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Sapling growth and survivorship as a function of light in a mesic forest of southeast Texas, USA

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Abstract For seven species in a mature mesic forest in southeast Texas, we estimated species-specific parameters representing radial growth in high light and low light for tree saplings. Shade-intolerant species had higher asymptotic growth rates and lower low-light growth than tolerant species. Inspection of species positions on graphs of low-light growth versus high-light growth suggested that there was a trade-off between these two processes across species. By linking functions of growth versus light and mortality versus growth, we also found that shade-intolerant species had higher mortality risk at low light and stronger sensitivity of mortality to light than shade-tolerant species. Moreover, we found that low-light survival and high-light growth were negatively correlated across species. In contrast to northern hardwood forests, where sapling survival in low light may be achieved at the expense of growth, our results suggested that shade-tolerant species in this southern mixed forest can grow faster as well as survive better than shade-intolerant species in low light. We conclude that both sapling growth and survival are important components of shade tolerance and their relationships may be system-specific.

Keywords Tree sapling · Radial growth · Mortality risk · Shade tolerance · Forest dynamics

Introduction

Light competition is a central process in forest dynamics and succession (Horn 1971; Bormann and Likens 1979; Shugart 1984; Glitzenstein et al. 1986; Pacala et al. 1996). Plants have evolved suites of traits that optimize carbon gain under different light conditions. Investigators have given these strategies labels such as “shade tolerant” or “shade intolerant” (e.g. Boardman 1977; Givnish 1988). In adopting such strategies, plants are presumed to have faced evolutionary trade-offs in carbon allocation.

A number of authors has investigated the putative trade-off between high-light growth and low-light growth: shade-tolerant species may grow faster than shade-intolerant species in low light, and vice versa (e.g. Lorimer 1981; Givnish 1988; Popma and Bongers 1988). The higher growth rates of intolerant species in high light have been attributed to physiological and morphological advantages (Loach 1970; Bazzaz1979; Walters et al. 1993; Walters and Reich 1996; Beaudet and Messier 1998; Coomes and Grubb 1998; Huante and Rincon 1998; Reich et al. 1998). The success of shade-tolerant species in low light has been attributed to more efficient use of light and faster growth in shade (e.g. Boardman 1977; Bazzaz 1979; Walters and Reich 1996; Agyeman et al. 1999; Williams et al. 1999). This trade-off of high-light growth versus low-light growth has been widely viewed as the general explanation of shade tolerance.

However, the generality of this trade-off was called into question by the finding that shade-tolerant species do not always grow faster than intolerant species in low light but they may survive better (e.g. Kitajima 1994; Kobe et al. 1995; Kobe and Coates 1997). The high survivorship of shade-tolerant species in low light has been attributed to carbon allocation to storage that acts as a buffer against mortality agents (Kobe 1997; Reich et al. 1998; Veneklaas and Poorter 1998; Canham et al. 1999). These results led the authors to conclude that juvenile tree survivorship plays a more important role than growth in determining success in low light, and that the trade-off between growth in high light and survival (rath-

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er than growth) in low light is the key explanation for variation among species in shade tolerance.

In this paper, we present results of mortality and growth responses of saplings to light availability in a southeastern Texas forest. We aim to test the hypothesis that shade tolerance involves a trade-off between high-light growth and low-light survivorship. If shade-intolerant species grow faster than shade-tolerant species in high light, and if shade-tolerant species survive better than shade-intolerant species in low light, we will expect to see a negative correlation between measures of high-light growth and low-light survivorship across species. Further, if survival in low light has been achieved by carbon allocation to storage at the expense of growth as suggested by several authors, a negative correlation between low-light growth and low-light survival across species would be predicted.

To test this hypothesis, we estimated species-specific parameters representing high-light growth and low-light survivorship. The parameters were chosen to be consistent with parameters introduced in growth and mortality subroutines of SORTIE, a forest dynamics model (Pacala et al. 1996). The test is based on earlier sets of studies that identified survival as a key element of the trade-off (Pacala et al. 1994, 1996; Kobe et al. 1995).

Regardless of the nature of the trade-off, the existence of a range of strategies implies segregation of juveniles along a light gradient, i.e., species occupy their own niches along the light gradient (e.g. Latham 1992; Kobe 1999). The "gap partitioning hypothesis" states that the light environment under a forest canopy is a gap-understory mosaic which provides different niches and allows coexistence of tree species that differ in their resource (light) requirements for growth, survival and establishment (Ricklefs 1977; Denslow 1980, 1987; Orians 1982). Studies on tropical and temperate tree species have provided support to this hypothesis (e.g. Latham 1992; Kobe 1999). In this study, we ask whether light gradient partitioning occurs in a warm temperate forest in southeast Texas, USA.

