

SEASONAL WATER STRESS TOLERANCE AND HABITAT ASSOCIATIONS WITHIN FOUR NEOTROPICAL TREE GENERA

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Abstract. We investigated the relationship between habitat association and physiological performance in four congeneric species pairs exhibiting contrasting distributions between seasonally flooded and terra firme habitats in lowland tropical rain forests of French Guiana, including *Viola* and *Iryanthera* (Myristicaceae), *Symphonia* (Clusiaceae), and *Eperua* (Caesalpiniaceae). We analyzed 10-year data sets of mapped and measured saplings (stems ≥ 150 cm in height and < 10 cm diameter at breast height [dbh]) and trees (stems ≥ 10 cm dbh) across 37.5 ha of permanent plots covering a 300-ha zone, within which seasonally flooded areas (where the water table never descends below 1 m) have been mapped. Additionally, we tested the response of growth, survival, and leaf functional traits of these species to drought and flood stress in a controlled experiment. We tested for habitat preference using a modification of the torus translation method. Strong contrasting associations of the species pairs of *Iryanthera*, *Viola*, and *Symphonia* were observed at the sapling stage, and these associations strengthened for the tree stage. Neither species of *Eperua* was significantly associated with flooded habitats at the sapling stage, but *E. falcata* was significantly and positively associated with flooded forests at the tree stage, and trees of *E. grandiflora* were found almost exclusively in nonflooded habitats. Differential performance provided limited explanatory support for the observed habitat associations, with only congeners of *Iryanthera* exhibiting divergent sapling survival and tree growth. Seedlings of species associated with flooded forest tended to have higher photosynthetic capacity than their congeners at field capacity. In addition, they tended to have the largest reductions in leaf gas exchange and growth rate in response to experimental drought stress and the least reductions in response to experimental inundation. The corroboration of habitat association with differences in functional traits and, to a lesser extent, measures of performance provides an explanation for the regional coexistence of these species pairs. We suggest that specialization to seasonally flooded habitats may explain patterns of adaptive radiation in many tropical tree genera and thereby provide a substantial contribution to regional tree diversity.

Key words: drought tolerance; French Guiana; photosynthetic capacity; phylogenetically independent contrast; relative growth rate; seasonally flooded forest; specific leaf area; torus translation method; tropical forest.

INTRODUCTION

One of the classical explanations for regional patterns of species diversity proposes that some species are limited to a subset of local abiotic or biotic conditions in which they outcompete other species (MacArthur and Levins 1964, Chase and Leibold 2003). Such niche differentiation in concert with habitat heterogeneity has been argued to permit coexistence and the maintenance of regional diversity (Tilman 1982, Kneitel and Chase 2004). In sessile species such as plants, strong associations between abundance and habitat descriptors have been interpreted to reflect habitat specialization (Clark et al. 1998, Svenning 2001). However, the contribution

of habitat specialization to patterns of regional diversity in species-rich plant communities such as tropical trees has been questioned because most species exhibit naturally clumped distributions (Hubbell 1979, Condit et al. 2000), which may reflect a process other than habitat specialization, such as dispersal limitation (Condit et al. 2000, Dalling et al. 2002) or random events (Hubbell 2001).

Recent evidence for habitat associations among tropical trees has been provided by studies addressing this problem using at least one of four approaches. Most studies have focused on small-scale (50 ha) permanent plot data, using randomization tests such as the torus model (Harms et al. 2001) or Poisson cluster model (Plotkin et al. 2000) to account for spatial aggregation when computing correlations with environmental variables such as topography. A second approach has used distribution data from larger spatial scales (1000 km²) to

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examine the consistency of patterns of habitat association across large distances (Fine et al. 2005). Other studies have provided evidence that species perform better in the habitat in which they are aggregated, using either long-term census data (Russo et al. 2005) or reciprocal transplant experiments with seedlings (Fine et al. 2004, Palmiotto et al. 2004, Baltzer et al. 2005).

