

Seedling co-tolerance of multiple stressors in a disturbed tropical floodplain forest

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Abstract. Differential stress tolerance among species is a central concept for understanding coexistence in diverse ecosystems. Although multiple co-occurring stressors are present in many ecosystems, relatively little is understood as to how communities are shaped by interacting stressors at multiple scales. We use a regression design to test the effects of two environmental stress gradients, flooding and shade, as well as herbivore activity, mechanical damage, on first-year transplanted seedling survival and growth in twenty-one common garden plots in secondary Amazonian floodplain forests. Among ten woody species varying in flood and shade tolerance, half of the seedlings were clipped at 5 cm aboveground, removing ~50% of plant biomass. Damage reduced seedling survival by ~50% and aboveground biomass by 94% of undamaged seedlings. Despite declines in relative growth rates with increasing flood duration, the survival of most flood-tolerant species was unaffected by variation in prolonged submergence of 3–6 months. Meanwhile, low-flood-tolerant species displayed clear thresholds in survival of flood duration <150 d. The effects of all three stressors were largely independent, with the exception of two species whereby light availability interacted with flood duration to enhance seedling survival during prolonged floods and one species whereby flood duration interacted with damage. Trade-offs in stress tolerance among species were not apparent. Rather, damage, shade, and flood tolerance among species were all positively correlated, suggesting that combined stresses favor the persistence of a few highly stress-tolerant species—characterized by slow growth rates, high root:shoot ratios, and short stems—in this disturbed ecosystem. This study highlights the importance of dry season stressors (e.g., light availability, herbivore activity, and drought) as strong selective forces for the establishment and persistence of tropical floodplain communities. Furthermore, in an ecosystem where relatively little is known as to how seedlings persist in forest understories, we demonstrate how biotic and abiotic stressors ultimately shape woody species composition and richness.

Key words: drought; plant strategy theory; resource allocation trade-offs; seedling ecology; *várzea*; wetland forests.

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INTRODUCTION

Multiple stressors play a critical role in structuring plant communities and driving their recovery following disturbance (Chapin et al.

1987). A central tenet of community ecology is that species distribute differentially across stress gradients as a function of stress tolerance (Grubb 1977, Grime 1979). As multiple stressors co-occur in most natural environments, some species

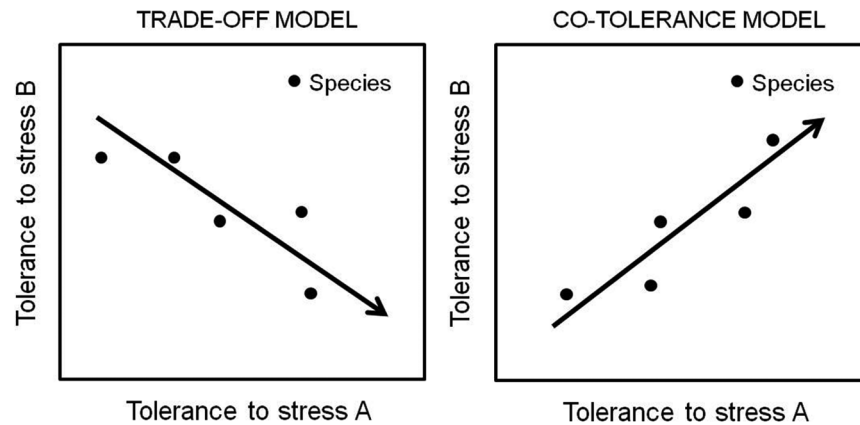


Fig. 1. Two models for species strategies for survival of multiple stressors: a trade-off model whereby resource allocation to tolerance of stress A compromises resources available for tolerance to stress B; and a co-tolerance model whereby high stress tolerance to stress A enhances tolerance to additional stressors.

possess a suite of traits that permit broad tolerance to many stresses, thus thriving under limited resources (Chapin et al. 1993). Alternatively, interspecific differences in resource allocation to stress tolerance could cause trade-offs among species, supporting co-existence under combined stresses (Fig. 1; Battaglia and Sharitz 2006). The effect of multiple stressors is of pressing concern due to the introduction and intensification of stressors associated with climate change (e.g., flooding and drought) and anthropogenic disturbance (e.g., introduced vertebrates and logging, Shears and Ross 2010, Tockner et al. 2010). Drought sensitivity plays an increasingly important role in mediating moist tropical forest species distribution (Engelbrecht et al. 2007), while herbivory and fire frequency together drive forest-grassland dynamics in savannas (Holdo et al. 2009). Tolerance to multiple stresses among seedlings—a bottleneck in tree life history—is critical for forest persistence under altered stress regimes (Aber et al. 2001).

Tree seedlings in Amazonian floodplain forests have adapted tolerance to submergence by floods ≤ 7 months in duration, a phenomenon unparalleled among temperate and boreal trees. Over 1000 tropical tree species (Wittmann et al. 2006) successfully establish under variable stresses of submergence, shade, and herbivory in Amazonian floodplains. A tolerance vs. escape model (Parolin 2002) describes two strategies for seedling establishment in floodplains, whereby some

species escape submergence via rapid height growth (Parolin 2003), while others tolerate submergence via various physiological traits (e.g., reduction of toxic by-products from aerobic respiration, Ferreira et al. 2009). A trade-off among species for shade and flood tolerance is another model for species establishment in seasonally flooded forests, whereby shade-tolerant species persist at high elevations with short flood duration and highly flood-tolerant species require high-light habitats (Hall and Harcombe 1998, Battaglia and Sharitz 2006). The former model predicts that fast-growing species dominate higher elevations, while the latter model predicts slower-growing species will persist. While flooding and light gradients affect species composition of saplings in floodplains (Wittmann and Junk 2003), little is understood as to how flooding and light mediate seedling communities during the first year of establishment—a critical period for survival in this ecosystem.

Tropical floodplains are subject to major anthropogenic impacts, including intensification of cattle and water buffalo herds at alarming rates in many of the world's large river basins (Gatewood and Cornwell 1976, Robertson and Rowling 2000, Junk and de Cunha 2005, Dahdouh-Guebas et al. 2006). In Lower Amazon floodplains, cattle and water buffalo move through forest understories throughout the low-water season and could have a potentially large impact on seedling recruitment via mechanical damage to plant tissues (Sheikh 2002). Seedlings

are particularly vulnerable to damage as a result of their size, shallow root system, and limited reserves for tissue repair and defense (Weisberg et al. 2005, Holdo et al. 2009). Tolerance to mechanical damage varies with species traits such as seed size (Harms and Dalling 1997), cotyledon morphology (Green and Juniper 2004), storage reserves (Canham et al. 1999), and relative growth rates in first-year seedlings. In floodplain forests, the carbon costs of damage recovery (e.g., resprouting) and limited carbon assimilation during flooding (Kozłowski and Pallardy 1997) could place an additional stress on seedlings that limits growth and survival (Waring 1987). Nonetheless, regeneration via sprouting is a common survival strategy for many flood-tolerant species (Frangi and Lugo 1991, Deiller et al. 2003, Ernst and Brooks 2003). If flood tolerance and sprouting place competitive demands on plants for resources, a trade-off between flood and damage tolerance and may explain species differences in survival.

The goal of this study is to test the combined effects of environmental stress gradients, flood duration and shade, and a biotic stress, mechanical damage, on the growth and survival of woody species from secondary Amazonian floodplain forests. In one of the few garden experiments on seedlings in Amazonian floodplain forests, we used a regression design to compare seedling growth and survival across a fine gradient of change in flood duration. We compare the responses of ten species across a suite of traits, including relative growth rates (RGR), root:shoot ratios, and cotyledon morphology, to understand the potential strategies for seedling persistence under seasonal flooding stress and increasing disturbance by introduced livestock. We address the following questions: (1) How do flood duration, light availability, and mechanical damage affect seedling survival? (2) How do species life history traits such as RGR, root:shoot ratios, and cotyledon morphology affect survival and stress tolerance? (3) Are there trade-offs in species tolerance?