Materials and methods

Study site and species

The study site, Wier Woods, is located in Hardin County, Texas (30°16′ N, 94°12′ W) approximately 16 km north of Beaumont. Species composition is typical of many mesic sites throughout the coastal plain of the southeastern United States (Marks and Harcombe 1981). Except for a selective cutting of pines that occurred around 1910 (Glitzenstein et al. 1986), the forest has been free from direct human influences. Hurricane Bonnie passed over Wier Woods in 1986 causing a decline in tree basal area of about 5%, but basal area recovered from hurricane damage to the pre-hurricane level by 1990. Basal area has varied between 33.7 m^2/ha (after hurricane) and 35.1 m^2/ha over the last 20 years. The hurricane had little effect on understory mortality. The soil is a fine, loamy, thermic Glossaqualf (Harcombe et al. 1998). Based on analysis of fisheye photographs, the understory light availability ranged from 0.5% full sun to 15.2% full sun (a total of 75 out of 100 plots were involved in light measurement) with a mean of 6.1% (±0.5%) in mid-summer of 1994. The climate is humid subtropical with an average precipitation around 1,341 mm/year evenly distributed throughout the year. The average annual temperature is 20.4°C. Mean average temperature exceeds 10°C for all months. The growing season is long, from March to November, with approximately 240 consecutive frost-free days. 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.). Loblolly pine, American holly and southern magnolia are evergreen; the other species are deciduous. Deciduous species start leafout in early March and the new leaves are fully expanded within a few weeks after leafout (Harcombe and Marks 1977).

Table 1 Density (stems/ha) of the seven species as trees (DBH>4.5 cm) and saplings ((height ≥140 cm and DBH ≤4.5 cm) at the study site (From Harcombe et al. 1998). Species are coded as following: QUNI, *Quercus nigra* (water oak); LIST, *Liquidambar styraciflua* (sweetgum); QUAL, *Quercus alba* (white oak); ACRU *Acer rubrum* (red maple); MAGR, *Magnolia grandiflora* (southern magnolia); ILOP, *Ilex opaca* (American holly); FAGR, *Fagus grandifolia* (American beech)

Species	Shade tolerance	Tree	Sapling
QUNI	intolerant	16	22
LIST	intolerant	80	16
QUAL	intermediate	43	11
ACRU	tolerant	89	36
MAGR	tolerant	76	87
ILOP	very tolerant	350	274
FAGR	very tolerant	45	43

The seven species included in this study have a wide range of shade tolerance levels according to a published shade tolerance classification (Burns and Honkala 1990). Sweetgum and water oak are shade-intolerant; white oak is intermediate; red maple and southern magnolia are shade-tolerant; American beech and American holly are very shade-tolerant species. The seven species vary in their relative abundance (Table 1) both as canopy trees and saplings (height ≥140 cm and DBH ≤4.5 cm).

Sapling measurements

Growth

The study site is 4 ha divided into 100 contiguous tree plots. Each plot is 20×20 m. Sapling plots (a total of 16) are randomly distributed within the 100 tree plots. Each sapling plot is circular with an area of 250 m^2. In each sapling plot, DBH is measured annually to the nearest 0.1 cm with a DBH tape. Such surveys have been performed annually for saplings with a size range of height ≥140 cm and DBH ≤4.5 cm since 1981, resulting in a long-term data set that provides the demographic data for this study. In addition to DBH measurements, heights of the saplings that were selected for light measurements (see light measurement section below) were measured with a measuring pole reading 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. Growth of each sapling alive in 1998 was radial increment between 1998 and 1995 divided by 3. We chose to calculate annual growth as the average over 3 years instead of 1 year to reduce measurement variation. Sapling growth between 1995 and 1998 was used in this study because growth history during this period is most likely to be correlated with light measurements taken in 1998.

