

Are rare species less shade tolerant than common species in fire-prone environments? A test with seven *Amorpha* (Fabaceae) species

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Abstract Increases in tree density resulting from fire suppression have contributed considerably to the loss of savanna and grassland habitats in North America. Inability to tolerate shade is likely an important cause of species loss in areas that have not maintained historical burning regimes. We conducted an experiment to test whether differences in shade tolerance can explain rarity within the genus *Amorpha*. Four common and three rare species of *Amorpha* were grown in a greenhouse for 100 days in direct sun or under 90% shade. Overall, shading significantly reduced growth and survival and affected allocation among species, but these differences did not differ consistently between common and rare species. Ability to tolerate shade was best explained by phenotypic plasticity, with greater shade survival being exhibited by species with the largest

changes in leaf area ratio. Furthermore, this study demonstrated that all three of the rare species can be readily cultivated under greenhouse conditions.

Keywords *Amorpha* · Growth analysis · Shade tolerance · Conservation biology · Rare species

Introduction

There is little doubt that humans are directly or indirectly responsible for the rarity of many species through over-harvesting (Mulligan and Gorchov 2004; Tabuti 2007), introduction of invasive species (Mooney and Cleland 2001; Seabloom et al. 2006), habitat destruction and fragmentation (Alho 2008; Burgman et al. 2007; Duncan and Young 2000), and changes in disturbance regimes (Brown et al. 2003; Loehle 2006). In the grassland and savanna ecosystems of eastern North America, the primary threats have been a combination of widespread habitat loss and fire suppression (Bachelet et al. 2000; Leach and Givnish 1996; Loehle 2006). While fire suppression may directly affect species that depend on burning for completion of their life cycles (e.g., fire-induced flowering, heat-stimulated germination (McCormac and Windus 1993), smoke-stimulated germination, serotiny, and disturbance dependence), the greatest driver of ecosystem change may arise indirectly

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through the encroachment of woody plants (Briggs et al. 2005). Recent reductions in fire frequency have caused an increase in tree encroachment in these otherwise open plant communities (Briggs et al. 2002; Hoch et al. 2002; Varner et al. 2005). The consequences of this community transition range from changes in avian abundance and diversity (Grant et al. 2004; Krannitz 2007) to altered soil carbon and nitrogen pools (Billings 2006) and reduced diversity and abundance of ground layer plants (Brockway and Lewis 1997; Kush and Meldahl 2000). The latter response is of particular concern for conservation, since the ground layer accounts for the vast majority of plant species richness in these systems (Leach and Givnish 1999; Walker and Peet 1984).

In the southeastern United States, the combined effects of habitat loss and fire suppression have caused many of the rare vascular species associated with the highly geographically restricted longleaf pine-wiregrass ecosystem to be either federally or state protected (Estill and Cruzan 2001; Gray et al. 2003; Sorrie and Weakley 2003; Van Lear et al. 2003). Understanding what biological factors may have predisposed these species to be rare, while others remain abundant in the remaining habitat, is an important challenge to conservation biology. Most research on rare species has focused on the biology and ecology of individual plant species (but see Baskauf and Eickmeier 1994; Lloyd et al. 2002), allowing no comparison with common species that have similar traits, and thus preventing generalizations about the causes and consequences of rarity. Inability to tolerate the increased shade associated with woody plant encroachment may be an important cause of rarity among species native to savanna and

grassland ecosystems. In order to test this hypothesis, we performed a greenhouse experiment that compared the shade tolerance of three rare and four common species of the genus *Amorpha*.

Methods

Study species

The genus *Amorpha* (false indigo), Fabaceae, includes 15 species of perennial shrubs indigenous to North America (Mabberly 1997; Weakley 2008; Wilbur 1975). The genus is not only primarily distributed through the American prairies to the southeastern United States but also extends into the western US and northern Mexico. Approximately half of *Amorpha* species are rare and have restricted ranges, while the other half are common and much more widespread (Britton and Brown 1913; Weakley 2008) making the genus a promising model system for understanding the biological causes of rarity in plants. Habitat requirements for *Amorpha* range from grassland to open woodland environments and from xeric to mesic conditions (Britton and Brown 1913; Miller 2004; Weakley 2008).