A fourth approach has addressed the mechanisms underlying differential performance and/or distributions, testing for differences in traits hypothesized to confer a performance advantage in a particular environment. Trait screening that explicitly incorporates evolutionary relationships among species can provide considerable insight into adaptive evolution and niche assembly (Webb et al. 2002, Ackerly 2003). For example, Fine et al. (2006) show that seedling performance differences between Peruvian tree congeners that are white sand or clay specialists can be explained by a trade-off between investment in defense and rapid growth. Clearly, a more complete understanding of habitat specialization would result from studies integrating measures of distribution, performance, and traits in a phylogenetic context, yet few examples exist to date (Cavender-Bares et al. 2004, Fine et al. 2005, 2006).

A large number of recent studies have tested for edaphic habitat specialization among tropical trees by examining habitat types defined by soil nutrient availability (Harms et al. 2001, Potts et al. 2002, Palmiotto et al. 2004, Russo et al. 2005). However, despite the strong seasonality of most Neotropical forests (Losos and Leigh 2004), relatively little attention has been paid to how habitats with seasonal differences in water stress can limit species distributions (Prance 1979, Lopez and Kursar 2003, Parolin et al. 2004). In particular, seasonally flooded forests inundated by high precipitation (floodplain forests, *sensu* Prance 1979) have been differentiated from terra firme forests for at least two reasons that might affect tree species distributions. First, seasonally flooded forest is characterized by periods of inundation, with soils saturated to the surface, for periods that may last several weeks during the height of the rainy season in many forests (Prance 1979, Parolin et al. 2004). In fact, the lower species richness found in seasonally flooded forest has been attributed to flood intolerance among species that occur in terra firme forest (Duivenvoorden 1995). Second, trees in seasonally flooded forest may be less susceptible to drought during the dry season because the water table in many of these lowland areas remains within 60 cm of the soil surface (Salvado 2002). Severe drought has been shown to affect species composition in several tropical forests (Wright 1992, Condit et al. 1995, 2004). However, it remains unknown whether seasonally flooded forest may represent a refuge for species that are drought intolerant (Parolin 2001).

The lowland tropical forests of French Guiana provide good opportunities to examine tree associations with seasonally flooded forest because they contain

frequent examples of congeneric species exhibiting divergent patterns of habitat associations in a heterogeneous landscape of seasonally flooded and terra firme forest (Sabatier et al. 1997, Koponen et al. 2004). To examine the relationship between habitat association and physiological performance within four congeneric species pairs across seasonally flooded and terra firme forest, we combined experimental and observational data for species traits with patterns of performance and distribution of saplings and adult trees in the field to address the following questions. (1) Is a positive association with seasonally flooded forest accompanied by a negative association with terra firme forest? Does preference or avoidance of seasonally flooded forest occur at different developmental stages for these species? (2) Are performance measures of growth and survival consistent with habitat associations for each developmental stage? (3) Are flood-tolerant species characterized by particular combinations of morphological or physiological traits? (4) To what extent do traits that confer advantages in flooded forest and/or seasonal drought explain contrasting distributions for the four congener pairs?

METHODS

Overview and species

In lowland forests of French Guiana, at least 17 genera include congener pairs that exhibit contrasting distributions in seasonally flooded vs. terra firme forest. We chose four of these pairs for study because they are common, easily distinguished morphologically, and their fruit was available in 2003 when we began trait screening for juveniles. These four pairs show strong evidence of spatial aggregation at scales of 0.5–10 ha (Collinet 1997) and have been the subject of general consensus about habitat association among foresters, ecologists, and botanists in French Guiana. One species in each genus is associated with seasonally flooded forest, as reflected in local common names (Gourlet-Fleury et al. 2004), including *Iryanthera hostmanii* and *Virola surinamensis* (Myristicaceae), *Symphonia globulifera* (Clusiaceae), and *Eperua falcata* (Caesalpinaceae). Four common congeners have been associated with terra firme forest, including *I. sagotiana*, *V. michelii*, *S.* sp. 1, and *E. grandiflora* (Sabatier et al. 1997). Nomenclature follows Boggan et al. (1997), with an undescribed but morphologically distinct species of *Symphonia* (*S.* sp. 1) as reported earlier by Molino and Sabatier (2001).