Table 2 Estimates of the Michaelis-Menten parameters, A and S for different species (refer to Eq. 2). *A* and *S* are indices of high-light growth and low-light growth, respectively. Confidence intervals (*CI*) were constructed using both likelihood ratio test and bootstrapping (*italics*). Size is the stem radius at breast height. N is the sample size. Species are coded as in Table 1

Species	Shade tolerance	*N*	Size range (mm)	A (95%CI)	S (95% CI)
QUNI	Intolerant	42	1.0–18.0	2.219 (1.204–5.820) *(0.942–4.515)*	0.190 (0.098–0.425) *(0.092–0.583)*
LIST	Intolerant	35	6.0–24.5	2.176 (1.410–3.866) *(1.266–3.729)*	0.232 (0.128–0.382) *(0.104–0.369)*
QUAL	intermediate	35	0.5–10.0	1.102 (0.735–1.601) *(0.690–1.633)*	0.971 (0.493–2.118) *(0.454–2.315)*
ACRU	Tolerant	44	3.0–21.0	1.086 (0.840–1.370) *(0.833–1.346)*	0.724 (0.439–1.275) *(0.468–1.341)*
MAGR	Tolerant	73	4.0–21.5	1.019 (0.808–1.225) *(0.824–1.245)*	1.769 (1.085–3.026) *(1.062–3.219)*
ILOP	Very tolerant	82	2.0–22.5	0.610 (0.447–0.813) *(0.446–0.809)*	1.981 (1.081–5.321) *(1.053–5.373)*
FAGR	Very tolerant	50	3.5–23.5	0.565 (0.418–0.768) *(0.415–0.811)*	12.283 (3.187–∞) *(2.575–∞)*

Mortality

In addition to measuring saplings, we checked each sapling annually to see whether it was dead or alive. 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 of time between the year of death and the year when it entered the study. If a sapling was still alive at the end of the study (year 1998), its survival time was the difference between 1998 and the year when it entered the study. Saplings that were alive in 1998 were flagged as right censored (Cox and Oakes 1984; Lee 1992). For dead saplings, growth was the difference in radius over the last 3 years prior to death divided by 3. We included all saplings (dead or alive) that had been recorded since the beginning of the long-term study (1981). The final sample size (including dead and live) varied from 252 (red maple) to 1,917 (American holly) saplings per species.

Light

A subset of live saplings was selected from the database for light measurements. Saplings were selected in a stratified random fashion by plots to obtain a broad range of light conditions. Following Pacala et al. (1994), we originally set a sample size of at least 50 saplings per species. However, because of low density of some species, the final sample size ranged from 35 to 82 saplings per species (see Table 2). Light availability was quantified by taking a fish-eye photograph at the top of the each sapling (following Rich 1989; Pacala et al. 1994). Photographs were taken in mid-summer (late June to mid-July), 1998, by placing the camera with an Olympus 8-mm fisheye lens directly above each sapling. To increase contrast, all photographs were taken early in the morning before sunrise and late in the afternoon after sunset when skylight is evenly distributed. Moreover, all photographs 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). When analyzing the images, appropriate thresholds were set to minimize the halo effects (Anderson 1964). The global site factor (GSF) was estimated from each photograph. GSF is a quantitative index of the total amount of light availability (both diffuse and direct) that a sapling experienced during the growing season. The GSF value was then converted to percent of full sun by multiplying by 100. Since no major canopy disturbances occurred during the 1995–1998 period, the light level in 1998 was taken to be a reasonable representation of average light environment over the 3 year period at a given location.

Data analysis

In a previous study (Lin et al. 2001), sapling mortality risk was modeled as a function of growth. In the present study, we modeled sapling growth as a function of light. In addition, a mortality-light model was developed by combining the mortality-growth model with the growth-light model.

Growth as a function of light

We used a nonlinear regression model to quantify sapling growth with light availability. Maximum likelihood methods (Edwards 1992) were applied in model fitting. For a given species, if growth rates follow a normal distribution, then the likelihood function is:

$$\prod_{i=1}^{n}[\frac{1}{\sqrt{2\pi\sigma^2}} - \exp(-\frac{(G_\mathrm{i}-\mu)^2}{2\sigma^2})] \qquad (1)$$

where G_i is the annual radial growth rate of sapling i (3-year average); n is the sample size; μ and σ^2 are mean and variance of the growth distribution, respectively.

We used absolute growth rates G_i instead of relative growth rates for two reasons. First, absolute growth rates did not show dependence on size for six out of seven species (for the seventh species, water oak, the dependence was weak). Second, if large saplings tend to be more common in high light, and if large saplings grow faster than small saplings, there could be a secondary effect of size on growth as well. In fact, we found no indication of unevenly distributed plant size across the light gradient.

