

Interannual variation in rainfall, drought stress and seedling mortality may mediate monodominance in tropical flooded forests

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Abstract Flood tolerance is commonly regarded as the main factor explaining low diversity and monodominance in tropical swamps. In this study we examined seedling mortality in relation to seasonality, i.e., flooding versus drought, of the dominant tree species (*Prioria copaifera*), and three associated species (*Pterocarpus officinalis*, *Carapa guianensis* and *Pentaclethra macroloba*), in seasonally flooded forests (SFF) in Darien, Panama. Seedling mortality differed among species, years and seasons. *Prioria* seedlings experienced the lowest overall mortality, and after 3 years many more *Prioria* seedlings remained alive than those of any of the associated species. In general, within species, larger seedlings had greater survival. Seed size, which can vary by close to 2 orders of magnitude in *Prioria*, had a confounding effect with that of topography. Large-seeded *Prioria* seedlings experienced

1.5 times greater mortality than small-seeded seedlings, as large-seeded *Prioria* seedlings were more likely to be located in depressions. This finding suggests that seed size, plant size and topography are important in understanding SFF regeneration. For all species, seedling mortality was consistently greater during the dry season than during flooding. For *Prioria*, dry season seedling mortality was correlated with drought stress, that is, high mortality during the long El Niño dry season of 1998 and the normal dry season of 2000, but very low dry season mortality during the mild dry season of 1999. *Prioria*'s ability to dominate in seasonally flooded forest of Central America is partly explained by its low drought-related mortality in comparison to associated species.

Keywords Low diversity · Seasonality · Seed size · Swamps · Topographical relief

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Introduction

In the tropics, low tree species diversity and monodominance is associated with seasonally flooded conditions (Janzen 1974; Campbell et al. 1986; Hart 1990; Richards 1996; Ferreira and Stohlgren 1999). The paucity of species in seasonally flooded forests (SFF) has been attributed to the inability of most species to tolerate flooding (Duivenvoorden 1996; Marques and Joly 2000). However, flood tolerance among tropical tree species remains poorly understood. Recent studies suggest that *terra firme* species (i.e., species from non-flooded habitats) are relatively flood tolerant, even though they do not occur in inundated habitats (Joly and Crawford 1982; ter Steege 1994; Lopez and Kursar 2003). In fact, the post-flooding environment may be an important determinant of species' distributions in

flooded habitats (Crawford and Braendle 1996). Hence, flood tolerance alone cannot explain low diversity in SFF (Lopez 2001).

Neotropical SFF are strikingly dynamic habitats (Golley et al. 1975; Junk 1989). Flooding due to a rise in river levels or poor drainage is common during the rainy season, while drought is more likely to occur during the dry season. Alternation of flooding, which restricts root growth, and drought, which selects for more extensive or deeper root systems, is likely to exert a physiological constraint for plants, as adaptations to both of these conditions might be difficult (Bertness et al. 1992; Baruch 1994; Loreti and Oosterheld 1996). The length and strength of both flooding and drought might be critical in determining species composition and low diversity of SFF. For example, when compared to their contiguous *terra firme* forests, Amazonian SFF are more diverse than those in northern South and Central America (Appendix 1). This pattern may arise from the latter experiencing severe droughts while central and western Amazon experience relatively mild dry seasons, which should result in less physiological stress than if flooding is followed by drought. Although biogeographical differences in species diversity may be attributed to ecological and geological history (i.e., Pleistocene refugia), a functional relationship between seasonality and low species diversity in SFF also appears likely.

Within seasonal forests, the strength of the dry season varies considerably among years. In particular, interannual variation in Neotropical precipitation is associated with the El Niño–Southern Oscillation (ENSO) (Ropelewski and Halpert 1987; Kiladis and Diaz 1989). During warm phases of ENSO (El Niño), the Pacific lowlands of Costa Rica and Panama experience severe droughts, while the Atlantic region receives increased precipitation and flooding. The opposite pattern occurs during the cold phase (La Niña) (Estoque et al. 1985; Waylen et al. 1996; Gutierrez and Dracup 2001). In this study, we focus on interannual variation in seasonality and its effects on population dynamics of four SFF species in Darien Province, Panama. We evaluate the importance of interspecific differences in drought-related mortality (i.e., low water potentials) in seedlings of four common SFF species, including the dominant species *Prioria copaifera* Griseb (Caesalpinioideae), as an alternative mechanism explaining low diversity and monodominance in inundated habitats. Additionally, we ask whether initial seedling size (i.e., stem diameter, seedling height, number of leaves), seed size and micro-topographical relief influence seedling survivorship in *Prioria*. If flooding stress were the most important factor in SFF, we would expect greater mortality during flooding than during the dry phase.