Seven taxa in the genus *Amorpha* were chosen for the study, including the common species *A. canescens*, *A. fruticosa*, *A. herbacea*, and *A. nana*, and the rare congeners *A. georgiana* var. *georgiana*, *A. georgiana* var. *confusa*, and *A. schwerinii* (Table 1). Of the common species, the distribution of *A. fruticosa* extends from southern Canada to northern Mexico, west to California, and east to Florida (Gleason and Cronquist 1991), while *A. herbacea* is restricted to the southeastern US, and *A. canescens* and *A. nana* are

Table 1 The seven *Amorpha* taxa used in this study

Taxon	Vegetative community	State status	Location of seed origin
<i>A. georgiana</i> var. <i>confusa</i>	Pine savanna (wet)	NC Threatened	Brunswick County, NC
<i>A. georgiana</i> var. <i>georgiana</i>	Pine savanna, River terrace	NC Endangered	Cumberland County, NC
<i>A. schwerinii</i>	Dry forest	NC Significantly Rare	Montgomery County, NC
<i>A. canescens</i>	Upland prairie	Common	Columbia County, WI
<i>A. fruticosa</i>	Marsh, Shrub swamp, Woodland	Common	Durham County, NC
<i>A. herbacea</i>	Pine savanna, Scrub oak forest	Common	Brunswick County, NC
<i>A. nana</i>	Mesic prairie	Common	Central South Dakota

common to the mid-western and central US. *A. georgiana* var. *confusa* is a narrow endemic restricted to one county in South Carolina and three counties in North Carolina, where it is listed as a state threatened species (NCNHP 2006). *Amorpha georgiana* var. *georgiana* is a state-endangered species in North Carolina (NCNHP 2006), but it has a somewhat broader distribution of scattered populations throughout South Carolina and Georgia. Both morphological and molecular data indicate that *A. georgiana* var. *georgiana* and *A. georgiana* var. *confusa* should be considered distinct species (Straub, personal communication), and a revision of their status is underway (Weakley, personal communication). The third rare species, *A. schwerinii*, is found in a limited number of isolated populations from Alabama to North Carolina.

Habitat requirements vary considerably among the species, with *A. canescens*, *A. nana*, and *A. schwerinii* occurring on well-drained soils and the remaining species occurring either on moist soils or over a range of well-drained and moist soils (Miller 2004; Weakley 2008). Additionally, there is a wide range of known national vegetation associations, indicating individual species are capable of surviving in diverse light environments (Table 1). While *A. nana* and *A. canescens* are most commonly associated with open prairies, the remaining species may be found in communities ranging from coastal plain swamps and marsh edges to pine savannas, scrub oak forests, and dry forests (Britton and Brown 1913; NCNHP 2006; Weakley 2008).

Growth experiments

We used classical growth analysis to compare the morphological and growth responses of all seven species of *Amorpha* to light availability. Seeds were collected for five of the study taxa (*A. fruticosa*, *A. herbacea*, *A. georgiana* var. *georgiana*, *A. georgiana* var. *confusa*, and *A. schwerinii*) from populations in the coastal plain and piedmont of North Carolina (Table 1) in November 2007. The number of populations sampled ranged from two to five populations per species. The seeds for *A. canescens* and *A. nana* originated from populations in the upper mid-western United States and were purchased from Prairie Moon Nursery (Winona, Minnesota, USA). Mean seed mass was estimated by weighing 15 seeds per population.

Prior to planting, seeds were scarified by nicking the seed coat with a razor blade and were placed in a Petri dish on damp blotter paper. The Petri dishes were kept moist in a growth chamber with temperature alternating from 30°C during the day to 20°C at night, under a photosynthetic photon flux density level (PPFD) of 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and a day-length of 8 h (North Carolina State University Phytotron, Raleigh, NC, USA). Initial trials, however, suggested that the study species do not require a well-controlled environment for successful germination. In December 2007, after a mean time of 7 days in the growth chamber, germination was considered complete when the seed coat became separated from the emerging cotyledons. The radicles of the germinated seeds were then covered with an inoculum of *Rhizobium* specific for *Amorpha* (Prairie Moon Nursery, Winona, MN, USA) before being planted into a mixture of 50% peat and 50% sand in 225 ml pots. Pots were placed in a greenhouse with temperature alternating between 25°C during the day and 22°C at night (North Carolina State University Phytotron, Raleigh, NC, USA). Thirty plants per species were divided evenly and randomly among three replicates of a full sun treatment and three replicates of a 90% shade treatment, achieved with neutral-density shade cloth hung 45 cm above the plants. The 90% shade treatment was chosen to provide lower PPFD than typical for frequently burned habitats, such as long-leaf pine savanna (Battaglia et al. 2003; Miller 2004), but higher than closed-canopy temperate forest (Canham et al. 1990). Plants were watered twice daily by misting to saturation with deionized water in the morning and with a complete nutrient solution (NCARS 2008) in the afternoon.

Destructive harvests of randomly chosen individuals were performed at the time of planting and at 50 and 100 days after planting. At the time of planting, 15 recently germinated seedlings were harvested, but for the subsequent harvests, sample sizes differed among species due to unequal survival rates. For the full sun treatment, 7–10 individuals were harvested per species, except for *A. canescens*, for which only five or six individuals were harvested. For the 90% shade treatment, sample sizes ranged from 3–10 individuals for the 50-day harvest. Due to low sample sizes at the 100-day harvest, the only parameter analyzed was survival. Stem height was measured from the base of the stem to the apical meristem. Leaf

area was measured on a CI-202 leaf area meter (CID, Inc., Camas, WA, USA). For recently germinated seedlings, length (l) and width (w) of cotyledons were measured and the area was calculated based on the area of an ellipsis ($A = l \cdot w \cdot \pi/4$). Each harvested plant was separated into leaf, stem, and roots for biomass measurements. Each fraction was weighed separately after drying for at least 48 h at 70°C. Due to low seedling availability, the initial dry mass of *A. schwerinii* seedlings was estimated from the linear regression between seed mass and seedling dry mass for the other six *Amorpha* species ($y = 0.5525x + 0.0113$, $R^2 = 0.999$).