The goal of this analysis is to predict mean growth response (μ) from light availability. The Michaelis-Menten function gave a good fit. The model takes the following form:

$$\mu = \frac{AL}{A/S + L} \qquad (2)$$

where μ is the mean response of radial growth given light (mm/year); L is the percent of full sun; A and S are species-specific parameters which represent asymptotic growth rate (A) and slope of growth response at low light (S), respectively. Asymptotic growth rate is an index of high-light growth; slope at low light is an index of low-light growth (Pacala et al. 1993, 1994, 1996; Wright et al. 1998).

Because the growth distribution has variable variance, the variance σ^2 can be modeled as a function of μ (See Pacala et al. 1994):

$$\sigma^2 = C\mu^{D} \tag{3}$$

where C, D are two parameters that account for heteroscedasticity.

The final likelihood function was built by replacing μ and σ^2 in the likelihood function 1 with Eqs. 2 and 3. Maximum likelihood estimates of parameters A (asymptotic growth rate), S (slope of growth response at low light), C and D were found by maximizing the following likelihood function:

$$\prod_{i=1}^{n}\left[\frac{1}{\sqrt{2\pi C[AL/(A/S+L)]^{D}}} - \exp\left(-\frac{[G_i - AL/(A/S+L)]^2}{2C[AL/(A/S+L)]^{D}}\right)\right] \tag{4}$$

where L is the percent of full sun; G_i is the radial growth rate of sapling i; A, S, C, D are species-specific parameters.

We did not report maximum likelihood estimates for C and D because they are not relevant to the conclusions of the study. We used both likelihood ratio test and bootstrapping (Huet et al. 1996) to find 95% confidence intervals for A and S. The bootstrapped confidence intervals were based on 1,000 iterations of subsampling with replacement (Chernick 1999). Both model fitting and bootstrapping were done using Splus 5.1 on Unix (Mathsoft, 1999).

Mortality as a function of growth

We used survival analysis to model sapling mortality as a function of growth (Lin et al. 2001). An exponential distribution was used to describe the underlying distribution of the survival time. Therefore, the likelihood function for right-censored and non-censored saplings is (Lee 1992):

$$\prod_{i=1}^{r}\lambda e^{-\lambda T_i}\prod_{i=1}^{n-r}e^{-\lambda t_i} \tag{5}$$

where r is the number of saplings that died during the study (non-censored) 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 (i.e. annual death rate).

The goal of this analysis is to predict λ from radial growth rate. A negative exponential function gave a good fit:

$$\lambda = e^{-\beta_0-\beta_1 x}\times\theta \tag{6}$$

where x is the radial growth rate (mm/year); λ is the species-specific parameter of mortality risk. The parameters to be estimated are the βs. We used a multiplicative error term θ so that the model could be linearized to a familiar form. Estimates of parameters β_0 and β_1 were found by maximizing the likelihood function Eq. 5. Parameter estimates (βs) and detailed methods are described in Lin et al. (2001).

Mortality as a function of light

By combining Eq. 2 and Eq. 6, we were able to predict mortality risk directly from light. The function that predicts sapling mortality risk from light availability is:

$$\lambda = \exp[-\beta_0 - \beta_1 AL/(A/S+L)] \tag{7}$$

where λ is mortality risk, L is light availability (% full sun). A, S and βs are parameters that we obtained from model fitting above.

To test the trade-off of high-light growth versus low-light survivorship, it is necessary to compute an index of survival in low light. We chose probability of survival at 1% full sun over 3 years as an index of low-light survivorship:

$$P_3 = \exp(-\lambda\times 3) \tag{8}$$

where $\lambda=\exp[-\beta_0-\beta_1\times A/(A/S+1)]$. A, S, and βs are the parameters in Eqs. 2 and 6.

Probability of reaching 50 mm radius (10 cm DBH)

To further explore the relative performances of different species over a gradient of light availability, we computed the probability of reaching a given size (50 mm radius) for each species across the light gradient. Since radial growth rate can be modeled as a function of light (Eq. 2), the reciprocal of Eq. 2 multiplied by 50 gives the time (t) to reach 50 mm radius (assuming constant growth rates over time). Given an exponential distribution of survival time, the probability of survival in time T is then:

$$P_s = \exp(-\lambda T) \tag{9}$$

where both λ and T are functions of light (so that P_s is also a function of light).