METHODS

Study site

This study was conducted in three floodplain forests near Santarém, Pará, Brazil (02°25' S,

54°42' W; Appendix: Fig. A1). The region lies in the Lower Amazon Basin, with a rainfall of 1800–2000 mm yr⁻¹ and five consecutive dry months with rainfall ≤100 mm (July–November; Sombroek 2001). Flood waters of the Amazon River peak in May–June at 7.7 ± 2.4 m asl (*unpublished data*; Capitania dos Portos-Santarém 2008) 1–3 months after the mid-rainy season. Many of the region's forests are ~20–80 years old, having regenerated on abandoned jute (*Corchorus capsularis*) plantations (WinklerPrins 2006). Currently, cattle and water buffalo move through forests in the low-water season to reach grasslands for pasture (Sheikh 2002).

Using a regression design (Cottingham et al. 2005), we established 21 fenced plots of 5 × 5 m (*N* = 7 per forest) in random locations across a flood gradient. Plots were located off trails and cattle were excluded from plots with barbed wire fences >0.5 m from the nearest planted seedling. We measured water column depth in plots at peak flooding (15 May 2008) with a weighted line suspended from a canoe into the water. Daily river levels in 2008 were obtained from the Capitania dos Portos database in Santarém. Relative flood level was calculated as the difference between maximum river level (8.36 m asl) and water column depth (0.7 to 2.5 m in 2008). Flood duration was then calculated as the number of days for the river to rise and fall between relative flood level and 8.36 m. Flood duration (113–208 d) is thus the days seedlings were waterlogged in saturated soil as complete submergence time varied with height. Based on an average height of 25 and 12 cm for undamaged and damaged seedlings after one year, the average estimated duration of plant submergence was 100–200 d and 107–200 d, respectively.

Field methods

Seedlings were germinated from seeds collected from nearby floodplain forests in the flood season (May–July 2007) and grown in shaded nursery beds in a mixture of composted cattle manure, palm fibers and floodplain soil. We selected ten species (referred to by genus; species names in Table 1) that varied in flood tolerance, cotyledon morphology, and seed size. Species were grouped into light-demanding and shade-tolerant based on cotyledon morphology and leaf phenology (Table 1; Appendix: Fig. A3). After

Table 1. Physiological traits of ten floodplain forest study species, ordered by flood tolerance and ecological guild. Species were assigned to two ecological guilds, light-demanding (LD) or shade-tolerant (ST), based on cotyledon morphology and leaf phenology (Appendix: Fig. A3). Abbreviations for Cotyledon morphology (Cot): Phanerocotylar epigeal foliaceous (PEF), Cryptocotylar hypogeal storage (CHS), Cryptocotylar epigeal storage (CES). Seed size is the average wet weight from a subsample of seeds. Average one-year survival and relative growth rates (means \pm SD) are shown for undamaged seedlings and damaged seedlings.

Species	Family	Flood tolerance	Cot	Guild	Seed (mg)	Survival (%)		RGR ($\text{cg g}^{-1} \text{mo}^{-1}$)	
						Undam.	Dam.	Undam.	Dam.
<i>Psudobombax munguba</i>	Malvaceae (Bombacoideae)	High	PEF	LD	45	74 \pm 28	29 \pm 37	19 \pm 10	12 \pm 11
<i>Cordia tetrandra</i>	Boraginaceae	High	PEF	LD	140	81 \pm 29	29 \pm 29	17 \pm 11	7 \pm 7
<i>Vitex cymosa</i>	Lamiaceae	High	PEF	LD	350	87 \pm 17	61 \pm 36	14 \pm 6	7 \pm 9
<i>Coccoloba ovata</i> †	Polygonaceae	High	PEF	LD	39	94 \pm 13	82 \pm 21	13 \pm 8	7 \pm 7
<i>Mouriri acutiflora</i>	Melastomataceae	High	CHS	ST	230	79 \pm 22	4 \pm 10	14 \pm 6	2 \pm 3
<i>Garcinia brasiliensis</i>	Clusiaceae	High	CHS	ST	2930	86 \pm 20	59 \pm 29	17 \pm 6	12 \pm 4
<i>Trichilia singularis</i> †	Meliaceae	High	CHS	ST	390	85 \pm 14	56 \pm 32	16 \pm 6	8 \pm 4
<i>Ormosia paraensis</i>	Fabaceae	Low	CES	ST	600	14 \pm 29	0 \pm 0	26 \pm 7	...
<i>Guarea guidonia</i>	Meliaceae	Low	CHS	ST	580	11 \pm 23	2 \pm 7	18 \pm 5	8 \pm 3
<i>Hevea brasiliensis</i>	Euphorbiaceae	Low	CHS	ST	3930	0 \pm 0	1 \pm 4

†Woody shrubs \leq 8 m tall.

expansion of first true leaves, seedlings were transplanted to perforated bags in a forest understory and watered daily for 2–8 weeks. After floodwaters receded, seedlings ($N = 2268$) were transplanted into plots at randomly assigned locations 50 cm apart. Newly planted seedlings had 2–9 true leaves (± 1 within species).

Three weeks after transplanting (October 2007), all seedlings were measured and a subset ($N = 21$ per species) was harvested for initial biomass. Seedlings were then randomly assigned to a treatment, damaged or undamaged. Damaged seedlings had stems clipped with scissors at 5 cm aboveground (Green and Juniper 2004) and all remaining true leaves removed. Clipping removed most aboveground biomass without removing dormant buds at cotyledon nodes that provide the physiological capability to sprout (Harms and Dalling 1997, del Tredici 2001). Foliar cotyledons (when present) were not removed. There were five seedlings per species per treatment per plot, except for *Guarea guidonia* (4 seedlings). Seedlings that experienced natural hazards and stress once transplanted into plots (e.g., litterfall, herbivory, drying) were classified as “broken stems” or “dried apex”. We observed natural damage among 4% of 1117 undamaged seedlings in the low-water season and 7% of 579 undamaged seedlings in the flood season.

We measured seedling survival, height, and diameter seven times at 5-week intervals over one year (October 2007–February 2008; August–

September 2008), sampling before and after a single annual flood pulse (Appendix: Fig. A2). Because plots emerged from flood waters at different times, the February and August censuses of 2008 excluded 7 and 9 plots, respectively, that were underwater. All seedlings were harvested after one year to measure final above- and belowground biomass after drying to a constant weight. Relative growth rate (RGR) was calculated as $[\ln(\text{biomass}_{\text{final}}) - \ln(\text{biomass}_{\text{initial}})]/\text{time}$ for the change in total dry plant biomass from initial (October 2007) to final harvest (September 2008), where time = 11.25 months. Initial biomass for damaged seedlings was considered as biomass after damage. Initial biomass of unharvested seedlings was estimated by the linear regression equation for plant biomass as a function of stem volume of all species ($h \cdot \pi \cdot (\text{mid-stem diameter}/2)^2$; $r = 0.84$).

Light availability was estimated with hemispherical canopy photos taken at 50 cm aboveground at the center of each plot in the late dry season (November 2007), after most deciduous species had already flushed new leaves. Photos were taken just before sunrise and oriented to magnetic north with a Nikon Coolpix 990 and FC-E8 Fisheye lens, with an F-stop of 5.8 and automatic speed (Frazer et al. 2001). Photos were analyzed with Gap Light Analyzer Version 2.0 to calculate percent transmitted light $[100 \cdot (\text{transient diffuse} + \text{direct light})/(\text{direct} + \text{diffuse radiation incident})]$, accounting for both direct light from

overhead gap openings and diffuse light reflected off leaves (Frazer et al. 1999).

Soil cores were collected at four points 1.5 m from the plot center in the low water season (January 2008). At each point, litter depth was measured with a ruler and averaged across the plot. The 7×10 cm soil cores were extracted with a PVC tube and divided in half, 0–5 cm and 5–10 cm depth, placed in plastic bags, and weighed in the lab. A 25 g subsample from each core was dried at 105°C for 48 h to calculate volumetric soil water content, SWC [$1 - (\text{Mass}_{\text{dry}}/\text{Mass}_{\text{wet}})$], and soil bulk density [$1 - (\text{SWC} \times \text{Mass}_{\text{wetcore}})/\text{Vol}_{\text{core}}$]. Soil pH was measured with an Oyster portable pH kit and standard polymer pH electrode (Model #6015WC, Extech, Waltham, MA) from 20 g of wet soil mixed with 40 ml of deionized water. To measure soil texture, sand particles were extracted with a sieve (#230: 0.063 mm), silt was decanted, and the clay fraction was estimated by subtracting the sand and silt fractions from total dry weight in the LBA-Santarém soil laboratory (Kettler et al. 2001, adapted by Beldini). Soil samples collected in September 2008 were sent to Embrapa-Belém in Brazil for soil nitrogen (organic N, NH_3 , and NH_4) concentration, using the Kjeldahl method, and extractable soil phosphorous, using the Mehlich method (Embrapa 1997).