Gas exchange

Remaining plants from the high-light treatment in the aforementioned experiment were grown in a greenhouse with temperature alternating between 23°C during the day and 20°C at night (North Carolina State University, Raleigh, NC, USA) for 8 months. Plants were watered daily to saturation and were given a complete nutrient solution (Peters Professional, St. Louis, MO, USA) thrice per week. There were no remaining individuals for *A. canescens* and *A. nana*, but at least five individuals remained for each of the other species. Maximal rates of net photosynthesis (A_{\max}) were measured for one fully mature, sun-exposed leaf per individual for each of the five remaining species. A_{\max} was measured with an open-flow infrared gas analyzer equipped with a red–blue light source (LI-6400, Li-Cor, Lincoln, NE). Inside the cuvette, the CO₂ concentration was set to 400 ppm, PPFD was set to a saturating level of 1,500 $\mu\text{mol m}^{-2} \text{s}^{-1}$, and the leaf block temperature was set to 28°C. Leaves were allowed to equilibrate inside the cuvette for 30 min before eight measurements were recorded over a period of 3 min and averaged to determine A_{\max} for each leaf. Since leaflets did not entirely fill the cuvette, measurements were corrected for leaf area.

In order to provide more detail regarding how these species respond to light, photosynthesis was measured over a range of light intensities (PPFD = 0, 25, 50, 100, 250, 500, 1,000, 1,500, and 2,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$). As before, these light curves were performed with the LI-6400 on five individuals of each of the five species. The same settings were used inside the cuvette and the same procedure

followed for the measurement of photosynthesis as described above. The following parameters were calculated for each light curve: dark respiration rate (R_d), light compensation point (the light level at which net CO₂ gas exchange is zero), and quantum yield (ϕ). Quantum yield is the initial slope of the light curve and was calculated by dividing the change in CO₂ uptake by the change in light level from 0 $\mu\text{mol m}^{-2} \text{s}^{-1}$ to 50 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

Analyses

Classical growth analysis was used to examine patterns of growth and allocation. Relative growth rate (RGR) was calculated as

$$\text{RGR} = \frac{\overline{\ln(M_2)} - \overline{\ln(M_1)}}{t_2 - t_1}$$

where $\overline{\ln(M_1)}$ and $\overline{\ln(M_2)}$ are the mean ln-transformed plant dry masses at times t_1 and t_2 , respectively (Hoffmann and Poorter 2002). Net assimilation rate (NAR) was calculated as

$$\text{NAR} = \frac{(M_2 - M_1)[\ln(A_2) - \ln(A_1)]}{(A_2 - A_1)(t_2 - t_1)}$$

where A_1 and A_2 are total leaf area at times t_1 and t_2 , respectively (Williams 1946). Leaf area ratio (LAR) was calculated by dividing total leaf area by plant dry mass. Specific leaf area (SLA) was calculated by dividing total leaf area by leaf dry mass. Survival was calculated by dividing the number of individuals who survived to the 50-day harvest by the total number of seedlings planted.

Analysis of variance (ANOVA) was used to test for the effects of light and species on stem height, plant biomass, root:shoot, LAR, SLA, and survival (JMP 7.0, SAS Inst, Cary, NC, USA). The effect of species on A_{\max} , R_d , ϕ , and light compensation point was also tested with ANOVA. Each response was tested for normality with the Shapiro and Wilk's test ($P \leq 0.05$), and logarithmic transformations were used to achieve normality, when necessary. Additionally, to compare shade tolerance in individual *Amorpha* species, the difference between trait means in the full sun and deep shade treatments were analyzed with ANOVA as above. For the derived variables RGR and NAR, which are based on intervals, the values were calculated for each interval

and also analyzed with ANOVA. In order to test for a significant effect of light availability on survival within each species, we used the chi-square test.

For comparisons between common and rare plant types, each species was treated as a statistical replicate, as is appropriate in comparative studies to avoid greatly inflating the error degrees of freedom. This was done by performing the ANOVA on the species means for a given dependent variable. Since the *Amorpha* species originated from habitats with moisture conditions ranging from swamp to upland prairie, we tested whether adaptation to moisture conditions could be a confounding factor in our analyses by classifying habitat conditions as “wet” or “dry” for each species according to their Wetland Indicator Status (USDA 2009) and testing species trait means with ANOVA as above. Only *A. herbacea* could not be designated as either wet or dry, as it is a facultative species. All data were tested for normality with the Shapiro and Wilk’s test ($P \leq 0.05$).