Materials and methods

Study site

We conducted this study in Casarete, a SFF located in the floodplains of Rio Balsas, near Darien National Park, a World Heritage site and Man and the Biosphere reserve, Republic of Panama (8°07'N, 77°52'W). Low tree diversity and the dominance of *Prioria* characterize SFF in Darien, while adjacent non-flooded forests are highly diverse (Golley et al. 1975; Grauel and Kursar 1999). In addition to *Prioria*, *Carapa guianensis* Aubl. (Meliaceae), *Pterocarpus officinalis* Jacq. (Papilionoideae), and *Pentaclethra macroloba* Willd. Kuntze (Mimosoideae) occur in nearby SFF. With the exception of *Pterocarpus*, these species also occur in non-flooded habitats.

The climate in Darien is warm and seasonally wet. The mean annual temperature is 27.4°C with average temperatures of 1°C above the annual mean during April. The annual rainfall averages 2,300 mm at Camogantí, 8 km north-east of Casarete ($n = 14$ years), with about 90% occurring between May and December (Estadística Panameña 1987). Hence, while periodically flooded during the rainy season, SFF in Darien also experience a 3-month-long dry season (Estoque et al. 1985; Bush and Colinvaux 1994).

Seedling dynamics

Prioria seeds fall during the transition from dry to rainy season, approximately from April to June (Croat 1978; O. Lopez unpublished data). We followed the dynamics of a 1997 *Prioria* seedling cohort in seven 20 × 20-m plots randomly distributed along a 2-km-long transect. In September 1997, after most seeds had germinated, we surveyed each plot, tagged, and mapped 700 first year seedlings. For each *Prioria* seedling, we measured width and length of the attached seed, stem diameter at 3 cm above the soil, height and the total number of leaves. Additionally, we scored the topographical site in which each seedling established as topographical relief can influence flooding or drought effects (Huenneke and Sharitz 1986). Microsites were typified as lower than average (depressions), average (flat areas) or as higher than average (mounds). The maximum difference in relief between these microsites was 20 cm. *Prioria* seedlings were censused every 2 months for 3 years ending in August 2000 (964 days). At each census, we noted seedling death and the total number of leaflets. Stem diameter and plant height were re-measured at 427 and 781 days, respectively.

In addition to *Prioria*, we monitored seedling mortality in three other species. *Pterocarpus* produced seeds near the

end of the rainy season (i.e., October–December) but did not germinate until a few months later, during the following dry season. Thus, in February 1998, after most *Pterocarpus* seeds had germinated, we tagged and mapped 365 seedlings in two of the 20 × 20-m *Prioria* plots, measured seedling height and the number of leaflets. *Pterocarpus* seedlings were censused along with the *Prioria* cohort throughout the remainder of the study (789 days), for survival, number of leaflets and plant height. In July of 1999, we tagged and mapped 155 and 315 seedlings of *Pentaclethra* and *Carapa*, respectively in two new, additional 20 × 20-m plots. For these two species, we measured mortality, seedling height and number of leaflets 4 times (285 days).

Rainfall and drought stress

We measured rainfall daily at Casarete from 8 December 1997 to August 2000. Under dry, sunny conditions, lowland tropical rainforests experience evapotranspiration rates of about 100 mm per month (Shuttleworth et al. 1984). Therefore, significant soil water shortage develops when rainfall is below this threshold. We quantified the strength of the dry season as the cumulative millimeters by which each dry month was below 100 mm rainfall, termed the rainfall deficit (Walsh 1996). At each census, starting in 1997 we assessed plant water stress as predawn and midday leaf water potentials (ψ_L) in from five to ten seedlings of *Prioria* and *Carapa* located adjacent to the plots using a Scholander pressure chamber (PMS Instruments, Corvallis, Oreg.) on dry days using mature healthy leaves. We also measured ψ_L in five seedlings of *Pterocarpus* during the dry season of 1998 and 1999.