Trade-offs between flood and shade tolerance as well as flood and damage tolerance were examined by comparing mean species survival under stressed conditions. Flood tolerance = the proportion of undamaged seedlings surviving during the flood season. Damage tolerance = the difference between seedling survival in damaged and undamaged treatments per plot during the low-water season. Shade tolerance = the survival of seedlings under low-light (9–12% canopy openness) in the low-water season. Growth-survival trade-offs were explored by comparing species mean RGR and percent survival of damaged and undamaged seedlings (Kitajima 1994, Sack and Grubb 2001). An index of stress tolerance was calculated as the average between flood, damage, and shade tolerance. We compared species traits—RGR, height, and root:shoot ratios—across stress tolerance to understand traits characteristic of highly stress-tolerant species.

Statistical analyses

Non-metric multidimensional scaling (NMDS) was used to illustrate graphically the relationship between species mortality and plot-level environmental variables including canopy openness, flood level, [N], [P], soil water content, percent sand, pH, litter depth, and initial seedling height. An NMDS was chosen given non-normal data, non-linear correlation among some environmental variables, and zero variation values in some plots. Environmental variables were relativized to a value between 0 and 1. Two dimensions were selected on the basis of a change in stress in the real data of less than 5. The ordination graph was rotated 125° to align major vectors with the axes and maximize orthogonality (90.8%). We ran Pearson's product-moment correlation coefficient tests across all variables, using the transformations: $\log([N])$, $\log(\text{litter depth})$, and $(\text{percent sand})^{0.25}$. Variables having low correlation with flood duration ($R > 0.32$; $P < 0.05$) were considered for hypothesis testing in models.

Analyses of seedling survival were conducted with generalized linear models (GLM) with a quasibinomial error structure (accounting for overdispersed data) and weighted by sample size using a two-vector response variable (Crawley 2007). For seedling growth analyses, we used linear models. We chose not to use forest as a random variable as the effects of flood duration were confounded with forest because each forest differed in the range of flood levels available (Appendix: Fig. A4). For both survival and growth we ran full models including all independent variables of primary interest (damage, flood duration, and canopy openness) and their interactions. In order to justify species-specific models for survival and growth, we used model comparison with likelihood ratio tests to test the effect of adding “species” to the full model. Based on the NMDS results, we also used model comparison to test the effects of adding litter depth and [N] to full models for seedling survival and growth of all species combined.

The significance of explanatory variables and their interactions were tested by comparing nested models using likelihood ratio tests with F-test statistics (Crawley 2007). Final models are fitted within the ANOVA function using sequential adding of terms to select the better of paired models (Bolker et al. 2009). The effects of

Table 2. Coefficients (and P values) estimated by generalized linear models for the effects of damage, flood duration, and light on seedling survival of all species for one year, the low-water season, and the dry season. Also shown are models for light-demanding species, shade-tolerant species, and $N = 9$ species (*Hevea* excluded due to 0% survival after one year).

Seedling survival	Damage	Flood duration	Light	Flood × damage	Light × damage	Light × flood	Light × flood × damage
One year	-1.19***	-0.001†	0.12***
Low-water season	-2.54***	...	0.15***
Flood season	-1.03***	...	0.08***
Light-demanding species	-1.76***	...	0.24***
Shade-tolerant species	-1.35***	-0.0093*
<i>Pseudobombax</i>	-2.24***	...	0.30***
<i>Cordia</i>	-6.01***	...	-1.16***	-0.13*	...	0.009**	...
<i>Vitex</i>	-7.64***	...	0.10***	...	0.45**
<i>Coccoloba</i>	-1.16*	...	0.21*
<i>Mouriri</i>	-4.57***	-0.015*	0.22	-0.0001†	...
<i>Garcinia</i>	-1.44***	-0.016**	0.13*
<i>Trichilia</i>	-1.70***	...	0.08***	0.001*	...
<i>Ormosia</i>	-21.2***	-0.097***	0.45**
<i>Guarea</i>	-2.04*	-0.09***

†0.10 < P ; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

additional categorical variables such as, seed size and seedling height on survival were tested separately using similar GLMs. The relationship between seed size and average sprout stem volume within species were explored with Pearson's product-moment correlation coefficients (Crawley 2007). To determine if there was a significant change in initial vs. final root biomass, we used two-way pair-wise t -tests within each species.

Seasonal differences in survival were explored with a repeated measures generalized linear mixed model (GLMM) with season, flooding, damage, and light as fixed effects (Crawley 2007). Based on seasonal differences in seedling survival, the effects of flood duration and mechanical damage on survival were tested over one year (October 2007–September 2008), as well as in the low-water season (October 2007–January 2008) and flood season (January–August 2008). For differences in survival between monthly censuses, a similar GLMM was constructed with census month as a fixed effect (Appendix: Table A1).

Species trade-offs between flood and shade tolerance, flood and damage tolerance, and survival and growth were explored with Pearson's product-moment correlation coefficient tests. Degrees of freedom for all t -tests are indicated as subscripts. All means are indicated with standard deviations (SD). All analyses were conducted using R 2.15.1 (R Development Core

Team 2012).

RESULTS

Effects of multiple stressors on first-year seedling survival

The NMDS yielded a 2-dimensional ordination showing that plot means for one-year survival fall along a gradient of increasing light availability (9–19% canopy openness; Kendall's tau = -0.50) and decreasing litter depth (0–4.0 cm; tau = 0.49). Axis 1 explained 77% of the variation in the distance matrix. Axis 2 explained 17% and was loaded by soil nitrogen (21–174 mg g⁻¹; tau = 0.34). Soil water content (21–37%), bulk density (0.84–1.34 g cm⁻³ at 0–10 cm depth), pH (4.7–6.7), phosphorus (5.6–33.4 mg g⁻¹), and sand content (0.4–13.6%) were all correlated with flood duration ($P < 0.05$).

Damage and light availability had the strongest effects on seedling survival, while flood duration (113–208 d) largely affected only shade-tolerant species (Table 2). Damage decreased one-year seedling survival by 29% (Fig. 2), with a wide range in differences between undamaged and damaged seedlings within each species (12–75%; Table 1). No difference in survival after damage was observed between light-demanding and shade-tolerant species ($t_{37} = 0.94$, $P = 0.37$), upon removing the two low-flood-tolerant species (*Guarea* and *Ormosia*; Table 1). Survival of light-demanding species (*Coccoloba*, *Cordia*, *Pseu-*