To address the first two questions, we analyzed data from long-term demographic inventories of trees and saplings of these species. To address the other questions, we integrated data from a shadehouse experiment on juveniles of the eight species grown under controlled conditions of water stress.

Demographic inventories

All inventories were conducted at the Paracou experimental site (5°18' N, 52°55' W), a lowland tropical

rain forest near Sinnamary, French Guiana (Gourlet-Fleury et al. 2004). The site receives nearly two-thirds of the annual 2875 mm (mean from 1986 to 2005, $SD = 540$ mm) of precipitation between mid-March and mid-June, and <50 mm per month in September and October (Bonafant et al. 2000). Topographic contours within the site range between 0 m and 35 m above sea level, and soil physical and chemical characteristics differ markedly between the resulting topographic classes of plateau, midslope, and bottomland (Baraloto et al. 2005, Epron et al. 2006). Bottomland sites can be further subdivided based on the depth of water availability in the wet and dry season. In particular, a zone of seasonally flooded forest has been defined as an area where periodic inundation at least to the soil surface occurs during the rainy season, and where a permanent water table supplied by the streams persists during the dry season, almost never receding below 1 m in depth. This area covers about 10% of the permanent study plots. We define all other zones as terra firme forest, with less severe flooding periods in the rainy season (despite important variations relative to topographic position) and without any access to the riparian water table during the dry season.

Tree census data are from a series of 15 permanent plots of 6.25 ha each, and an additional plot of 25 ha, in which all stems ≥ 10 cm dbh were censused every one to two years from 1984 to 2003 (Gourlet-Fleury et al. 2004). Some of the plots at Paracou were logged and subjected to silvicultural treatments in 1986. Therefore, we limited our analyses of adult trees to censuses conducted within the six unlogged plots because most trees were harvested in terra firme forest. We also limited our analysis to the census period during which all of the focal species were identified by botanists, beginning in 1995 to the most recent inventory in 2003.

Saplings were defined as individuals >150 cm tall but <10 cm in dbh. Sapling data are from a series of 768 fixed-radius subplots of 50 m^2 spaced every 20 m within an 8×8 grid centered within 12 of the Paracou plots. Within these subplots, saplings of 25 species, including the eight focal species of this study, were identified, mapped, and measured from 1995 to 2005 (Gourlet-Fleury et al. 2004). Patterns of habitat association for saplings did not differ between logged and unlogged plots, so we included the logged plots in subsequent analyses.

Association tests

To test for associations between trees and saplings in flooded vs. nonflooded forest habitats, we used a modification of the torus translation method described by Harms et al. (2001), which accounts for spatial aggregation by permuting rotations of habitat coordinates relative to those of trees. Our modifications are detailed in Appendix A. We also calculated density ratios as the relative density of stems in seasonally flooded vs. terra firme forest. To correct for the absence

of a species due to spatial aggregation unrelated to habitat preferences, we included only those sapling plots within the dispersal distance of extant trees of reproductive size for a given species calculation, using a modification of the procedure described in Baraloto and Goldberg (2004).

Field performance

For each species in each data set, we estimated performance parameters describing survival and growth. Survival was calculated as the mean proportion surviving between initial and final inventory dates (1995–2003 for trees; 1995–2005 for saplings). Growth was estimated as an average annual diameter increment. For saplings, this absolute growth rate may be influenced by size, because larger saplings tend to grow faster (C. Baraloto, *unpublished data*). Therefore, we calculated sapling growth as the relative growth rate (RGR) for dbh, as $RGR = (\log(\text{dbh}_{t_1}) - \log(\text{dbh}_{t_0})) / (t_1 - t_0)$. The original sapling data set measured dbh as 1 cm classes and not as a continuous variable, so we present growth data only from 2001, the first inventory date at which dbh measures were made to a precision of 0.1 mm.