Results

Growth responses to light

The species responded to light differently (Fig. 1). Asymptotes were reached below 50% full sun for three less-tolerant species (water oak, sweetgum and red maple), and below 30% full sun for the most shade-tolerant species (e.g. southern magnolia and American holly). Shade-intolerant species showed larger increases in growth rates than tolerant species as light levels increased. Species order in asymptotic growth rates corresponded to traditional ranks of shade tolerance (Table 2): very shade-tolerant American beech and American holly had lower asymptotic growth than intolerant species such as water oak and sweetgum. Growth rates of other species fell between the two extremes (Table 2, Fig. 2). The results support the expectation that intolerant species tend to have higher growth rates in high light than tolerant species.

Growth response to low light was evaluated by comparing the slopes of the initial growth curves at low light (the S parameter). Intolerant species (e.g. sweetgum and water oak) had shallower slopes than tolerant magnolia and very tolerant holly and beech (Table 2). The steep slopes of American beech and American holly suggested that their growth rates were quite responsive to light enhancement.

Differential growth responses among species resulted in a pattern wherein shade-intolerant species began to outgrow tolerant species as light availability increased. Above approximately 0.5% full sun, growth rates of very tolerant American beech and American holly were exceeded by the tolerant species southern magnolia. Southern magnolia remained the fastest growing species until the light level reached 8%, at which point intolerant water oak and sweetgum sur-

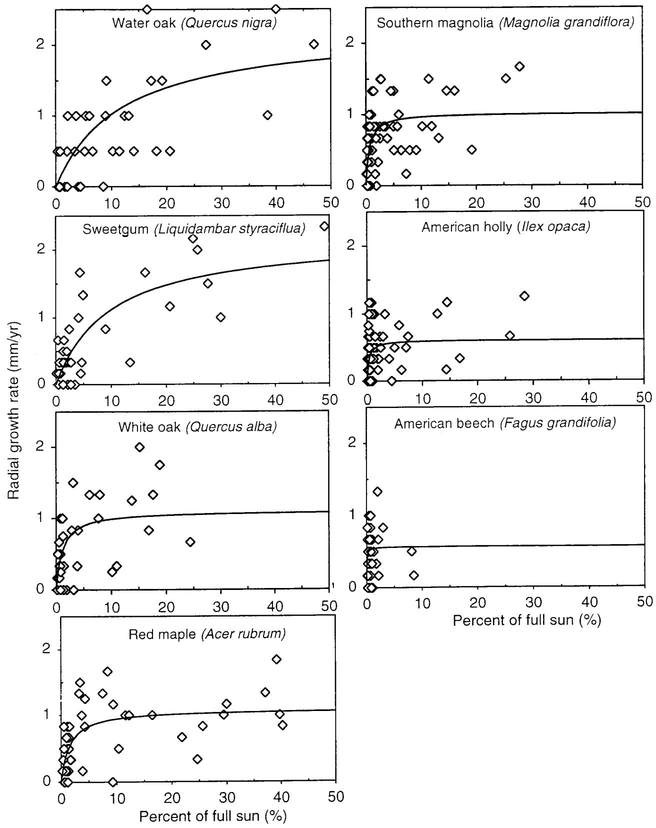

Fig. 1 Radial growth rate (mm/year) versus percent of full sun for the seven species. Radial growth rate was 3-year average (for water oak, growth rate was based on 1-year growth). Species are arranged in ascending order of shade tolerance from top to bottom and from left to right

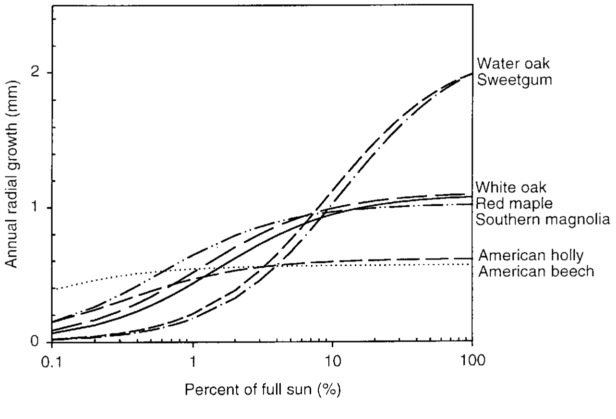

Fig. 2 Fitted growth-light regression curves using nonlinear model (2). The horizontal axis represents percent of full sun (Log scale). The vertical axis represents annual radial growth rate (mm/year). In contrast to Fig. 1, a log scale is used for percent of full sun to make the differences in performance in the 0.1 to 10% range more evident

passed southern magnolia. The three species that achieved the highest growth rate at some point along the light gradient were American beech, southern magnolia, and water oak.

