 0.05$). Compared with data shown by Kobe et al. (1995), all species tended to have a relatively high probability of survival in low light.

When the wet site data are combined with data from the mesic site (Lin et al. 2002), the negative correlation between high-light growth and low-light survival (Fig. 5a), as well as correlation between high-light growth and low-light growth (Fig. 5b) was strong. There was also a positive correlation between low-light growth and low-light survival across species ($R_s = 0.9, p < 0.01$; Fig. 5c): shade-tolerant species that grew fast in low light also survived well in low light.

Discussion

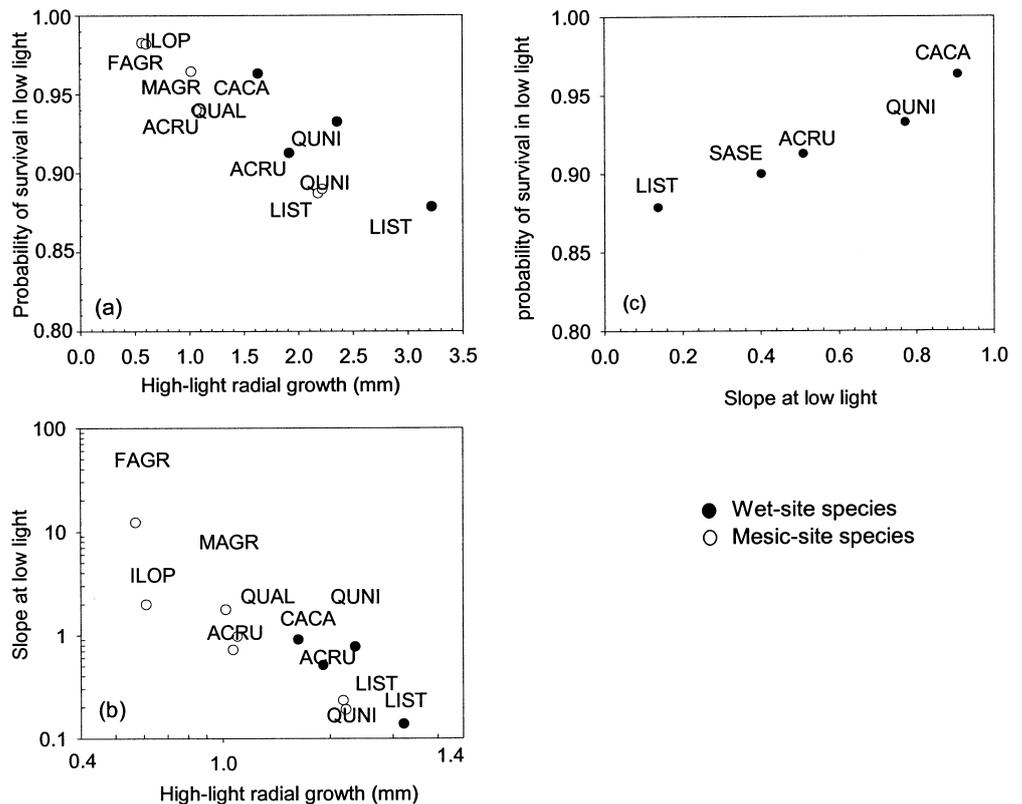
The results showed that the growth responses to light of different species were consistent with the expectation that shade-tolerant species grow faster than shade-intolerant species in low light and shade-intolerant species grow faster than shade-tolerant species in high light. That is, even at a wet site, growth-light responses did correspond to shade tolerance expectation, at least when flooding was not severe. When flooding was included, mortality risks of some shade-tolerant species were unexpectedly high

(Fig. 1) because flooding imposed extra mortality to saplings of shade-tolerant red maple and ironwood.

Several lines of evidence in our study suggest that flooding did not change actual shade tolerance: (1) the growth-light relationships were consistent with species rankings based on shade tolerance; (2) the mortality-growth curve of ironwood took the expected shape during the periods of low flood; and (3) both growth-light and mortality-growth relationships of water oak and sweetgum were very similar at the wet and mesic sites.