Data analysis

The effect of species (*Prioria* and *Carapa*), seasons (wet and dry) and time of the day (predawn and midday) on ψ_L was analyzed by ANOVA, using a fixed effects model. The relationship between ψ_L and monthly percent mortality was analyzed by regression analysis using the mean ψ_L experienced between censuses and the natural logarithm of the corresponding monthly percent mortality for the *Prioria* cohort only.

For each cohort of seedlings, we calculated the exponential mortality coefficients (λ) on a monthly basis as: $\lambda = [\ln(N_{t_2}) - \ln(N_{t_1})] / (t_2 - t_1)$, where N_{t_2} is the number of living seedlings at census t_2 , N_{t_1} is the number of living seedlings in the previous census (t_1), and $(t_2 - t_1)$ the time in months between censuses (days/30.4). Monthly exponential mortality coefficients were converted to monthly

percent mortalities by setting N_{t_1} to 100 and calculating N_{t_2} . Annual percent mortalities were calculated in an analogous manner. This equation represents the most commonly used formula for quantifying mortality in tropical trees (Clark and Clark 1992; Condit et al. 1995; but see Sheil et al. 1995). Because seedling mortality in each plot for each species is highly susceptible to the total number of seedlings remaining alive after each census (i.e., more seedlings at the beginning of the study), we have considered it appropriate to represent monthly mortality in Fig. 1 as the mean seedling mortality estimated in 20 random subsamples of 200 individuals for *Prioria* (100 in the other three species) with their respective 95% confidence intervals. This procedure guarantees that the expressed mortality represents the variance given by plots with low and high mortality and thus diminishes any potential skewness of the data. These values were highly congruent with our original mortality estimates ($r^2 = 0.98$, $P < 0.0001$ ANOVA), thus all other calculations and mortality analyses use the overall mortality for the whole cohort without resampling. A seedling was considered dead only when: (1) no stem was found but the tag was located; (2) a leafless stem and tag were found; (3) a broken stem and tag were found, and, for cases (2) and (3), no resprouts were observed in the following censuses.

We used a proportional hazards model in order to determine the effects of initial seed size, stem diameter, seedling height, topographical site, seedling density and number of leaves in explaining survival in *Prioria*. The interaction between seed size and topographical site was tested in a reduced model using only the significant parameters, i.e., stem diameter, seed size and topographical site. For *Pterocarpus*, *Pentaclethra* and *Carapa* only initial seedling height, number of leaflets and seedling density were tested in the model. The proportional hazards model is multivariate and semi-parametric, and is particularly powerful in examining the effect of explanatory variables on survival times when dealing with right-censored data, i.e., some of the individuals were still alive at the end of the study (Schupp 1990; Hosmer and Lemeshow 1999). A posteriori Tukey test was used for all group comparisons in seed size means across topographical sites and for the effects of site on mean survival of *Prioria* seedlings. The proportional hazards analysis was run independently for each species and the effect likelihood-ratio test (χ^2) was used to determine which of these parameters best explained seedling survival in each case. For each species, we also independently analyzed the effect of seedling size (i.e., diameter, height and number of leaflets), seed size and topographical site on mean survival time using a univariate Kaplan–Meier product–limit function in which each parameter (seed size, seedling diameter or seedling height) was grouped into either a large or small class in relation to

the mean. Differences in mean survival times between large and small groups and among topographical sites were tested using the Wilcoxon test of the Kaplan–Meier product–limit survival analysis. All parameters were tested for normality and only seedling density was log transformed. All statistical tests were conducted using JMP 4.0 (SAS Institute, Cary, N.C.).

Results

The 4-month-long dry season of 1998 was longer and stronger than average, due in part to its early onset in December of 1997, and accumulated a rainfall deficit of 257 mm. This deficit is 1.4 times greater than the 14-year average (180 mm, 8 km north-east from Casarete). The dry season of 1999 was shorter than average, lasting only 1 month (January) and accumulating 71 mm of rainfall deficit. In contrast, the dry season of 2000 was average, 3 months' duration (January–March), and accumulated 164 mm of rainfall deficit.