To understand which growth parameters influenced survival in deep shade among *Amorpha* species, we analyzed the ratios of species means in each treatment with its survival in the shade. We were thus able to compare not only the difference between performance in the sun and shade but also the plasticity of each trait response among *Amorpha* species.

Results

Growth response to shading

When tested over all species, shading significantly decreased RGR, NAR, total biomass, and root:shoot (Figs. 1a, b and 2a, c). Overall, LAR and SLA increased significantly in response to shading (Fig. 1c, d), though when tested within species, the increase was not always significant. The increase in LAR was significant in *A. fruticosa*, *A. georgiana* var. *confusa*, and *A. schwerinii* (Fig. 1c), while the increase in SLA was significant in all species except *A. herbacea* (Fig. 1d). Stem height did not differ consistently between the full sun and shade treatments (Fig. 2b). *A. fruticosa*, *A. georgiana* var. *georgiana*, and *A. schwerinii* were significantly taller in full sun, while *A. herbacea* and *A. nana* were significantly taller in the shade treatment.

In comparisons between common and rare *Amorpha* species, there was no significant difference in the mean shade:sun values for any of the growth or morphological traits measured, including RGR, NAR, LAR, SLA, total biomass, stem height, and root:shoot (Figs. 1e–h and 2e–g). Similarly, there were no significant differences in any of these traits between species originating from wet or dry habitats, regardless of whether *A. herbacea* was classified as a wet or dry species (data not shown). The results were marginally significant, however, for the differences in both total biomass and stem height between rare and common *Amorpha* species (Fig. 2e–f). While all species had higher total biomass in the sun treatment relative to the shade, there was a marginally significant trend for rare species of *Amorpha* to have a greater reduction in biomass under the shade treatment (Fig. 2e, $P = 0.074$). Among the common species, the biomass of the two species native to the prairies of the central US was more strongly affected by shading. If these species are removed from the analysis, leaving only the species native to the southeastern US, shading more strongly reduced the biomass of rare species ($P = 0.003$). Additionally, the common *Amorpha* species had a greater mean stem height in the shade than the sun treatment, while stem height was lower in the shade than the sun for rare species, although this difference was only marginally significant (Fig. 2f, $P = 0.078$).

Photosynthesis

Comparisons of light curves among *Amorpha* species also revealed significant differences in physiological responses to light intensity (Fig. 3). Specifically, there were significant differences in R_d , ϕ , and A_{\max} among five *Amorpha* species. *Amorpha georgiana* var. *georgiana* ($-1.12 \pm 0.09 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) had a significantly lower mean R_d than *A. herbacea* ($-0.68 \pm 0.09 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, $P = 0.011$). Additionally, *A. georgiana* var. *georgiana*, *A. fruticosa*, and *A. georgiana* var. *confusa* all had significantly higher ϕ than *A. herbacea* and *A. schwerinii* ($P < 0.0001$). There was also a large range in mean A_{\max} (4.05 ± 1.22 to $15.12 \pm 1.12 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) among the *Amorpha* species measured. *Amorpha georgiana* var. *georgiana* had significantly higher A_{\max} values than *A. georgiana* var. *confusa*, *A. herbacea*, and *A. schwerinii* ($P < 0.0001$). There