The low intraspecific difference in mortality-light and growth-light functions between the flooding site and the mesic site for the shade-intolerant species sweetgum and water oak (Fig. 4a,b,d,e) is an indication that flooding may not have substantial influence on growth and mortality of these species. This stands in contrast to the situation for the shade-tolerant red maple whose mortality risk was much higher at the wet site than the mesic site under low light conditions (<5% full sun) during the flooding period (Fig. 4f), but not during the pre-flooding period (Fig. 4g). The difference in mortality responses between pre-flooding and flooding periods suggests an interaction of light and flooding, with saplings growing in low light suffering greater flood-related mortality than saplings growing in high light (Menges and Waller 1983; Hall and Harcombe 1998, 2001; Battaglia et al. 2000). This comparison involves only three species; a more complete evaluation of flooding effects would require comparison of death rates over time for all species. Nevertheless, the cross-site comparison shows how flooding might have different

Fig. 5 Low-light survival vs high-light radial growth (a) and low-light growth vs high-light growth (b) for mesic-site species and wet-site species. c Low-light survival (probability of survival at 1% full sun in 3 years, see Eq. 6 in text) vs low light growth (slope at low light, S in Eq. 1)



effects on mortality of floodplain species with different shade tolerances.

We did not find strong evidence for the tradeoffs proposed by Pacala et al. (1993, 1994, 1996) and Kobe et al. (1995) at this site, though the trends are suggestive. One possible cause of the non-significant results may be low statistical power, since the correlation analysis was based on only five species. For this reason, increasing the number of species could be valuable in providing a more reliable answer. The consistent results using two sites combined suggest that the shade tolerance tradeoffs of wet-site species may not be very different from those of mesic-site species.

A final point regarding tradeoffs is that, consistent with previous work (Lin et al. 2002), we found a positive correlation between low-light growth and low-light survival (Fig. 5c). We argued that the positive relationship between low-light growth and low-light survival may suggest a post-photosynthetic carbon allocation “decision” that favors allocation to continued growth rather than storage that presumably contributes to survivorship (Kobe 1997; Canham et al. 1999). Such a decision would be even more advantageous at the wet site because allocation to continued growth seems to be an effective sapling strategy to cope with flooding hazard (Fulton 1991; Hall and Harcombe 1998, 2001). Added growth improves survival because species with faster DBH and height growth will have better survival by virtue of a shorter duration of high risk of flood-related mortality. Bigger individuals are less-susceptible to flooding mortality than are smaller individuals (Hall 1993).

Returning to the question of community level effects, a complete evaluation of the reason why river floodplain forests are often dominated by shade-intolerant species (e.g. Hall 1993; Jones et al. 1994; Harcombe et al. 1998) would require comparison of death rates for flooded vs non-flooded conditions for both shade-tolerant and intolerant species. Although data are not available to do such comparisons, both growth and mortality of shade-intolerant juveniles (sweetgum and water oak) at the flooding site were similar to their mesic background levels, suggesting that flooding might have little impact on performance of these species. In contrast, both cross-site and temporal comparisons have provided evidence that flooding did increase mortality risks of shade-tolerant juveniles and may consequently act as a major bottleneck for regeneration of these species. The dominance of shade-intolerant species at the flooding site may be partially explained by this process.