ψ_L varied in relation to season and time of day. On average, *Prioria* and *Carapa* seedlings had significantly lower ψ_L during the dry season than those measured throughout the wet season (mean \pm SE; -1.04 ± 0.03 MPa vs. -0.70 ± 0.02 MPa, for dry and wet seasons, respectively; $F_{1,367} = 99.74$, $P < 0.001$ ANOVA; see also Fig. 1). Similarly, predawn ψ_L were significantly higher than those measured at midday (-0.48 ± 0.02 MPa vs. -1.17 ± 0.02 MPa, for predawn and midday, respectively; $F_{1,367} = 427.19$, $P < 0.001$ ANOVA). Interestingly, the ψ_L of *Prioria* and *Carapa* seedlings differed significantly when season and time of day were taken into account (i.e., species \times season \times time of the day interaction effect, $F_{1,367} = 5.25$, $P < 0.02$, ANOVA). Midday ψ_L of *Prioria* seedlings were consistently lower than those of *Carapa* seedlings during the dry season (-1.61 ± 0.05 MPa vs. -1.19 ± 0.05 MPa, for *Prioria* and *Carapa*, respectively). During the dry season of 1998, the most severe dry season, seedlings of *Prioria* developed a midday ψ_L as low as -2.2 MPa.

Across all species seedling mortality differed between seasons and years. Although it is difficult to assess and infer the influence of interannual variation in drought strength across cohorts of different ages, mortality varied greatly among years and seasons (Table 1). Nonetheless, dry season monthly percent mortality was 3 times greater than wet season mortality ($F_{1,32} = 11.67$, $P = 0.0017$, ANOVA). Although this pattern was consistent across species, monthly percent mortalities varied greatly among species (Fig. 1, Table 1). Very few seedlings of *Pterocarpus*, *Pentaclethra* and *Carapa* survived the first year (<8%), whereas 50% of *Prioria* seedlings survived and

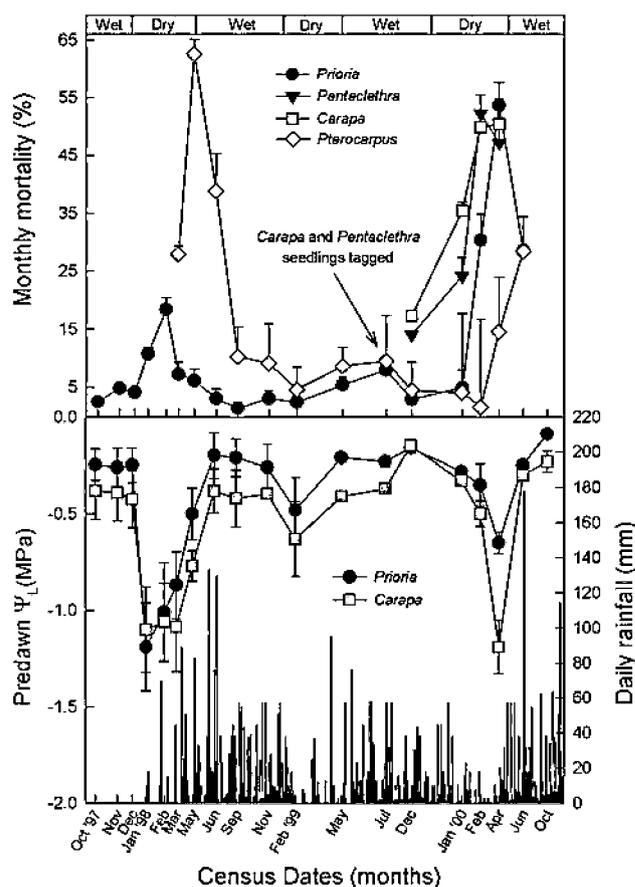


Fig. 1 Mean monthly percent mortality with their respective positive 95% confidence intervals by census date for all species (top). Mean seedling mortality was estimated in 20 random subsamples of 200 and 100 individuals of the whole cohort for *Prioria* and the other three species, respectively. Mean leaf predawn water potentials (± 1 SE) for *Prioria* and *Carapa* seedlings and daily rainfall per census date (bottom)

4.5% remained alive after 3 years. *Prioria* annual percent mortality for the first year of the study was 1.3 greater than mortality in the second year, but nearly 2 times greater in the third year compared to the first year.