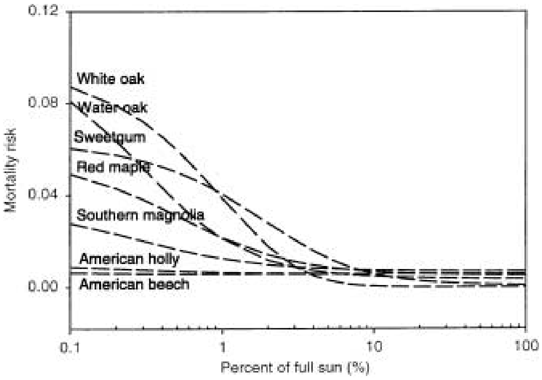

Fig. 3 Fitted mortality risk as a function of percent of full sun (Log scale) using model (7)

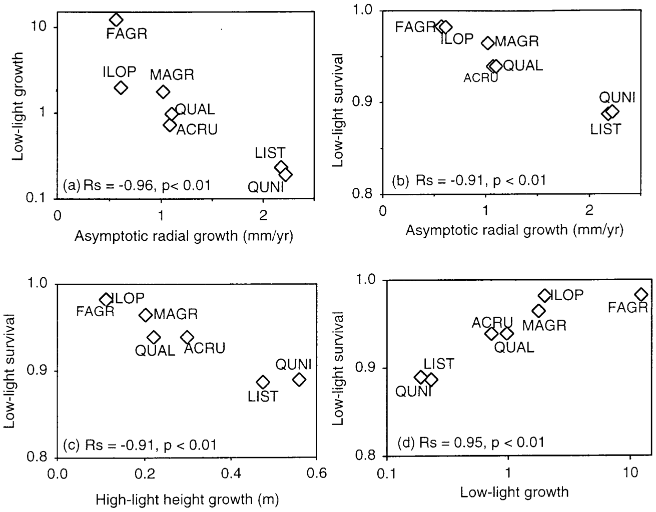

Fig. 4a–d Scatter plots of performance at low light (growth or survival) vs. performance at high light (radial or height growth). Species are coded as in Table 1. **a** Low-light growth (slope of the growth response at low light, *S*) versus asymptotic radial growth (*A*). The two parameters *A* and *S* were estimated by fitting model (2). **b** Low-light survivorship (probability of survival at 1% full sun in 3 years, see Eq. 8 for calculation) versus asymptotic radial growth. **c** Low-light survivorship versus high-light height growth. Asymptotic radial growth was converted to height growth using regression of height on radius. **d** Low-light survivorship versus low-light growth. Note the Log scale on the *x*-axis

Mortality response to light

Mortality risk decreased as light increased for most species (Fig. 3). In low light, intolerant and intermediate species showed higher mortality risk than tolerant species. As light increased, mortality risk of very shade-tolerant species (e.g. American beech and holly) remained constant while mortality risk of less tolerant species (e.g. white oak, water oak) decreased rapidly. That is, higher light availability significantly increased the chance of survival for intolerant species but had little effect on survival for very tolerant species. In high light, all species had low mortality and there was little interspecific difference.

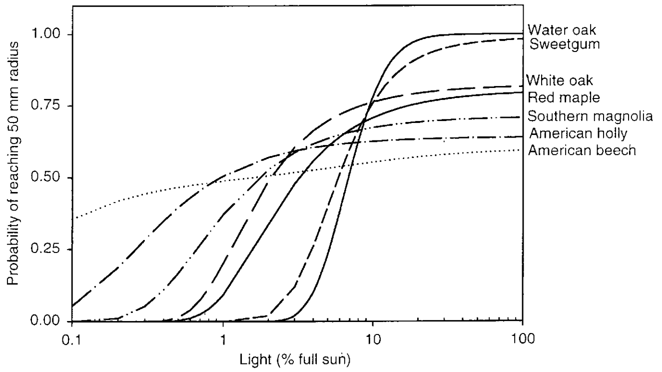

Fig. 5 Probability of reaching 50 mm in radius at breast height (10 cm DBH) versus light for different species. Computation was based on Eq. 9