To evaluate species performance in seasonally flooded vs. terra firme forest, we superimposed maps of stems for each species onto the maps of seasonally flooded forest in the GIS database, and we assigned the categorical variable of seasonally flooded/terra firme to each stem. Effects of seasonally inundated habitats on growth may occur because these sites tend to have fewer stems and lower basal area than terra firme forest (Prance 1979, Koponen et al. 2004), so we calculated a covariate describing neighborhood competition as the sum of basal areas of all stems ≥ 10 cm dbh within a radius of 20 m from trees, and 10 m from saplings. We then analyzed survival and growth for each species with individual stems as replicates, using logistic regression and ANCOVA, with independent variables of seasonally flooded/terra firme forest (binary) and neighborhood basal area (continuous, log-transformed). *Viola surinamensis* was excluded from the analyses because assumptions of the parametric models could not be met due to limited sample size.

Shadehouse experiment

We also tested the response of growth, survival, and leaf functional traits of these species to drought and flood stress in a controlled experiment in a shadehouse at the INRA research facilities in Kourou. Juveniles were grown in pots from 18 to 22 months of age, during which we measured six variables that have been linked to drought and/or flood tolerance and that describe performance (relative growth rate for biomass, RGR), morphology (specific leaf area, SLA; root:shoot ratio, R:S), and ecophysiology (carbon assimilation, A ; stomatal conductance, g_s ; water use efficiency, WUE). Full details of the experimental design and measurements are provided in Appendix B.

TABLE 1. Associations with seasonally flooded and terra firme soils for trees (≥ 10 cm dbh) and saplings (>150 cm tall, <10 cm dbh) of four congeneric species pairs in the Paracou plots, French Guiana.

Species	Stage	Seasonally flooded†			Terra firme		
		<i>N</i>	<i>p</i>	Association	<i>N</i>	<i>p</i>	Association
<i>E. falcata</i>	tree	183	0.973	(+)*	1395	0.099	NS
	sapling	15	0.809	NS	183	0.467	NS
<i>E. grandiflora</i>	tree	10	0.004	(-)**	405	0.996	(+)**
	sapling	7	0.383	NS	84	0.445	NS
<i>I. hostmanii</i>	tree	111	1.000	(+)**	168	0.000	(-)**
	sapling	28	0.980	(+)*	105	0.082	NS
<i>I. sagotiana</i>	tree	3	0.000	(-)**	264	0.999	(+)**
	sapling	8	0.029	(-)*	206	0.900	NS
<i>S. globulifera</i>	tree	72	1.000	(+)**	10	0.000	(-)**
	sapling	32	1.000	(+)**	17	0.002	(-)**
<i>S. sp. 1</i>	tree	22	0.001	(-)**	407	0.996	(+)**
	sapling	10	0.029	(-)*	197	0.904	NS
<i>V. surinamensis</i>	tree‡	3	0.974	(+)*	2	0.011	(-)*
	sapling	3	0.912	NS	28	0.160	NS
<i>V. michelii</i>	tree	2	0.081	NS	58	0.933	NS
	sapling	7	0.605	NS	172	0.777	NS

Notes: The table reports the total number of stems censused (*N*), the proportion of permutations with lower relative density within that category (*p*), and the corresponding positive (+) or negative (-) association.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ (one-tailed); NS, not significant.

† The water table never descends below 1 m in depth.

‡ Trees were tested in an adjacent 25-ha plot because the species is rare at the site and does not occur in the main plots.

We used two approaches to test the effect of watering treatment on these correlated dependent variables based on multivariate analyses of variance (MANOVA). First, we analyzed the entire data set using three-way MANOVA to test the effects of genus, habitat preference (seasonally flooded or terra firme forest), treatment, and their interactions. We then performed MANOVA for each species to test for treatment effects. We compared means among treatments using Tukey's hsd post hoc test.