Species differed in their response to seasons. With moderate mortality during the dry season and very low mortality during the wet season, *Prioria* represents a species well adapted to flooding followed by drought. *Pterocarpus* appears to be more sensitive to flooding with moderate mortality during both dry and the wet seasons. *Pentaclethra* and *Carapa* represent species that are not well adapted to flooding followed by drought, with moderate mortality during the wet season and very high mortality during the dry season (Table 1, Fig. 1). A simple model illustrates the effects of these three distinct mortality patterns on annual survivorship (Fig. 2). In *Prioria* seedlings, the high mortality observed during the dry seasons appears to result from plant water stress as mortality was

Table 1 Annual percent mortality and average monthly percent mortality during the dry and wet seasons for seedlings of the study species

Species ^a	Annual mortality (%)			Average monthly mortality (%)	
	1998	1999	2000	Dry season	Wet season
<i>Prioria</i>	49.8	37.5	91.9	13.6	3.3
<i>Pterocarpus</i>		93.4	39.6	14.6	13.7
<i>Carapa</i>			97.4	39.2	10.5
<i>Pentaclethra</i>			96.9	43.0	9.4

^a For *Prioria*, the monthly percent mortality during the dry season includes dry seasons of 4, 1, and 3 months in length for 1998, 1999, and 2000, respectively. For all species the first census of the rainy season (May or June) was treated as the final dry season census for the purpose of determining mortality during the dry season. All the other censuses made during the wet season were included in the calculation of monthly mortality during the wet season. The number of wet season censuses was 7, 5, 2, and 2 for *Prioria*, *Pterocarpus*, *Carapa* and *Pentaclethra*, respectively. The annual mortality in *Carapa* and *Pentaclethra* is based on 7 months

negatively correlated with predawn ψ_L ($r^2 = 0.2$, $F_{1,16}$, $P < 0.05$, linear regression, Fig. 3).

When the six size and topographical variables were incorporated into the proportional hazards model, only stem diameter, topographical relief and seed size significantly explained survival of *Prioria* seedlings (Table 2). In contrast, the univariate Kaplan–Meier analysis showed that, on average, seedlings of *Prioria* with greater stem diameter, greater height and smaller seeds lived longer than smaller diameter, shorter and bigger-seeded seedlings (Table 3). Similarly, seedlings of *Prioria* that were located on mounds or flat sites had twice the survival of those

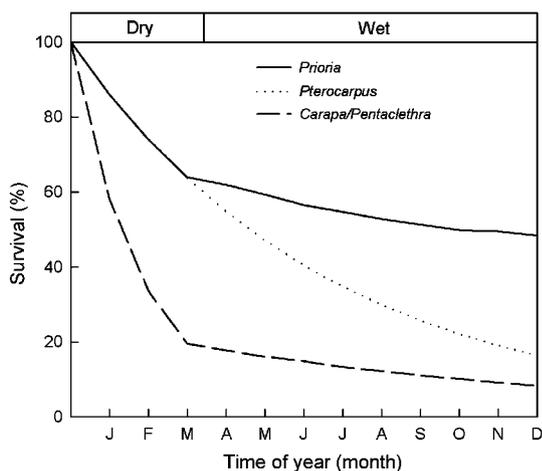


Fig. 2 Seedling mortality modeled for 1 year for all study species. Each species curve was generated using the average dry and wet season (i.e., flooding) monthly mortality in Table 1. A 3-month dry season was assumed

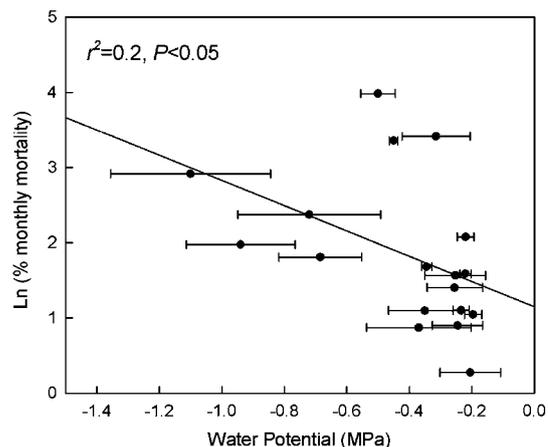


Fig. 3 Correlation between monthly percent mortality and leaf water potentials for *Prioria* seedlings. Each point represents the percent mortality (ln transformed) at a particular census expressed on a monthly basis and the predawn leaf water potential. $r^2 = 0.2$, $P < 0.05$

found in depressions (Fig. 4, Table 3). Although no seed size by topographic site interaction was found within the *Prioria* cohort (Table 2), large-seeded seedlings were more likely to be found in depressions and small-seeded seedlings on flats (all pairs comparisons Tukey–Kramer honestly significantly different test $P < 0.05$), perhaps explaining the higher long-term survival of small-seeded seedlings. To provide a more direct test of the importance of seed size for survival, we compared seed size within each topographic class and found that only in depressions did small-seeded seedlings have higher seedling survival times (511 days) than did large-seeded seedlings (363 days, Wilcoxon, $\chi^2 = 7.7$, $P < 0.005$).