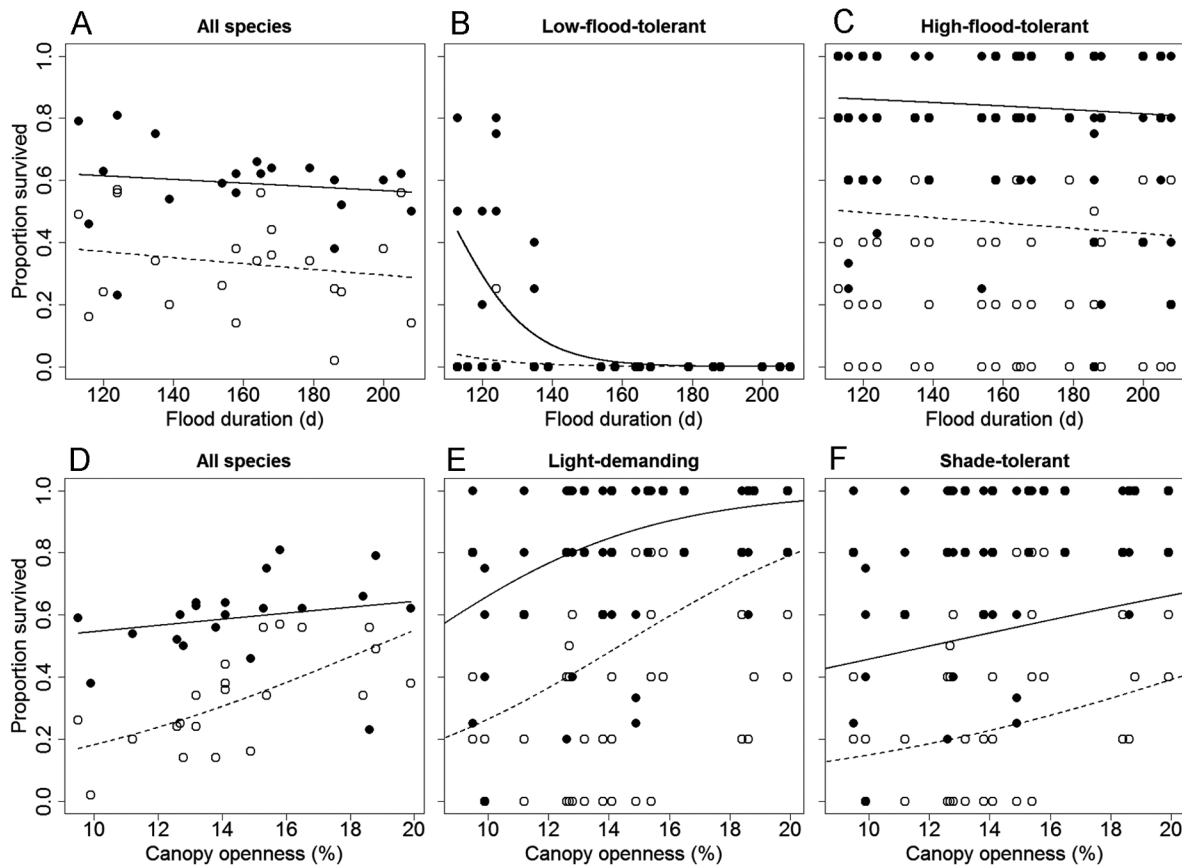


Fig. 2. Seedling survival across a flood gradient for all species combined (A), low-flood-tolerant species (B), and flood-tolerant species (C) and survival across light availability (D), light-demanding species (E), and shade-tolerant species (F). Mean species survival per plot is shown, fitted by a weighted regression model, for undamaged (filled dots, solid line) and damaged (open dots, dashed line) seedlings. Statistical tests and P values for the effects of damage, flooding, and light are indicated in Table 2.

dobombax, and damaged seedlings of *Vitex* increased with more light availability, as did shade-tolerant species, *Ormosia*, *Trichilia* and *Guarea* (Table 2). Sharp declines in survival of the low-flood-tolerant species occurred within 140 d of flooding. Some flood-tolerant species also had decreasing survival with increased flood duration (*Cordia*, *Garcinia*), while others showed slight increases with increasing flood duration (*Vitex*, *Trichilia*; Table 2; Appendix: Fig. A5). Increasing litter depth decreased average seedling survival ($F = 23.2$, $P < 0.001$), but soil nitrogen concentration had no effect on survival ($F = 14.9$, $P < 0.001$). Seed size did not predict survival ($R^2 = 0.11$, $t_8 = 0.98$, $P = 0.35$).

Seasonal patterns in survival differed among

damaged and undamaged seedlings. Damaged seedlings were susceptible to death in both the dry and flooded seasons, while undamaged seedlings only suffered declines in survival in the flood season (Fig. 3; Appendix: Table A1). The drop in damaged seedling survival at the end of the dry period (December 2007) occurred following three consecutive months of low rainfall < 100 mm (Fig. 3). Accordingly, soil water content at the end of the dry period (range: 21–37% in soils of $3 \pm 3\%$ sand, $79 \pm 5\%$ silt, and $18 \pm 5\%$ clay) had a positive effect on survival ($F = 12.7$, $P = 0.001$).

Interactive effects of damage, flood duration and light availability on annual survival of all seedlings and individual species were often non-

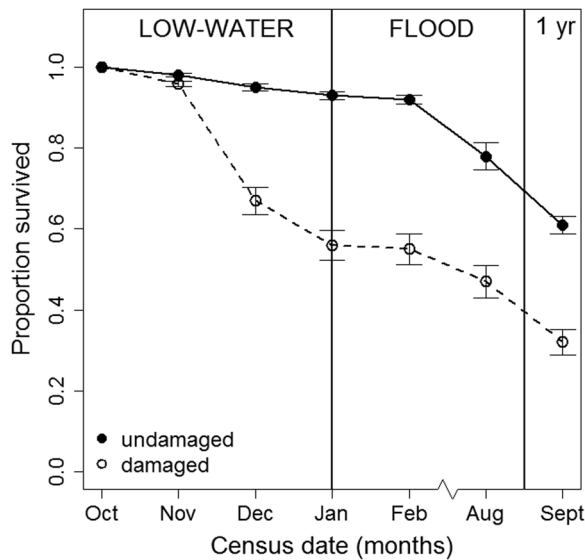


Fig. 3. Seedling survival (means \pm SE) of undamaged (filled dots) and damaged (open dots) seedlings of all species over one year. Survival is broken into three periods: low-water season (October to January), flood season (February–September), and one year (September). The time gap during flooding (February–August) is indicated by a zig-zag on the x -axis.

significant (Table 2), with the exception of a flood \times damage effect among *Vitex* seedlings ($\chi^2 = 9.06$, $P = 0.002$), whereby damaged seedlings were more vulnerable to death under prolonged flood duration. Additionally, there was a flood \times light interactive effect on annual survival of *Cordia* and *Trichilia* seedlings, whereby survival under moderate-high light availability (>13%) increased with increasing flood duration, but at lower light levels (9–13%) survival decreased with increasing flood duration (Table 2; Appendix: Fig. A5). These results show how increased flood duration can actually enhance survival of some highly flood-tolerant species, given adequate light in the forest understory.

Effects of multiple stressors on seedling growth and biomass allocation

Clipping initially removed $50 \pm 73\%$ SD of total plant biomass (ranging 19–65% within species; Table 1). Clipped seedlings sprouted 1–4 shoots from cotyledon nodes or leaf node closest to the point of damage. After one year,

total plant biomass of damaged seedlings was 22–53% and aboveground biomass was 4.4–9.6% of that of undamaged seedlings. For most species, damaged seedlings failed to recuperate lost biomass in one year. There was no difference in average biomass removed between shade-tolerant and light-demanding species (53% vs. 50%, $t_{10} = 0.86$, $P = 0.41$). We also found no differences in mean RGR between light-demanding and shade-tolerant species among undamaged ($t_4 = 1.20$, $P = 0.29$) or undamaged seedlings ($t_{20} = 3.82$, $P = 0.16$). Damaged seedlings had higher root:shoot ratios than undamaged seedlings (1.08 ± 0.64 vs. 0.67 ± 0.35 , respectively). When comparing initial and final root biomass for all species, an increase in root biomass was observed only for *Coccoloba*, *Garcinia* and *Trichilia* ($t = 2.5$, $P = 0.015$; $t = 6.9$, $P < 0.001$; $t = -3.6$, $P < 0.001$, respectively).

Increasing light availability enhanced RGR for both light-demanding and shade-tolerant species, excepting *Mouriri* (Table 3, Fig. 4B). As expected, mechanical damage decreased RGR of all species, but flood duration only decreased RGR for the shade-tolerant species *Mouriri*, *Garcinia* and *Ormosia* (Table 3, Fig. 5A). High RGR among light-demanding species was due in part to large stem height increments immediately after flood drawdown when many deciduous canopy trees have dropped leaves. Interactive effects on species RGR were largely nonsignificant, with the exception of a flood \times light effect for two species (Table 3). Finally, higher litter depths decreased RGR ($F = 10.3$, $P = 0.012$) and nitrogen enhanced RGR when litter depth was low ($F = 28.0$, $P = 0.0007$). A positive correlation between root:shoot ratios and flood duration suggested that seedlings may allocate more reserves below ground with prolonged flooding (Appendix: Table A2). There was a strong flood duration \times damage interaction ($F = 17.0$, $P < 0.001$), whereby damaged and undamaged seedlings had similar root:shoot ratios at shorter flood durations, but damaged seedlings had lower root:shoot ratios during longer floods.

Growth-survival relationships

Among undamaged seedlings, species with rapid RGR had lower survival rates ($r = -0.72$; Fig. 5C). This trend was largely driven by two extremes: the rapid RGR/low survival of low-

Table 3. Coefficients (and P values) estimated by linear models for the effects of damage, flood duration, and canopy openness (light) on seedling relative growth rate (RGR) for all species combined, light-demanding species, shade-tolerant species, and $N=9$ species (excluding *Hevea*). Adjusted R^2 values show the total amount of variance explained by the final model.