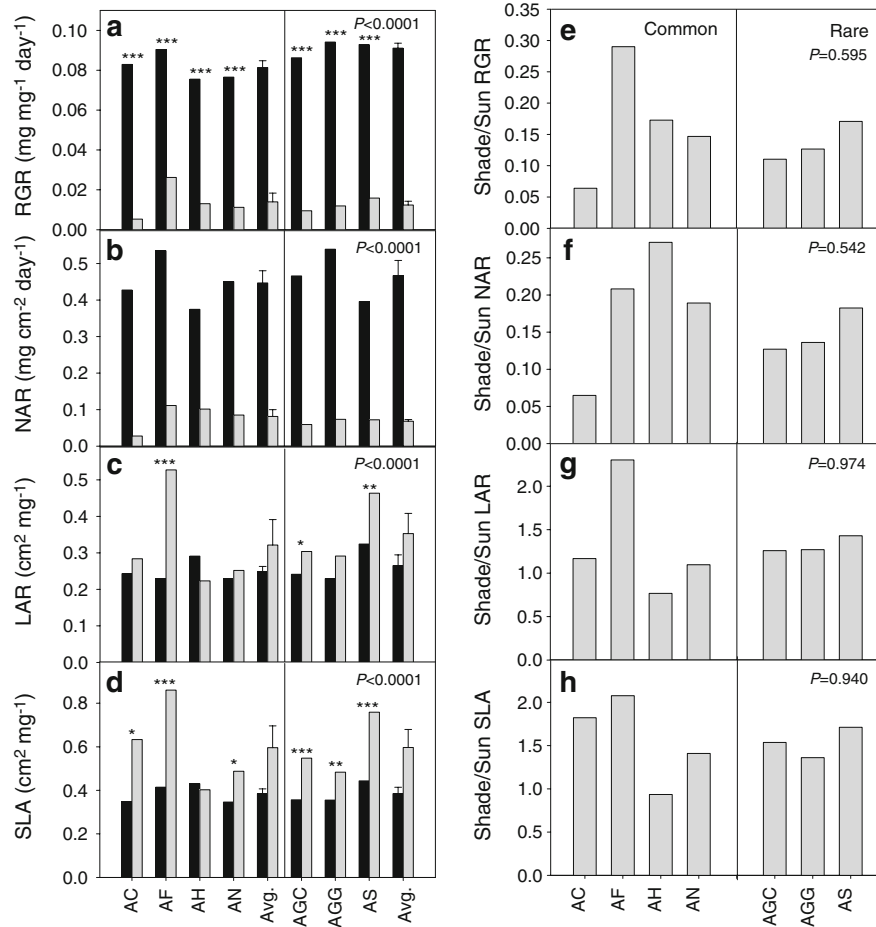


Fig. 1 The effect of full sun (black bars) versus 90% shading (gray bars) on **a** relative growth rate, RGR (mg mg⁻¹ day⁻¹), **b** net assimilation rate, NAR (mg cm⁻² day⁻¹), **c** leaf area ratio, LAR (cm² mg⁻¹), and **d** specific leaf area, SLA (cm² mg⁻¹) in *Amorpha* species. Ratios for the relative difference between sun and shade treatments for each species are reported for all parameters (**e–h**). LAR and SLA were calculated at the 50-day harvest, and RGR and NAR were calculated for the 7–50 day interval. *P*-values for **a–d** represent

significance of the treatment effect for all species combined, while *P*-values for **e–h** represent significance between common and rare species types. Significant treatment effects within species are denoted by stars: * *P* < 0.05, ** *P* < 0.01, and *** *P* < 0.001. Error bars represent standard errors. Species codes: AC, *A. canescens*, AF, *A. fruticosa*, AGC, *A. georgiana* var. *confusa*, AGG, *A. georgiana* var. *georgiana*, AH, *A. herbacea*, AN, *A. nana*, and AS, *A. schwerinii*

was, however, no significant difference in light compensation point among these five *Amorpha* species (mean = 14.8 ± 0.62 μmol m⁻² s⁻¹, *P* = 0.286).

Shade effects on survival

For all species, seedling survival in full sun was significantly higher than that in the shade treatment (Fig. 2d, *P* = 0.005). When species were tested separately, the increased mortality in shade was significant only for *A. nana* and *A. georgiana* var.

confusa. In the sun treatment, most mortality occurred early in the experiment, while seedlings were quite small (mean mortality for 7–50 days = 53.7%), with little mortality occurring between 50 and 100 days (mean mortality = 6.0%, data not shown). In contrast, in the shade treatment, mortality remained relatively high throughout the duration of the experiment, with mean mortality decreasing from 69.3% in the first interval to 38.8% in the second. There were large differences in the sensitivity to shading, but there was not a significant

Fig. 2 The effect of full sun (black bars) versus 90% shading (gray bars) on **a** total biomass (mg), **b** stem height (cm), **c** root:shoot, and **d** mean survival (%) in *Amorpha* species. Ratios between sun and shade treatments for each species are reported for all parameters (**e–h**). All parameters were calculated at the 50-day harvest. *P*-values for **a–d** represent significance of the treatment effect for all species combined, while *P*-values for **e–h** represent significance between common and rare species types. Significant treatment effects within species are denoted by stars: * *P* < 0.05, ** *P* < 0.01, and *** *P* < 0.001. Error bars represent standard errors. Species codes are the same as in Fig. 1