With the proportional hazards analysis, plant height contributed to seedling survival in *Pterocarpus*, but not for *Pentaclethra* or *Carapa* (Table 2). In contrast, when seedling size categories were incorporated into a Kaplan–Meier univariate analysis, taller seedlings of *Pentaclethra* and *Carapa*, as well as *Pterocarpus*, lived longer (Table 3).

Discussion

Seasonal variation in seedling mortality and drought

In the tropics, tree diversity and distribution vary considerably with annual rainfall and dry season severity (Bongers et al. 1999). Hence, patterns of establishment, recruitment and mortality that result in monodominance or low species diversity in SFF might be controlled by flooding during the rainy season, drought during the dry season or both. Our data suggest that tree seedling mortality at Casarete, Darien is strongly influenced by the strength of the dry season and

Table 2 Proportional hazards likelihood ratio χ^2 -test for parameter effects on seedling survival of *Prioria*, *Pterocarpus*, *Carapa* and *Pentaclethra*. NS Not significant

Species and parameter	df	χ^2	P-value
<i>Prioria</i>			
Seed size	1	3.83	<0.050
Seedling density	1	0.07	NS
Stem diameter	1	9.96	<0.001
Plant height	1	1.06	NS
Leaf number	1	0.82	NS
Topography	3	11.13	<0.01
Seed size \times topography	3	4.23	NS
<i>Pterocarpus</i>			
Plant height	1	11.58	<0.001
Seedling density	1	2.16	NS
Leaf number	1	2.41	NS
<i>Carapa</i>			
Plant height	1	0.31	NS
Seedling density	1	0.40	NS
Leaf number	1	0.76	NS
<i>Pentaclethra</i>			
Plant height	1	0.70	NS
Seedling density	1	0.18	NS
Leaf number	1	11.97	NS

Table 3 Kaplan–Meier Wilcoxon χ^2 statistics for group differences on mean survival times of *Prioria* seedlings in relation to size traits^a and topographical site

Species and parameter	df	χ^2	P-value
<i>Prioria</i>			
Seed size (large vs. small)	1	5.86	<0.02
Stem diameter (large vs. small)	1	27.82	<0.0001
Plant height (tall vs. short)	1	8.23	<0.005
Topography (flats, mounds and depressions)	3	13.08	<0.001
<i>Pterocarpus</i>			
Plant height (tall vs. short)	1	42.61	<0.0001
<i>Carapa</i>			
Plant height (tall vs. short)	1	3.48	0.06
<i>Pentaclethra</i>			
Plant height (tall vs. short)	1	3.70	<0.05

^a Only seedling height was analyzed for seedlings of *Pterocarpus*, *Carapa*, and *Pentaclethra*

its effects on seedling water stress. Among our study species, seedlings of *Prioria*, the dominant canopy tree in SFF in Darien, experienced significant drought stress shown by a threefold increase in mortality during the unusual dry season of 1998 (4 months). The following dry season (1999) was relatively wet and did not cause drought or high mortality, while the average, 3-month-long, dry season of 2000

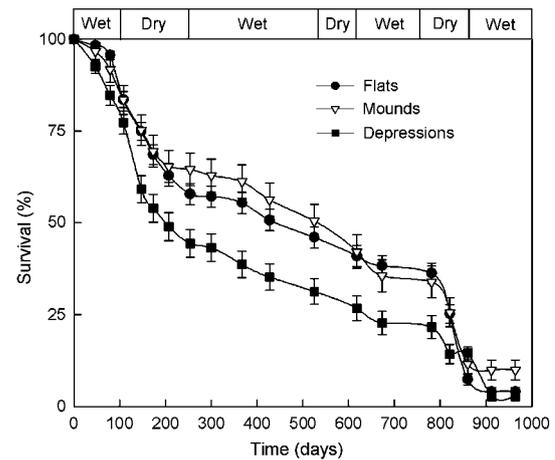


Fig. 4 Survival probability of *Prioria* seedlings, expressed as percentage, by time in days in relation to topographical site. Each seedling was classified according to soil elevation: average (*Flats*), higher than average (*Mounds*) and lower than average (*Depressions*). $P < 0.001$; Wilcoxon test

increased *Prioria* seedling mortality to even greater levels than in the longer 1998 dry season. Maximum seedling mortality also occurred during the dry season for *Carapa*, *Pentaclethra* and *Pterocarpus* (Fig. 1). Despite differences in cohort size and years of study across the study species, the relative impact of drought-related mortality appears greater in *Carapa*, *Pentaclethra* and *Pterocarpus* than in the dominant *Prioria* species. We conclude that relatively lower drought-related mortality for *Prioria* during years with a severe dry season might be the main factor maintaining its dominance.