Species	Damage	Flood duration	Light	Flood \times damage	Light \times damage	Light \times flood	Light \times flood \times damage	R^2
All species	-0.079***	-0.0008***	0.011***	0.65
Light-demanding species	-0.085***	-0.0009***	0.015***	0.56
Shade-tolerant species	-0.19***	-0.0008***	0.0068***	0.0008**	0.72
<i>Pseudobombax</i>	-0.10*	-0.00091**	0.017**	0.43
<i>Cordia</i>	-0.098**	0.016**	-0.0013**	0.46
<i>Vitex</i>	-0.067**	0.014***	-0.0011***	0.51
<i>Coccoloba</i>	-0.063***	-0.00067***	0.013***	0.50
<i>Mouriri</i>	-0.14***	-0.00079***	0.011**	0.72
<i>Garcinia</i>	-0.053***	-0.00042**	0.0064**	0.47
<i>Trichilia</i>	-0.19***	-0.00074**	0.007**	0.00067†	0.66
<i>Ormosia</i>	0.50
<i>Guarea</i>	0.82

†0.10 < P ; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

flood tolerant species, *Ormosia* and *Guarea*, and the slow RGR/high survival of high-flood tolerant *Coccoloba* and *Vitex* (Fig. 5C). In contrast, there was a positive correlation between RGR and survival of damaged seedlings ($r = 0.43$, Fig. 5C). In terms of height, undamaged seedling height at the end of the dry season (January) increased survival in the following flood season ($\chi^2 = 13.3$, $P = 0.0003$), suggesting that taller seedlings were more tolerant of flooding. Damaged seedling height in the low-water season (December) increased survival at the onset of the rainy season ($\chi^2 = 162$, $P < 0.001$). Heights of undamaged and damaged seedlings were negatively correlated with flood duration ($r = -0.43$ and -0.38 , respectively), indicating that seedlings subjected to longer flood periods are shorter.

Species tolerance trade-offs

Species stress tolerance levels were positively correlated, supporting a co-tolerance model for species survival in floodplains (Fig. 1B). There was a positive correlation between flood tolerance and damage tolerance among species ($r = 0.84$, Fig. 4A). Highly flood and damage tolerant species *Coccoloba* and *Garcinia*, both had relatively slow RGR and high root:shoot ratios. *Garcinia*, a species with large belowground cotyledons, also had the lowest percent biomass removed by clipping (21% vs. an average of 50%). A positive correlation between shade tolerance and flood tolerance was also found ($r = 0.64$, Fig. 4B). Species with high survival in low

light conditions also displayed high survival after flooding. The two woody shrub species, *Coccoloba* and *Trichilia*, were highest in shade and flood tolerance. Stress tolerant species had low RGR, high root:shoot ratios, and small shoots after one year of growth in the floodplain forest understory (Fig. 6). No differences in stress tolerance were found between light-demanding and shade-tolerant species ($t = 0.32$, $P = 0.76$).

DISCUSSION

Co-tolerance as a strategy for survival in floodplains

Species trade-offs in resource allocation are considered a key mechanism for maintaining species diversity in tropical forests (Wright 2002). Plants possess a suite of physiological and life history traits that permit flood tolerance or avoidance (Blom and Voisenek 1996, Kolb et al. 2002). Given limited reserves to allocate towards tolerance, species should display different strategies for survival and growth in response to different stressors (Fig. 1; Grime 1977). Here, species responses to prolonged submergence, mechanical damage, and limited light availability suggest that some species possess a suite of traits permitting co-tolerance as a strategy for seedling survival in disturbed floodplains (Fig. 1). Those species share traits of high root:shoot ratios and low RGR, suggesting that high allocation to belowground reserves is advantageous for both damage and flood tolerance (Kozlowski 1984, del

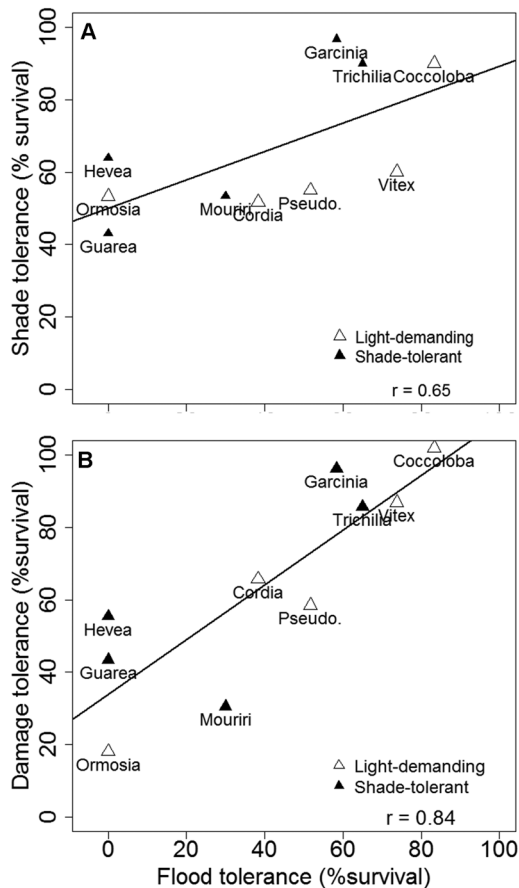


Fig. 4. Correlation between damage tolerance and flood tolerance (A) and shade tolerance and flood tolerance (B) for light-demanding (white triangles) and shade-tolerant (black triangles) species, indicated by genus. Pearson's correlation coefficients indicated as R.

Tredici 2001, Myers and Kitajima 2007). If ample belowground reserves facilitate damage and stress tolerance, then such an attribute may represent a single strategy to cope with a combination of stress and disturbance (Craine 2005). Seedlings may also simply remain dormant during flooding, thus consuming relatively little storage reserves and effectively providing very low competition with allocation of carbohydrate reserves to new shoots or defense in the shade.

A growth-survival trade-off was apparent among undamaged seedlings. Species in upland tropical forests tend to fall along a continuum of fast-growing pioneer species with low survival to slow-growing, long-lived species with high sur-

vival (Kitajima 1994, Wright 2002). In this study, species were not positioned along the growth-survival continuum according to cotyledon morphology or previously determined shade-tolerance (see also Parolin 2002, Battaglia et al. 2004). Rather, species fell roughly along a survival-growth continuum of fast-growing, low-flood tolerant and slow growing high-flood tolerant, among undamaged seedlings. In contrast, damaged seedlings with faster RGR displayed slightly higher survival. High RGR could increase storage reserves available for survival and recovery after damage in the dry season (Myers and Kitajima 2007) and avoid burial by litter and sediments during flooding.

A tolerance vs. escape model proposes that species occupying lower elevations have strategies to tolerate submergence, while species at higher elevations escape submergence by rapid RGR and height growth in the initial growth season (Parolin 2002). The escape strategy has been documented in both pioneer and non-pioneer species (Parolin 2002, 2003). We found that low-flood-tolerant species (*Guarea*, *Hevea*, and *Ormosia*) displayed relatively early fruit maturation, seed germination, and high RGR to escape flooding. Low-flood-tolerant species were among the first seeds collected prior to or during peak flooding and the first to germinate, thus increasing the growth window in the low-water season (Trowbridge et al. 2005). In particular, *Hevea*, reaching an average of 55 cm in height prior to flooding, was intolerant of submergence (70–230 cm depth), suggesting that rapid shoot extension is a strategy for survival. Given the importance of height growth for low-flood-tolerant species, submergence intolerant species are particularly vulnerable to mortality from trampling and browsing by herbivores.