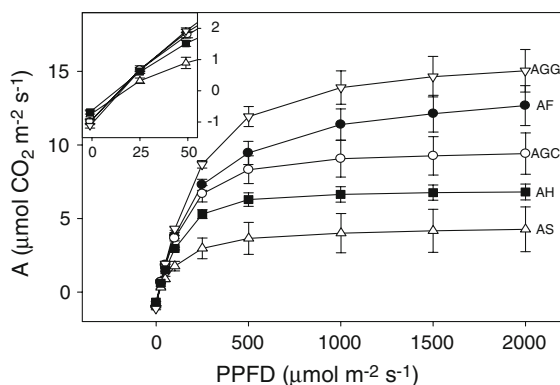
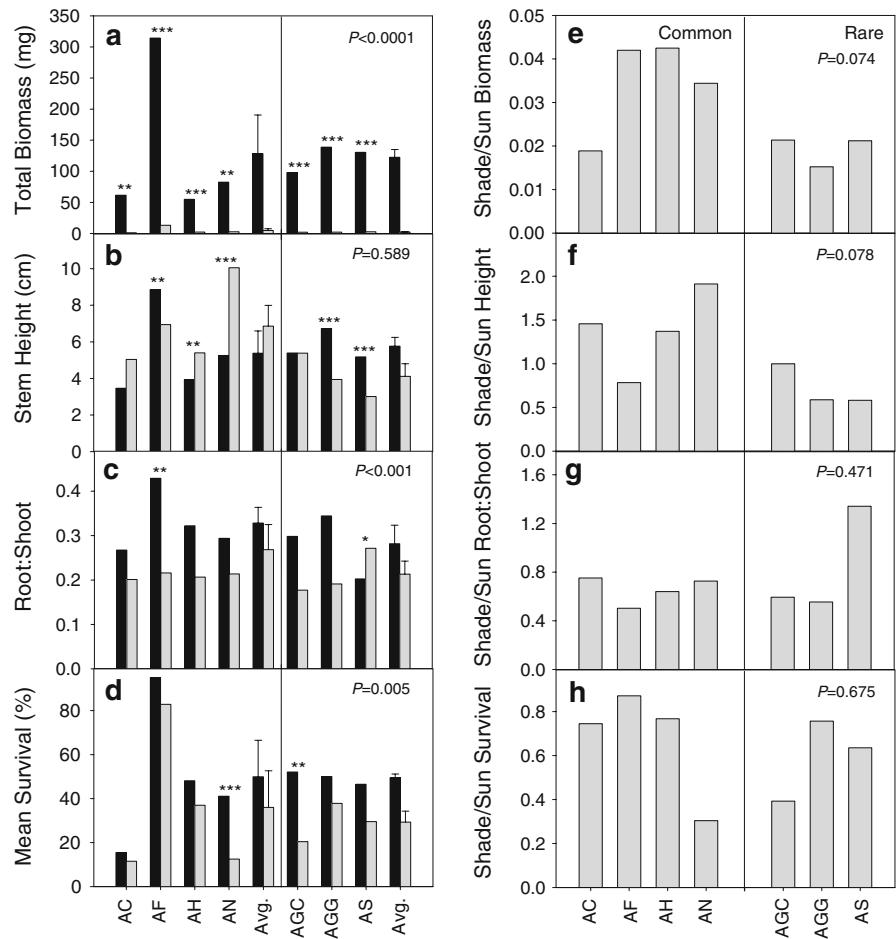


Fig. 3 Light response curves for five species of *Amorpha* grown in full sun. Each curve represents an average of five individuals. Open symbols represent rare species, and solid symbols represent common species. Error bars represent standard errors. Species codes are the same as Fig. 1

difference in survival between common and rare *Amorpha* species (Fig. 2h). In fact, mean survival rates were very similar between common and rare species under full sun ($49.9 \pm 16.6\%$ SE vs. $49.5 \pm 1.6\%$) and under deep shade ($36.0 \pm 16.7\%$ vs. $29.3 \pm 5.0\%$).

For most species, there were too few individuals to estimate shade survival rates for the 50–100 days period. Of the common species, higher shade survival rates were found for *A. fruticosa* (100%, *n* = 17, data not shown) and *A. herbacea* (44%, *n* = 9). The rare species *A. georgiana* var. *georgiana* had a shade survival rate of 71% (*n* = 7). The combined shade survival of the remaining species was only 25% (*n* = 16) for the 50–100 days period.

In *Amorpha*, survival in shade was significantly correlated with the ability to maintain relatively high growth rates (Fig. 4c). Species that had high survival in shade also experienced the least reduction in