Our results suggest that greater dry season mortality was the result of drought stress in seedlings. Drought may kill plants due to run-away xylem embolism. This hypothesis is supported by the few cases in which field data on mortality and ψ_L have been correlated with species' sensitivity to xylem embolism (Davis et al. 2002). In the case of *Prioria* and *Carapa*, average midday ψ_L were -1.6 and -1.2 MPa, respectively. This implies that seedlings were operating near levels of catastrophic loss of hydraulic conductivity, as the water potential required to reduce hydraulic conductivity to 50% is -1.4 and -0.8 MPa for *Prioria* and *Carapa*, respectively (Lopez et al. 2005). The significant relationship found between mortality and low water potentials in *Prioria* seedlings also supports the hypothesis that mortality is increased by drought (Fig. 3).

Drought severity, differential mortality and changes in forest composition

In general, droughts may exert a strong selective pressure on tree seedling establishment and species composition of

tropical forests (Delissio and Primack 2003; Bebbler et al. 2004). On Barro Colorado Island, Panama, a species' preference for moist microhabitats and/or the swamp was not a definitive indicator for that species' change in abundance during an 8-year drying trend. Some moist-associated species increased, while others decreased in abundance (Condit et al. 1996). These findings denote the importance of understanding species-specific drought-related mortality and its potential role in shifting species composition of tropical forests.

Regardless of climatic variability, mortality of tropical tree seedlings is generally highest during the first year of establishment (Schupp 1990; De Steven 1994). Although we recognize the limitations of establishing unequivocal conclusions across all four species cohorts (i.e., seedling age, years), inter-specific differences in mortality during the first year of establishment might provide insight into species abundances and distributions. Despite severe drought stress, first year mortality in *Prioria* seedlings was 50% less than that of *Pterocarpus*, *Carapa* and *Pentaclethra* (Table 1), suggesting that, on average, *Prioria* will recruit a higher fraction of seedlings than coexisting species. While seeds of *Prioria*, *Carapa* and *Pentaclethra* germinate at the beginning of the rainy season, seeds of *Pterocarpus* are produced at the end of the flooding period and germinate during the following dry season. When compared to *Prioria*, *Pterocarpus*, as well as *Carapa* and *Pentaclethra*, experienced overall high seedling mortality during the first year; however, dry-season related mortality was the lowest for *Pterocarpus* (Table 1). Given the unusual pattern of dry-season germination, we believe *Pterocarpus* might experience markedly increased seedling establishment under dry seasons with high rainfall. In contrast, *Carapa* and *Pentaclethra* seedlings do not appear to be well suited for fluctuating flooding and drought conditions, as these species exhibit very high mortality during the dry season (Fig. 1a). *Pterocarpus* seedlings may establish better in intermediate to high light environments (Weaver 1997; O. R. Lopez, personal observation), suggesting that the moderate mortality observed during the wet season might also be the result of poor performance in low light (i.e., shade intolerant). *Pterocarpus* also appears to be found in clumps, a pattern in which disturbance (i.e., windblown by powerful storms) may play a role (Weaver 1997). Field observations indicate that *Carapa* and *Pentaclethra* are more abundant upstream and probably experience less inundation. Therefore, future changes in disturbance, flooding regime, or frequency of severe and mild dry seasons added to inter-specific differences in drought-related mortality could lead to shifts in the composition of SFF.