We also examined correlations among species traits and their response to water stress treatments using principal components analysis (PCA). To describe the general morphology of the species, we included the mean value for the control treatment. To describe a species response to water stress treatments, we calculated the response ratios of those variables for which significant effects were found for any species (see Appendix B: Table B1), calculated as the mean proportional change in that variable between the control treatment and either the inundation treatment or the drought treatment. The analysis was conducted in Statistica, Version 6.0 (StatSoft, Tulsa, Oklahoma, USA) based on a correlation matrix using a varimax normalized rotation of the axes.

We examined whether habitat associations of species were consistent with their experimental response by calculating for each genus pair the difference between slopes describing the relationship between the PCA axes and a demographic index of the sapling density ratio in seasonally flooded forest vs. terra firme forest. The sapling data were used because they represent a more similar developmental stage to the juveniles grown in the experiment.

RESULTS

Habitat associations

Contrasting associations with seasonally flooded forest and/or terra firme forest habitats were detected in all four genera, and the magnitude of these associations and the stage at which they occurred varied between genera (Table 1). The four species positively associated with seasonally flooded forest all have density ratios greater than the community average at the tree stage, and their association with seasonally flooded forest strengthened between sapling and tree stages (Fig. 1). The four species negatively associated with seasonally flooded forest all have density ratios less than the community average at both tree and sapling stages, and all but *S. sp. 1* exhibit strengthening of this repulsion between stages.

Field performance in contrasting habitats

Habitat-dependent survival was observed for only one species, and only at the sapling stage (Fig. 2). *Iryanthera sagotiana* saplings had a five times lower survival rate in seasonally flooded forest than terra firme forest (estimate = -1.87 , $P = 0.021$). Saplings of *I. hostmanii* and *S. globulifera* had about a 40% greater survival rate in flooded vs. nonflooded forest, but these patterns were not statistically significant ($P = 0.061$ and 0.073 , respectively). For no other species at the sapling stage, and for no species at the tree stage, did we detect an effect of habitat, or of the neighborhood basal area covariate, on survival.

Only within *Iryanthera* did we observe significant effects of habitat on tree diameter growth rate, with *I. hostmanii* growing faster in seasonally flooded forest

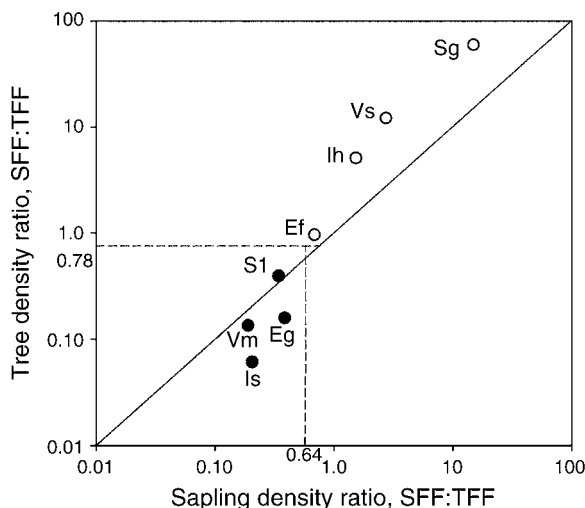


FIG. 1. Density ratios in seasonally flooded forest (SFF; water table never descends below 1 m depth) vs. terra firme forest (TFF) for four congeneric species pairs exhibiting contrasting distributions. Densities (no. stems/ha) were calculated as a proportion of total surface area sampled in each habitat for trees (dbh ≥ 10 cm) and as a proportion of the surface area sampled within dispersal areas of reproductive adults for saplings (>150 cm tall and <10 cm dbh). Dotted reference lines provide estimates of null density ratios, calculated for stems of all species combined based on sapling and tree stem densities in SFF:TFF of 3234:5062 and 498:642 stems/ha, respectively. Points above or below these reference lines indicate positive associations with SFF or TFF, respectively. Deviations above or below the solid diagonal indicate the strength of shifts between sapling and tree stages to associations with SFF or TFF, respectively. SFF-associated species based on torus translation tests (see Table 1) are indicated with open circles, and labels adjacent to each symbol are abbreviations for species epithets. Species abbreviations are as follows: *Eperua falcata*, Ef; *E. grandiflora*, Eg; *Iryanthera hostmanii*, lh; *I. sagotiana*, ls; *Symphonia globulifera*, Sg; *S. sp. 1*, S1; *Virola surinamensis*, Vs; and *V. michelii*, Vm. Note the log scale of both axes.