Flood tolerance and shade tolerance as coupled drivers of regeneration

In many floodplain ecosystems, both flooding and light availability drive seedling population dynamics and community structure (Menges and Waller 1983, Frangi and Lugo 1998, Battaglia and Sharitz 2006). Flood tolerance is a primary filter for species survival, whereby species known to have high flood tolerance had high survival under prolonged flooding, shade, as well as damage (Battaglia et al. 2000). Based on known

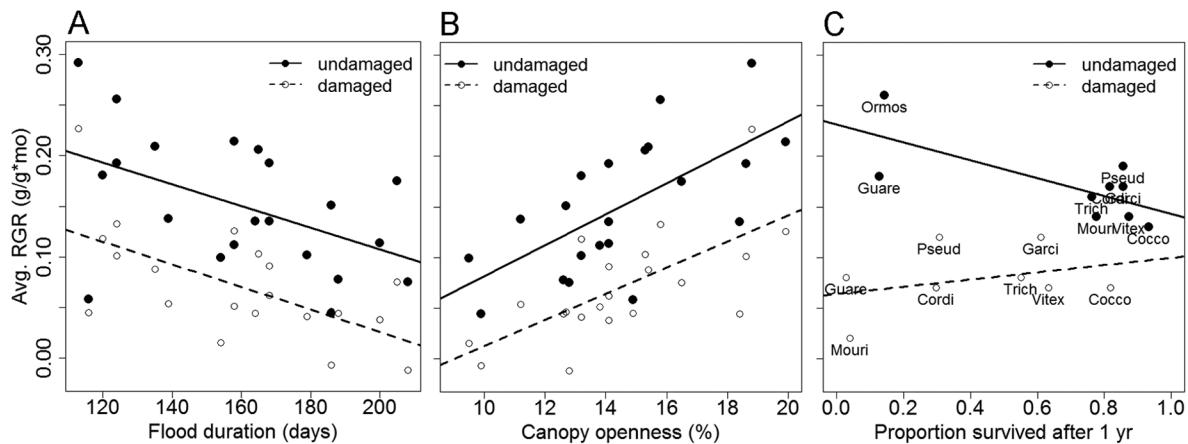


Fig. 5. Relative growth rates (RGR) of undamaged (filled dots) and damaged (open dots) seedlings across flood duration (A), light availability (B), and annual survival (C). Statistical tests for the effect of damage, light and flooding on RGR are indicated in Table 3.

species zonation along a flood gradient in Amazonian floodplains (Worbes et al. 1992), variable flooding stress should differentially affect seedling survival among species. While species differed in mean annual survival, we found no negative effect of increased flood duration on seedling survival among most flood-tolerant species. Flood-tolerant seedlings may survive prolonged flooding by maintaining high alcohol dehydrogenase (ADH) activity in root tissue, preventing the build-up of toxic acetaldehyde during anaerobic respiration over many months (Ferreira et al. 2009). Given the changes in climate and topography on a geological time scale in the Amazon River floodplain (Hoorne 2006), species occupying mid-low elevation sites appear to have very broad and variable ranges in flood tolerance.

We found no evidence for a flood-/shade-tolerance trade-off model to explain species coexistence among first-year seedlings. Despite the importance of light availability in enhancing survival for most species, species survival in the shade is often uncorrelated with species ranking for shade tolerance (Jones et al. 1994, Hall and Harcombe 1998). Low-flood-tolerant species (*Guarea* and *Ormosia*) also displayed low shade tolerance despite having large storage cotyledons and evergreen leaves, life history traits associated with shade tolerance in upland tree species. The highly flood-tolerant *Coccoloba* displayed high tolerance to shade despite having foliar epigeal

cotyledons and senescent leaves, traits associated with light-demanding species. Such responses suggest that high flood tolerance permits persistence in the shade (Hall and Harcombe 1998). Other studies have also found that *várzea* seedling survival and growth under submergence or waterlogging is unrelated to life history traits of pioneer vs. nonpioneer or evergreen vs. deciduous (Parolin 2001). Nonetheless, at the sapling phase, shade-tolerant species tend to dominate high-elevations (Wittmann and Junk 2003), indicating that over time shade-tolerant species do tend to persist in low-flood sites (Battaglia and Sharitz 2006).

In harsh physical environments, the amelioration of stress by additional abiotic and biotic factors is a proposed mechanism for plant community establishment (Bertness and Callaway 1994). Light availability in the flooded forest understory may ameliorate the negative effects of flooding on seedlings, permitting the establishment of light-demanding species at low flood levels (Battaglia et al. 2000). While light did enhance survival of most species here, particularly light-demanding species, we found few cases of interactive effects between light and flooding to suggest that the effect of flooding depends upon light availability. Only among two species did we find evidence to show that, given sufficient canopy openness, seedlings were unaffected by flood duration. The lack of an interaction is likely related to the lack of an

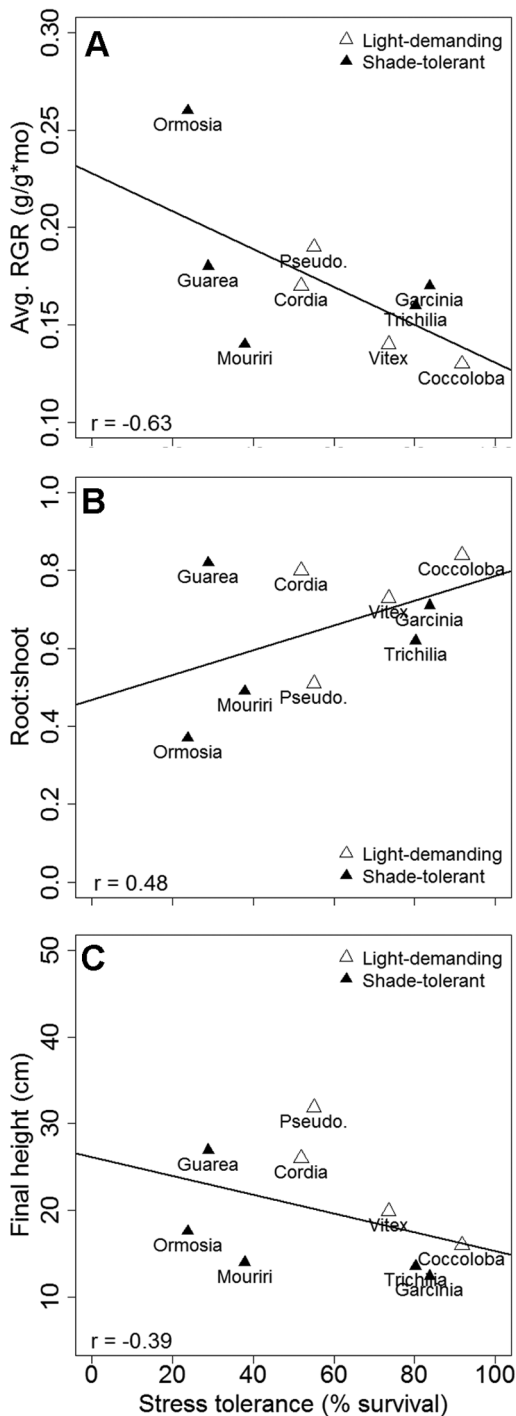


Fig. 6. Correlation between stress tolerance and species traits—RGR (A), root:shoot ratios (B), and final height after one year (C) for light-demanding and shade-tolerant species, indicated by genus.

effect of flood duration on survival for four of nine study species and potentially the relatively limited range in light availability (9–19%). An interaction between light availability and flood duration has been found for some seedlings in temperate forests, but depended upon seedling ontogenetic phase (Battaglia et al. 2000). No interaction between damage and shade stress in upland forest affected seedling survival (Baraloto and Forget 2007). Similarly, no interaction between herbaceous competition and water and nitrogen limitation affected seedling establishment in temperate oak forests (Dickie et al. 2007).

The role of mechanical damage for survival and growth in floodplains

Damage is pervasive in tropical forest understories (Clark and Clark 1989, Alvarez-Clare and Kitajima 2009). This study shows that damage differentially affects species growth and survival, ultimately driving patterns in community species composition and diversity. We found no interactive effect of mechanical damage and flood duration on seedling growth and survival. The time scale over which we measured interactive effects in this study is important for interpreting the combined effects of herbivore activity and variable flooding on seedling communities. A single damage event during the early growth season may have allowed recovery of photosynthetic tissue, shoots, and reserves that later facilitate flood tolerance. On the floodplain, seedlings are likely subject to multiple sequential damage events from herbivory, browsing, litter-fall, and trampling. The effect of repeated damage events throughout the growing season could select for highly damage-tolerant species, reducing seedling recruitment to zero in high-impact zones (Fig. 2A).