The effects of flooding followed by drought, topography, seed size and hydrochory on seedling survival

In contrast to the dry season, the rainy season, during which Casarete is periodically inundated, resulted in little seedling mortality. This result is consistent with our experimental demonstration that seedlings of many tropical tree species, both from SFF and *terra firme* forests, are tolerant to flooding (Lopez and Kursar 2003). What makes some seedlings more susceptible to drought than others under alternating flooding–drought cycles? Flooding reduced maximum root depth by 20% in seedlings of SFF species compared to 32% in those of *terra firme* species (Lopez and Kursar 2003). Thus, it is likely that shallow-rooted seedlings experience significantly more water stress under flooding–drought cycles than those with deeper roots (Rundel and Becker 1987; Tobin et al. 1999). In this study, we found high mortality in depressions, which are presumably wetter microsites than flats or mounds. This result is consistent with the hypothesis that anoxic soils inhibit root development during flooding, resulting in insufficient root growth and consequently high mortality during the dry season (Lopez and Kursar 2003). We conclude that, because flooding restricts root development, flooding followed by drought may impose severe stress for most tropical rain forest species. Hence, the capacity to make roots under flooding, and not flooding tolerance per se, may be a key factor allowing a few species to tolerate flooding followed by drought and thus to dominate SFF.

The effects of topography, seed size and hydrochory on seedling survival are equally important for understanding SFF. In temperate floodplain forests, seedling density and survival were greater in elevated microsites (Jones et al. 1994). Similarly, seed deposition and germination of temperate bottomland and tropical swamp species was greater in elevated sites such as stumps, logs or mounded soils than in depressions (Schneider and Sharitz 1988; Imbert et al. 2000). These observations suggest that debris accumulation, sediment deposition, erosion or any other processes that change elevation, if only by centimeters, may have substantial effects on the plant community. In our study, higher *Prioria* seedling survival was found on mounds or flat areas than in depressions, an elevation range of only 20 cm.

A larger seed and seedling may confer advantages during establishment as stress tolerance increases with size (Saverimuttu and Westoby 1996; Swanborough and Westoby 1996). Species from SFF tend to have large seeds. In addition, the ecological advantage of seed size might interact with other factors such as type and time of dispersal and germination, and site suitability for germination in relation to topography (Kubitzki and Ziburski 1994;

Parolin 2000; Lopez 2001). However, the effect of seed size on survival of *Prioria* seedlings was confounded by that of topography. On average, small-seeded *Prioria* seedlings lived about 1.8 times longer than large-seeded seedlings, probably because these were more frequently deposited on mounds, while large-seeded seedlings of *Prioria* were found more in depressions.

Finally, hydrochory, the common mode of seed dispersal for many SFF species, may be advantageous in habitats that experience seasonal flooding as floating seeds are deposited in elevated sites (Schneider and Sharitz 1988; Williamson and Costa 2000). Nevertheless, hydrochory could also reduce establishment success as prolonged flotation might hinder germination and survival through anoxic conditions and depletion of seed reserves (Lopez 2001). Evidently, tradeoffs between seed size and dispersal ability interact with both topography and seasonality to affect seedling establishment in SFF.

Monodominance and biogeographical trends in SFF

The mechanisms affecting seedling establishment, forest regeneration and species composition of inundated habitats are particularly complex because of the added effects of flooding and its interactions with drought, nutrients, soil-borne disease and mycorrhizae (Walker et al. 1989). Current explanations for the origin and maintenance of monodominance and low diversity of inundated forests favor the concept of niche specialization (Hart 1990; Duijvenvoorden 1996; Pitman et al. 1999). Flood tolerance, or the lack thereof, has implicitly been identified as the main mechanism controlling species diversity in SFF. There is no doubt that flooding plays a major role in tropical swamps, but why are SFF in Central America monodominant and those from Amazonia quite species rich? We hypothesize that the low diversity and monodominance of northern South and Central America's SFF is determined by the high level of environmental fluctuations caused by flooding–drought cycles rather than solely by flooding or flood tolerance. If habitats with more severe environmental fluctuations select for ecophysiologicaly similar species with overlapping niches (Hubbell 1979; Connell 1980; Hubbell and Foster 1986), then we would expect a much more reduced species pool in flooded habitats that also experience severe droughts relative to flooded habitats without such droughts. Relatively few species may have the specific suite of traits needed to disperse and establish in an alternating flood–drought regime. Consistent with this idea is the fact that when compared to their contiguous *terra firme* forests, SFF in eastern Amazonia, which lack a severe dry season, appear much more diverse relative to those in northern South and Central America that experience

drought (Appendix 1). Therefore, species diversity and patterns of monodominance among Neotropical SFF may possibly be the result of fundamental differences in the extent and severity of the dry season. In the case of Central American monodominant SFF, we believe that flooding followed by drought has selected against flood-tolerant *terra firme* species, which otherwise would persist in SFF.

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