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References

- Anderson MC (1964) Studies of the woodland light climate. I. The photographic computation of light conditions. *J Ecol* 52:27–41
- Battaglia LL, Fore SA, Sharitz RR (2000) Seedling emergence, survival and size in relation to light and water availability in two bottomland hardwood species. *J Ecol* 88:1041–1050
- Becker P, Erhart DW, Smith AP (1989) Analysis of forest light environments. Part I. Computerized estimation of solar radiation from hemispherical canopy photographs. *Agric For Meteorol* 44:217–232
- Boardman NK (1977) Comparative photosynthesis of sun and shade plants. *Annu Rev Plant Physiol* 28:355–377
- Burns RM, Honkala BH (1990) *Silvics of North America*. Vol 2. Hardwoods. U.S. Department of Agriculture Handbook 654, USDA, Washington, D.C.
- Canham CD, Kobe RK, Latty EF, Chazdon RL (1999) Interspecific and intraspecific variation in tree seedlings survival: effects of allocation to roots versus carbohydrate reserves. *Oecologia* 121:1–11
- Fulton MR (1991) Adult recruitment as a function of juvenile growth rate in a size-structured plant population. *Oikos* 62:102–105
- Givnish TJ (1988) Adaptation to sun and shade: a whole plant perspective. *Aust J Plant Physiol* 15:63–92
- Glitzenstein JS, Harcombe PA, Streg DR (1986) Disturbance, succession, and maintenance of species diversity in an east Texas forest. *Ecol Monogr* 56:243–258
- Hall RBW (1993) Sapling growth and recruitment as affected by flooding and gap canopy formation in a river floodplain forest in southeast Texas. Ph.D. Dissertation. Rice University, Houston, Tex.
- Hall RBW, Harcombe PA (1998) Flooding alters apparent position of floodplain saplings on a light gradient. *Ecology* 79:847–855
- Hall RBW, Harcombe PA (2001) Sapling dynamics in an Southeastern Texas floodplain forest. *J Veg Sci* 12:427–438
- Harcombe PA, Glitzenstein JS, Krusic P, Hall RBW, Cook ES, Fulton M, Streg DR (1998) Sensitivity of Gulf forests to climate change. In: *Vulnerability of coastal wetlands in southeastern United States*. Biological science report USGS/BRD/BSR-1998-0002, pp 45–66
- Jones RH, McLeod KW (1989) Shade tolerance in seedlings of Chinese tallow trees, American sycamore and cherrybark oak. *Bull Torrey Bot Club* 116:371–377
- Jones RH, Sharitz RR (1998) Survival and growth of woody plant seedlings in the understorey of floodplain forests in South Carolina. *J Ecol* 86:574–587
- Jones RH, Sharitz RR, McLeod KW (1989) Effects of flooding and root competition on growth of shaded bottomland hardwood seedlings. *Am Midl Nat* 121:165–175
- Jones RH, Sharitz RR, Dixon PM, Segal DS, Schneider RL (1994) Woody plant regeneration in four floodplain forests. *Ecol Monogr* 64:345–367
- Jones RH, Sharitz RR, James SM, Dixon PM (1995) Tree population dynamics in seven South Carolina mixed-species forests. *Bull Torrey Bot Club* 121:360–368
- Kobe RK (1997) Carbohydrate allocation to storage as a basis of interspecific variation in sapling survivorship and growth. *Oikos* 80:226–233
- Kobe RK, Pacala SW, Silander JA, Canham CD (1995) Juvenile tree survivorship as a component of shade tolerance. *Ecol Applic* 5:517–532
- Lee ET (1992) *Statistical methods for survival data analysis*. Wiley, New York
- Lin J, Harcombe PA, Fulton MR (2001) Characterizing shade tolerance by the relationship between mortality and growth in tree saplings in a southeastern Texas forest. *Can J For Res* 31:345–349
- Lin J, Harcombe PA, Fulton MR, Hall RW (2002) Sapling growth and survivorship as a function of light in a mesic forest of southeast Texas, USA. *Oecologia* 132:428–435

- Lorimer CG (1981) Survival and growth of understory trees in oak forests of the Hudson Highlands. New York. *Can J For Res* 11:689–695
- Marks PL, Harcombe PA (1981) Forest vegetation of Big Thicket, southeast Texas. *Ecol Monogr* 51:287–305
- Menges ES, Waller DM (1983) Plant strategies in relation to elevation and light in floodplain forests. *Am Nat* 122:454–473
- Pacala SW, Canham CD, Silander JA (1993) Forest models defined by field measurements. I. The design of a northeastern forest simulator. *Can J For Res* 23:1980–1988
- Pacala SW, Canham CD, Silander JA, Kobe RK (1994) Sapling growth as a function of resources in a north temperate forest. *Can J For Res* 24:2172–2183
- Pacala SW, Canham CD, Saponara J, Silander JA, Kobe RK, Ribbens E (1996) Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecol Monogr* 66:1–43
- Pacheco MA (2001) Effects of flooding and herbivores on variation in recruitment of palms between habitats. *J Ecol* 89:358–366
- Rich PM (1989) A manual for analysis of hemispherical canopy photography. Los Alamos National Laboratory Technical Report LA-11733-M, Los Alamos National Laboratory, Los Alamos, N.M.
- Rich PM (1990) Characterizing plant canopies with hemispherical photographs. *Remote Sensing Rev* 5:13–29
- Streng DR, Glitzenstein JS, Harcombe PA (1989) Woody seedling dynamics in an east Texas floodplain forest. *Ecol Monogr* 59:117–204
- Wright EF, Coates KD, Canham CD, Bartemucci P (1998) Species variability in growth response to light across climatic regions in northwestern British Columbia. *Can J For Res* 28:871–886