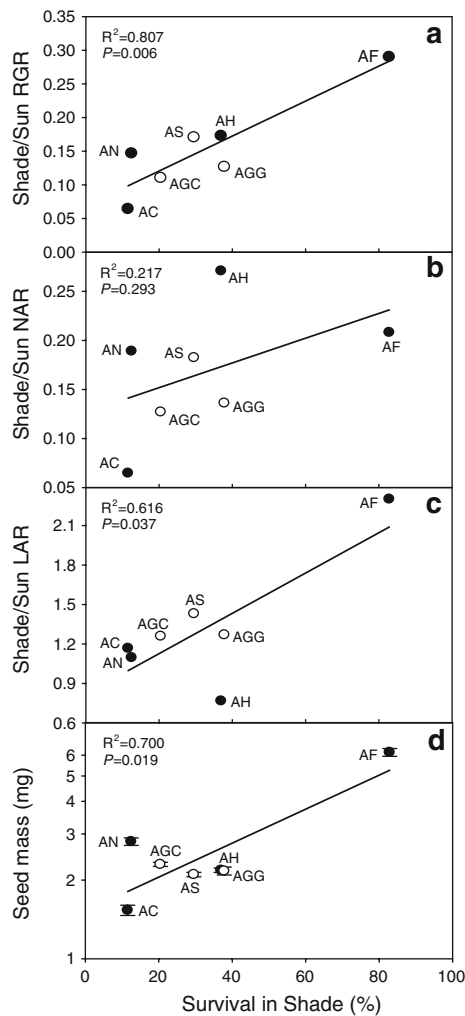


Fig. 4 Linear regressions among species of *Amorpha* between survival in shade (%) and **a** sun/shade relative growth rate, RGR, **b** sun/shade net assimilation rate, NAR, **c** sun/shade leaf area ratio, LAR, and **d** mean seed mass (mg). RGR and NAR were calculated for the 7–50 days interval, and LAR was calculated at the 50-day harvest. *Open circles* represent rare species, and *solid circles* represent common species. *Error bars* represent standard errors. Species codes are the same as Fig. 1

growth, relative to full sun. This ability to maintain relatively high growth rates in the shade was most strongly related to phenotypic plasticity in LAR ($R^2 = 0.616$, $P = 0.037$). Species with high survival and high RGR in the shade exhibited a greater increase in LAR under shade, while NAR was not significantly correlated with survival (Fig. 4b, c). Among all species, seed mass was significantly and positively correlated with shade survival (Fig. 4d), as

well as with RGR ($R^2 = 0.810$, $P = 0.006$, data not shown).

Discussion

Light availability had large effects on photosynthesis, allocation, growth, and survival of *Amorpha* plants. Mean survival was 1.5 times greater in full sun than under 90% shade (Fig. 2d), while RGR in sun was 6.4 times that in deep shade. RGR is determined by growth rate per unit leaf area (NAR) as well as leaf area per unit plant mass (LAR), according to the relationship $RGR = NAR \times LAR$ (Evans 1972). In *Amorpha*, the large decline in RGR in the shade was due primarily to the reduction in NAR (Fig. 1b), which averaged only 16.6% that of plants in full sun. The reduced NAR was partially offset by a mean increase of 31.2% in LAR in shade, relative to sun (Fig. 1c). This treatment effect on allocation patterns in *Amorpha* was also manifested as a decreased root:shoot (Fig. 2c) in the shade. Overall, these patterns are typical of plant responses to dense shade, which commonly reduces carbon assimilation, growth, and survival (Grubb et al. 1996; Montgomery and Chazdon 2002; Walters and Reich 1996), while resulting in an increase in LAR (Lusk 2002; Poorter 1999; Reich et al. 1998).

There was a considerable variation in shade tolerance among species. Contrary to the hypothesis, however, there was no consistent difference in shade tolerance between common and rare species of *Amorpha*. None of the measured growth traits differed significantly between common and rare species (Figs. 1 and 2). It does not appear that the different moisture conditions of habitat origin in *Amorpha*, which ranged from moist savanna to upland prairie, influenced our comparison of common versus rare species, since there were no significant differences in growth or allocation between species originating from wet or dry habitats. Survival under deep shade, which appears to be a better indicator of shade tolerance than growth (Kitajima 2007; Reich et al. 2003), also did not differ between rare and common species (Fig. 2d, h). Consequently, shade tolerance does not appear to explain the pattern of abundance among these seven species of *Amorpha*. Similarly, Baskauf and Eickmeier (1994) did not find any photosynthetic differences between a common

and rare species of *Echinacea*, while Lloyd et al. (2002) found only a non-significant tendency for common species to have higher RGR than rare species in the genus *Acaena* (Lloyd et al. 2002).

Munzbergova (2005) found significant differences between the population growth rate of a common and rare *Cirsium* species and suggests comparing only congeneric pairs of similar habitat requirements. Our study included *A. nana* and *A. canescens*, common species native to prairies of the central US, while the remaining five species are all native to the southeastern US. Among these five southeastern species, there was a tendency for rare species to be more strongly affected by shading. The two common southeastern species exhibited approximately a 25-fold decrease in plant mass in response to shading, while the three rare species exhibited approximately 50-fold decreases. The rare species also exhibited the greatest reductions in NAR and survival.

In *Amorpha*, shade tolerance was significantly correlated to seed size and phenotypic plasticity in LAR (Fig. 4c, d). The mean seed mass of *A. fruticosa* was over twice as large as all the other species studied here, which strongly influenced these correlations. Species with high survival in shade tended to have high seed mass, in *Amorpha* as well as a number of other plant species (Bruun and Ten Brink 2008; Moles and Westoby 2004). Larger seeds offer a recruitment advantage by containing larger reserves for young seedlings, although these benefits to survival have often been shown to be temporary (Walters and Reich 2000; Westoby et al. 1996). As seedlings age, other physiological traits are more influential to survival (Walters and Reich 2000), such as increases in LAR (Reich et al. 1998). Species of *Amorpha* with higher shade tolerance showed the greatest increase in LAR in response to shading. This increase in allocation to leaf area in shade appears to be critical to compensate for the reduced photosynthetic rates of many species in response to shade (De Lucia et al. 1998; Hoffmann and Franco 2003), thereby reducing the impact of shade on survival and growth. Overall, *A. fruticosa* was the most shade-tolerant species, maintaining the highest growth and survival rates under shade (Fig. 2a, d) and possibly contributing to its broad distribution range.