Large-seeded species with belowground storage cotyledons did not have higher survival after damage in comparison to small-seeded species (Harms and Dalling 1997, Green and Juniper 2004, Baraloto and Forget 2007). The lack of a relationship between seed size and survival may be due to clipping seedlings at 4–9 weeks after germination, when seedling dependence on cotyledon reserves for resprouting is low (Kitajima 1996, Myers and Kitajima 2007). Species differences in seed-derived energy reserves in root and stem tissues after damage may explain

differences in survival (Myers and Kitajima 2007). While root biomass is not directly correlated with storage reserves (Canham et al. 1999), the higher root biomass of stress-tolerant species may indicate larger storage reserves. Some species with epigeal cotyledons also displayed high root:shoot ratios and low RGR, contrary to the typical allocation patterns among upland light-demanding seedlings (Paz 2003). Future studies should investigate carbohydrate reserve availability in flood-tolerant seedlings and allocation to sprouts vs. anaerobic respiration and adventitious root production during flooding.

There was substantial decrease in survival of damaged seedlings during the peak dry season. Drought is a potentially important factor for floodplain seedling survival (Parolin 2001, Lopez and Kursar 2007, Parolin et al. 2010), but we were unable to provide direct evidence for limited water availability to seedlings. Following three consecutive months of extremely low and infrequent rainfall, damaged seedlings could experience drought stress that reduced survival. Although variation in soil water content did not explain dry season survival, the low rainfall and low water availability of silt-loam soils with 10–33% clay fraction (Brady and Weil 2000, Guyot et al. 2007) could limit water available to shallow roots. Nonetheless, the dry season decline in survival is confounded by the effect of seedling age, as the relative importance of mortality agents change with time (Alvarez-Clare and Kitajima 2009).

In conclusion, we show how the combined effects of stress gradients and disturbance mediate the establishment of seedlings in a disturbed tropical floodplain forest. Results support a co-tolerance strategy for survival under the multiple stresses related with disturbance and submergence by annual floods in this system. Increased stress tolerance of low-flood-tolerant species likely occurs in low-elevation forests of low-flooding years when seedlings are only waterlogged, as avoidance of complete submergence could enhance survival under additional stress. We show the relationship between stress tolerance and life history traits such as slow RGR and high root:shoot ratios, suggesting that allocation to storage reserves is critical for seedling persistence under stress and disturbance regimes. We also demonstrate the broad range of flood-

tolerance for species that have adapted to annual variation in flood levels of up to 6 months, as well as the potential threat to regeneration of low-flood tolerant species with increasing extreme flooding events (Chen et al. 2010), which make a substantial contribution to floodplain tree diversity (Wittmann et al. 2002). The prevalence of damage agents such as fire, logging, herbivores, and introduced ungulates in floodplain forests (Anderson et al. 1999, Finlayson 2005, Junk and de Cunha 2005), and the variation in seedling response to mechanical damage shown in this study suggest that sprouting among seedlings and trees is a strategy for survival on the floodplain (Kammesheidt 1998, Scariot 2000). Understanding the strategies for species persistence in tropical floodplains is critical, given the intensification of land-use as well as increased variability in flood regimes with global climate change (Tockner et al. 2010).

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SUPPLEMENTAL MATERIAL

APPENDIX

Table A1. Summary of repeated measures weighted regression mixed model for the effects of damage and census date on proportion of surviving seedlings. Damage treatment group and census date were included as fixed effects. Random effects include plot and group (seedlings in the same plot and damage treatment), nested in plot. The intercept coefficient is the log of mean survival of undamaged seedlings at month 1 (November), and remaining coefficients and standard error values are contrasts between the parameter and intercept values (Crawley 2007:365–368). *P* values indicate significant differences from the intercept.

Fixed effects	Coefficient	SE	z value	<i>P</i> value
Intercept (undamaged/census 1)	4.31	0.31	13.9	<0.0001
Damage treatment	–0.99	0.32	–3.12	0.0018
Census 2 (December)	–0.59	0.32	–1.86	0.063
Census 3 (January)	–0.27	0.34	–0.80	0.42
Census 4 (February)	0.39	0.52	0.76	0.45
Census 5 (August)	–3.63	0.28	–12.8	<0.0001
Census 6 (September)	–2.87	0.27	–10.7	<0.0001
Damage: census 2	–1.72	0.37	–4.69	<0.0001
Damage: census 3	–1.24	0.39	–3.14	0.0017
Damage: census 4	–0.84	0.60	–1.41	0.16
Damage: census 5	1.00	0.35	2.83	0.0047
Damage: census 6	0.34	0.33	1.03	0.30

Table A2. Summary of generalized linear model results (coefficients and *P* values) for the effects of damage, flood duration, light availability on three growth parameters of seedlings over one year: height, root:shoot ratios, and shoot growth immediately following flood drawdown, averaged across all species.

Growth parameter	Damage	Flood duration	Light	Flood × damage	Light × damage	Light × flood	Light × flood × damage
Height	-10.1***	-0.07***	1.11***	0.063**	-1.02**
Root:shoot	-0.68***	0.011***	0.072*	0.01***	-0.0005*
Post-flood growth	0.42**	0.012***	0.041***	-0.0004***	...

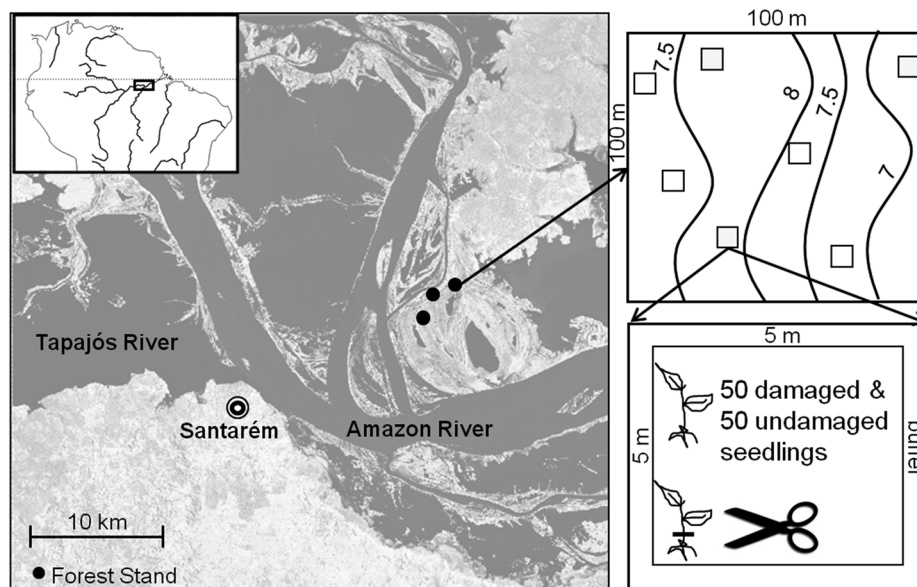


Fig. A1. Map of study region indicating three floodplain forest stands, within which 21 plots were established along a flood gradient.

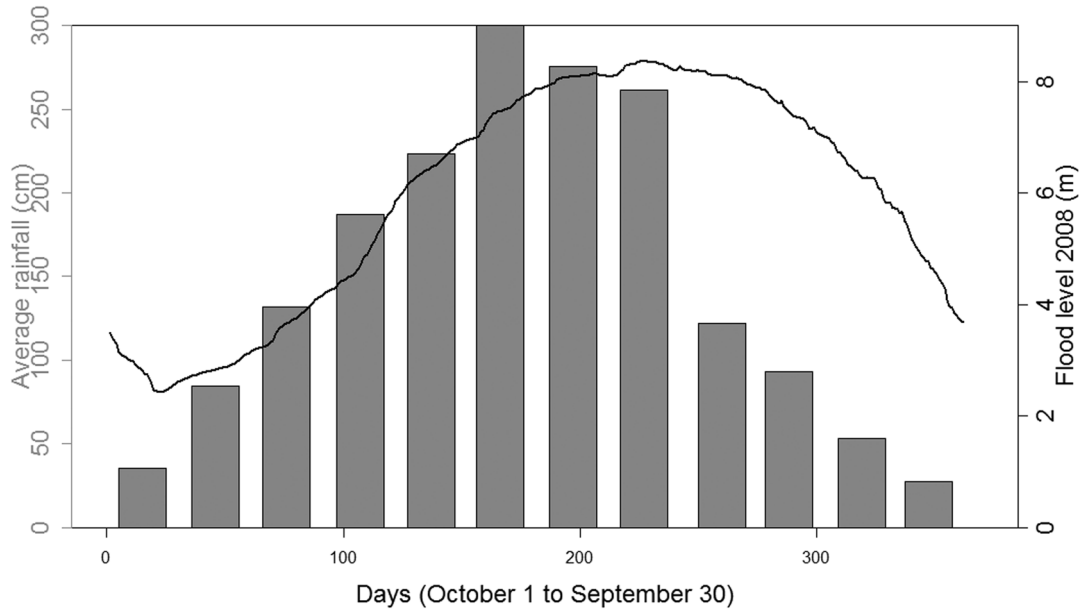


Fig. A2. Rainfall and flood pulse in the study region. Mean monthly rainfall from 1982–2008 on the left *y*-axis was provided by the Large-Scale Biosphere-Atmosphere (LBA) Station in Santarém-PA. Change in river level from day 0 (01 October 2007) to day 365 (30 September 2008) is indicated on the right *y*-axis (Capitania dos Portos–Santarém 2008).