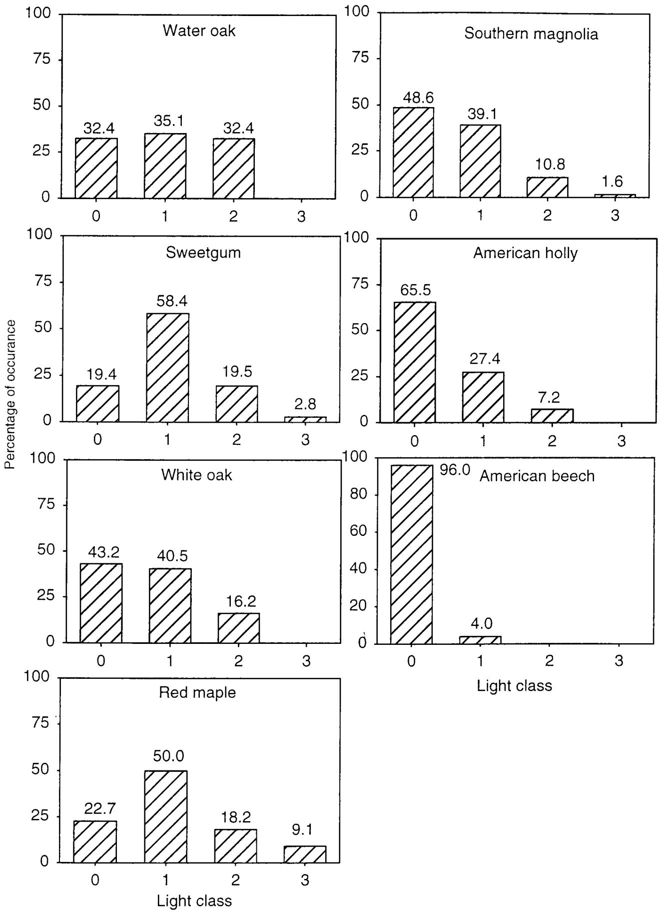

Fig. 6 Percent of saplings occurring at each of the four light levels. Light levels are as following: *0*: <1% full sun; *1*: 1–10% full sun; *2*: 11–40% full sun; *3*: 41–100% full sun. Species are arranged in ascending order of shade tolerance from top to bottom and from left to right

Interspecific trade-offs

To investigate interspecific trade-offs, species-specific measures of growth and survival in different light conditions were plotted (Fig. 4) since a negative correlation across species is an indicator of a trade-off (see Pacala et al. 1994; Kobe et al. 1995; Kobe and Coates 1997; Wright et al. 1998). Note that we used log scales for all but one variable, low-light growth, which we expressed on a log scale because of the large range of variation in that variable. The strongest negative correlation was between growth in low light and growth in high light ($R_s=-0.96$, $P<0.01$; Fig. 4a). Moreover, species alignments along the diagonal were consistent with published ranks of shade tolerance. For instance, very shade-tolerant American holly and American beech, the two most tolerant species were located at the upper left corner indicating high growth rates in low light and low asymptotic growth in high light. Shade-intolerant water oak fell in the lower right corner showing very high asymptotic growth and poor low-light growth.

There was also a negative correlation between low-light survivorship and high-light growth (radial and height) ($R_s=-0.91$, $P<0.01$; Fig. 4b, c). However, species showed relatively low variation in survivorship compared to that shown by Kobe et al. (1995). That is, all species tended to have a relatively high probability of survival in low light. More interestingly, our data suggested that shade-tolerant species, which grew faster in low light, also survived better than intolerant species ($R_s=0.95$, $P<0.01$; Fig. 4d).

Combined responses of growth and survivorship to light

Probability of reaching 50 mm radius was plotted as a function of light (Fig. 5). American holly and American beech ranked the top two species in the probability between 0.1% and 1% full sun. There was a dramatic increase in the probability of survival for red maple, white oak and southern magnolia between 0.1% and 1% full sun. Several species shifted ranks between 1% and 10% full sun. At light levels above 10%, intolerant water oak and sweetgum had the highest probability of reaching 50 mm radius. This shows that, in the context of resource partitioning, the full range of light was partitioned by species with different light requirement for growth and survival (Fig. 5).

The tendency toward light gradient partitioning was further illustrated by the spatial distribution of saplings across light microhabitats (Fig. 6). We found that 96% of the American beech saplings for which light measurements were made occurred in micro-habitats with less than 1% full sun. American holly and southern magnolia followed American beech with 65.5% and 48.6% of their saplings growing under 1% full sun. In contrast, only 19.4% of sweetgum saplings occurred in such dark microhabitats. In bright habitats with light ranging from 11% to 40% full sun, 32.4% of water oak saplings were found, followed by sweetgum (19.5%) and red maple (18.2%). None of the American beech saplings occurred in these bright microhabitats, and the other most shade tolerant species were also sparse in these areas.