The measurements of A_{\max} (Fig. 3) were highly correlated with NAR ($R^2 = 0.844$, $P = 0.028$, data not shown), indicating there is a close agreement

between the two methods of estimating rates of photosynthesis. The two highest rates of gas exchange, NAR, and shade survival were found in *A. georgiana* var. *georgiana* and *A. fruticosa* (Figs. 1b, 2d, and 3), although shade-tolerant shrub species often have lower A_{\max} than sun-adapted species (Chazdon 1992; Larcher 2003). Differences in quantum yield among species revealed that the leaves of *A. georgiana* var. *georgiana*, *A. fruticosa*, and *A. georgiana* var. *confusa* were more efficient than *A. herbacea* and *A. schwerinii* at light capture at low light levels. While A_{\max} was associated with performance in high light, there was little relationship between performance in the shade and dark respiration or quantum yield, parameters that determine assimilation under low light. This corroborates the result that changes in LAR were more important for determining species response to shading.

Survival, an important component of fitness, is perhaps the most relevant trait for examining how distribution patterns will be influenced by changing environments. Patterns of mortality in a greenhouse study may not be representative of natural rates, but can indicate overall susceptibility of seedlings to suboptimal conditions (Banack et al. 2002; Barton 1993). Ability of seedlings to survive in deep shade appears to be largely determined by ability to maintain positive growth rates, while allocating sufficient resources to defense and reserves (Kitajima 2007), the latter being critical for recovering from stress and disturbance.

Recently germinated seedlings of the study species were very small, delicate and susceptible to even the modest stresses and disturbances of a greenhouse environment. In temperate forests, shade-tolerant tree species can persist for long periods in a state of suppressed growth in the understory, but shade-intolerant species cannot survive when suppressed (Canham 1989; Kobe and Coates 1997). Similarly, seedling success in *Amorpha* will likely depend on rapid initial growth, which allows seedlings to quickly reach a size that buffers the effects of stress and disturbance. Inability to attain these larger sizes may explain the high mortality under shade, even after the seedlings were 50 days old. In the full sun treatment, mean RGR was $0.085 \text{ mg mg}^{-1} \text{ day}^{-1}$, corresponding to an 82-fold increase in plant mass over the first 50 days of the experiment. Correspondingly, in the full sun treatment, very little mortality

occurred after this time when the seedling had attained substantial size. In contrast, mean RGR in the shade treatment was $0.013 \text{ mg mg}^{-1} \text{ day}^{-1}$, which is not sufficient to double seedling mass in 50 days. Even in shade-tolerant shrubs, larger seedlings have been shown to have lower mortality rates (Hastwell and Facelli 2003).

Seed mass also plays an important role in determining seedling size. Seed mass is commonly associated with shade tolerance (Grime 1977; Poorter et al. 2008), as was shown here, being positively correlated with survival and RGR in the shade (Fig. 4d). The advantage of large seeds may not be primarily related to shade tolerance for these species, but rather to lowering risks, such as desiccation during dry spells or burial by leaf litter (Kostel-Hughes et al. 2005; Metcalfe and Grubb 1997). Leaf litter has been shown to greatly reduce establishment and survival of seedlings in woody species (Seiwa and Kikuzawa 1996), including *A. herbacea* var. *crenulata* (Wendelberger et al. 2007). Fire will likely benefit *Amorpha* seedling establishment by reducing litter as well as increasing light availability.

The three rare species were readily grown under greenhouse conditions, making this a viable option for propagation of these species for restoration efforts. Container-grown seedlings of the endangered subspecies, *A. herbacea* var. *crenulata*, have been successfully used to establish new populations (Wendelberger et al. 2007), and similar success may be possible with these species. The greatest impediment to producing seedlings appears to be an initial mortality when seedlings are small and delicate. Initially, seedlings were sensitive to even minor disturbances of the growing media caused by watering or stress imposed by drying of the soil media between daily waterings. Efforts to minimize such factors will likely result in considerably greater seedling survival than was attained in this study.

Determining the causes of rarity in groups of plants is a difficult but crucial task if we are to be successful in preventing the extinction of currently threatened and endangered species. Due to the complexity of natural ecosystems, it is often a combination of factors that can cause plant species to become rare (Kunin and Gaston 1993). Since RGR and total biomass were significantly reduced, it is likely that shade intolerance is a contributing factor to rareness for all the rare species studied here, at least

during the establishment phase. These species may benefit from a more active management of the fire regime and/or increases in practices to create more open habitats throughout their current range.

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