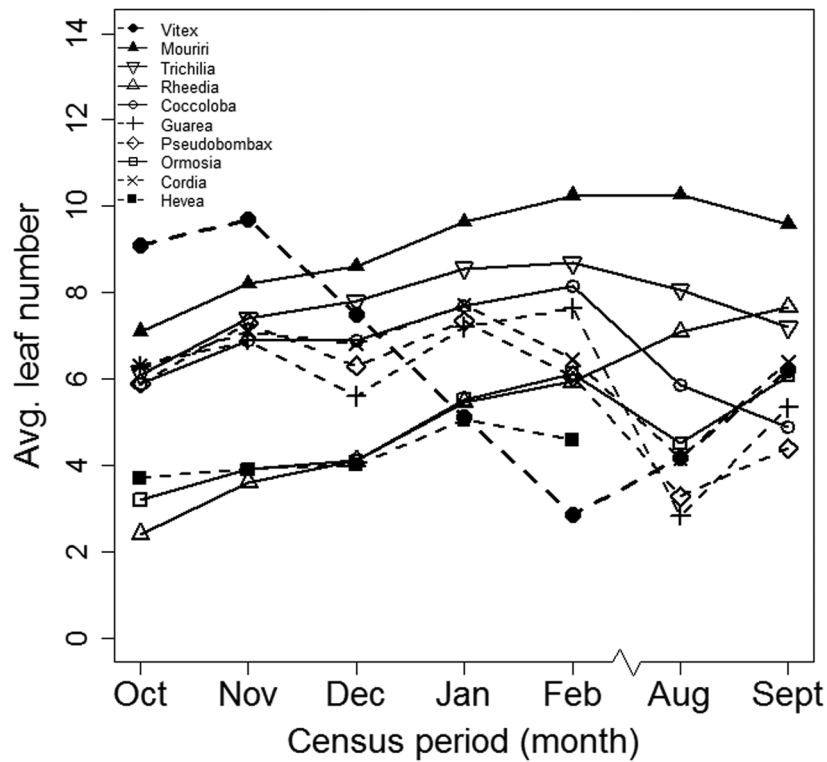


Fig. A3. Average leaf number of undamaged seedlings for all species over time. Deciduous species are indicated with dashed lines, evergreen species with solid lines. Note the early decline in leaf number for *Vitex cymosa*.

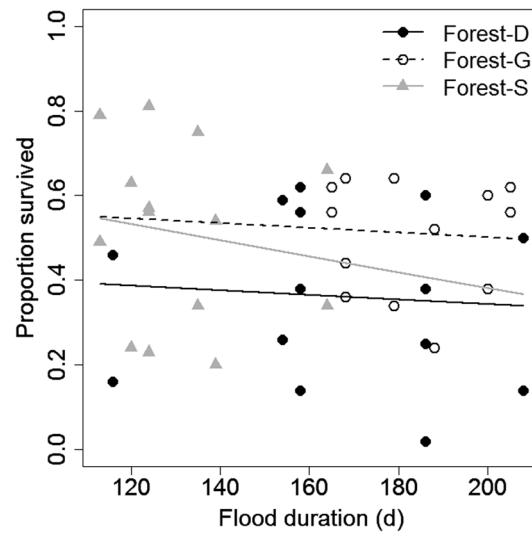


Fig. A4. Average seedling survival across flood duration in the three forests (D, G, and S) showing the differences in range of flood duration for each forest type.

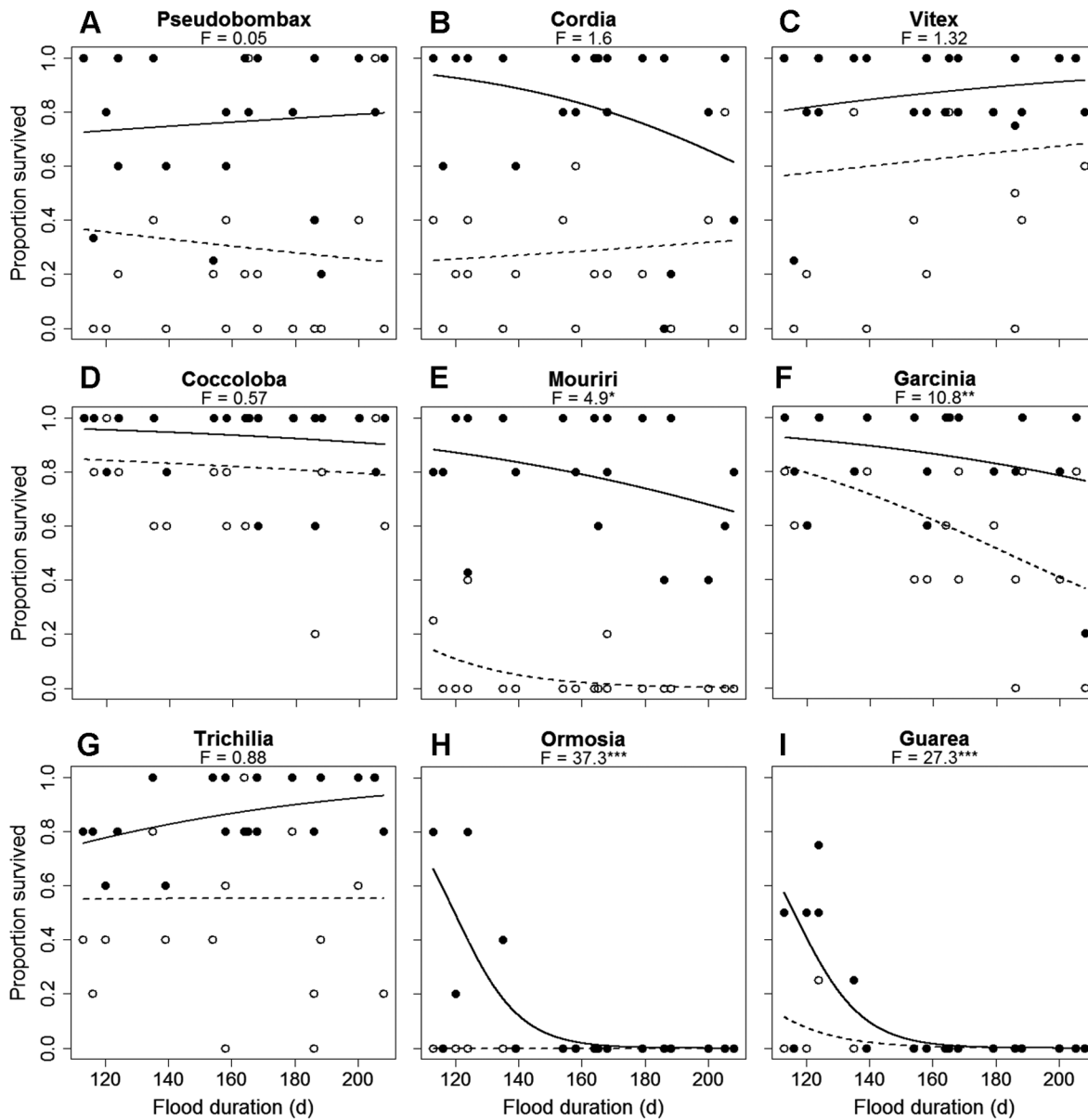


Fig. A5. Relationship between flood duration and survival among undamaged (filled dots) and damaged (open dots) species, indicated by genus. Flood duration had an effect on survival of *Vitex*, *Cordia*, *Garcinia* and the two low-flood-tolerant species *Ormosia* and *Guarea* (F-test values on top margin of each graph), but no interaction with damage was found (Table 2).