Discussion

Interspecific trade-offs in shade tolerance and carbohydrate allocation

In contrast to earlier work that focused on variation among species in growth (e.g. Loach 1970; Givnish 1988), recent workers have argued that survival is more important than growth in determining success in low light (e.g. Kitajima 1994; Kobe et al. 1995; Veneklass and Poorter 1998; Canham et al. 1999). This reasoning is based on graphs showing stronger negative correlation between low-light survival versus high-light growth than between low-light growth versus high-light growth (Pacala et al. 1993, 1996; Kobe et al. 1995). However, based on our work in the Coastal Plain forest, we do not find a compelling argument for favoring one trade-off over the other. Species did exhibit a slightly higher rank correlation for the trade-off involving low-light growth versus high-light growth than the trade-off involving low-light survival versus high-light growth, but the differences in strengths of correlations were not large. In the end, do our results support the old paradigm of shade tolerance? The answer may be yes, but, because we also find that low-light growth and survival are positively correlated (Fig. 4d), it is not necessarily appropriate to think of shade tolerance in terms of one trade-off as opposed to the other.

The key issue may be the relationship between growth and survival in low light. Working in a northern hardwood forest, Kobe (1997) pointed out that sapling survivorship was improved by carbon allocation to storage that acts as a buffer against abiotic stress (e.g. long dormant season) at the expense of growth. However, in contrast to the northern hardwood forest system, there are systems in which growth to escape abiotic stress may be favored over tolerance of stress. That is, while survivorship may be increased in some forest ecosystems by tolerating adverse conditions through large allocation to storage, it may be enhanced in other forest ecosystems by escaping the adverse conditions through allocation to continued growth (Fulton 1991; Walters and Reich 1996, 2000; Hall and Harcombe 1998). Indeed, carbohydrate allocation to storage could be disadvantageous under some circumstances because the stored reserves do not produce a direct return until mobilized for growth (e.g. Chapin et al. 1990; Kobe 1997). One possible specific scenario that is consistent with our results is that winters are mild enough to allow continued growth and reduce the risk of winter mortality such that the positive feedback between growth and survival can emerge. A general hypothesis that unifies the contradicting results of early work and recent studies is that shade tolerance involves carbon gain at low light rather than growth or survival, and that there may then be subsidiary allocation decisions that determine whether low-light growth or survival will show the strongest negative correlation with high-light performance. Selection on the allocation pattern may vary from place to place; that is, the relative importance of the survivorship and growth elements of shade tolerance may be system-specific.

Light gradient partitioning and species coexistence

In this study, we found that species changed ranks of performance (Fig. 5) and were differently distributed along the light gradient (Fig. 6). These results are consistent with reports for temperate species (e.g. Kobe et al. 1995; Walters and Reich 1996; Wright et al. 1998) and tropical species (e.g. Denslow 1980, 1987; Kobe 1999). Although the data show a degree of resource partitioning, almost all species have some possibilities to recruit into the adult tree class over a wide range of light conditions (Fig. 5). This is consistent with the assertion that niche partitioning is not characterized by mutually exclusive niches but by species with ranked probabilities of performance (Kobe 1999). Our data also indicate that all forest tree species in current study can tolerate shade as saplings by showing relatively high probability of survival in low light (Fig. 4). Thus, all species exhibit shade tolerance to some degree and coexistence may not require strict niche partitioning (Sipe and Bazzaz 1995).

Glitzenstein et al. (1986) investigated the role of disturbance (e.g. selective logging and windstorms) in maintaining tree species diversity in this forest. According to that study, because regeneration under the canopy of shade-tolerant dominants such as American beech and southern magnolia is low, disturbances that open light gaps in areas dominated by American beech and southern magnolia may favor regeneration of shade-intolerant species. On the other hand, since saplings of shade-tolerant species regenerate in areas dominated by shade-intolerant canopy trees, disturbances that remove shade-intolerant dominants will favor shade-tolerant species. It was hypothesized that this pattern of cyclic replacement driven by disturbance helps to preserve species diversity in this mesic forest. Our study further elucidates the mechanisms of species coexistence in this forest. That is, species show some degree of niche partitioning along the light gradient that is created by tree death. On the other hand, since no species die out quickly in low light, coexistence of these species may not require strict niche partitioning. Moreover, the conclusion from the growth-light and mortality-light models that shade-tolerant species should be the most successful is consistent with empirical observation of forest change over 20 years in this forest (Harcombe et al. 1998). This consistency further supports the idea that late-successional forests of this kind are structured in large part by competition for light.

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