(effect of seasonally flooded forest = 0.05, $t = 2.76$, $P < 0.001$) and *I. sagotiana* growing more slowly there (effect = 0.26, $t = -2.10$, $P = 0.037$; Fig. 2). As well, *S. globulifera* showed a trend of faster growth in seasonally flooded forest (effect = 0.13, $t = 1.49$, $P = 0.14$). In addition to *I. sagotiana*, three other species (*E. falcata*, *E. grandiflora*, and *S. sp.1*) showed lower growth with increasing neighborhood basal area but no effect of habitat.

For no species was growth at the sapling stage influenced by habitat when neighborhood basal area was included in the model (see Fig. 2). Nonetheless, *S. globulifera* grew more slowly in areas with higher neighborhood competition (effect of neighborhood basal area = -0.024 , $t = 2.22$, $P = 0.027$).

Experimental response to simulated flooding and drought

The effects of experimental treatments on juvenile performance varied among species. All juveniles of *V.*

michelii and *I. sagotiana* died within three weeks of inundation. Half of the juveniles of *S. sp. 1* also died in the inundation treatment, but only after more than six weeks. All of the other species had $>80\%$ survival over the four-month period during which the treatment was applied. No individuals expired under the drought treatment, although many of the plants had wilted leaves near the end of the treatment period.

Species within three of the four genera showed significant physiological responses to treatments, primarily a reduction in A and g_s in response to drought and/or inundation (Fig. 3). No significant effect of drought or inundation on any parameter was found in either species of *Symphonia*, and only the two species of *Eperua* showed significant growth reductions and changes in root allocation under water stress. These patterns contributed to the significant genus \times treatment interaction term in the MANOVA model (see Appendix B: Table B2). In addition, the magnitude of the differences between seasonally flooded forest/terra firme forest congeners for several parameters differed among genera, resulting in significant genus \times habitat preference interaction terms. This pattern was driven by differences between congeners only within *Eperua* for SLA, and only within *Symphonia* and *Virola* for R:S and RGR (Fig. 3).

The principal components analysis revealed the different patterns of traits and their response to water stress treatments both among genera and between seasonally flooded vs. terra firme forest species. The first axis (36.7% of variation) mostly represents flood tolerance, with strong positive loadings for the response ratio of relative growth rate and photosynthetic capacity to inundation (see Appendix B: Table B2 for full details). This axis also had a strong positive loading for WUE and a strong negative loading for SLA. The second axis (31.8% of variation) represents drought intolerance, with a strong negative loading for the response ratio of photosynthetic capacity to drought. This axis also had strong positive loadings for RGR, A , and g_s . Thus, the species least tolerant of inundation tended to have high SLA and low water use efficiency, whereas those least tolerant of drought tended to have higher leaf gas exchange and faster growth rates (Fig. 4A).

Patterns of experimental response were generally consistent with patterns of habitat association (Fig. 4B, C). Within all genera except *Eperua*, the species with the more positive values of the flood tolerance axis were more strongly associated with seasonally flooded forest as saplings, although with only three out of four genus pairs showing positive slopes in Fig. 4B. To a lesser extent, the species with more positive values of the drought intolerance axis were more strongly associated with seasonally flooded forest as saplings (three out of four genus pairs, including *Eperua*, show positive slopes in Fig. 4C).

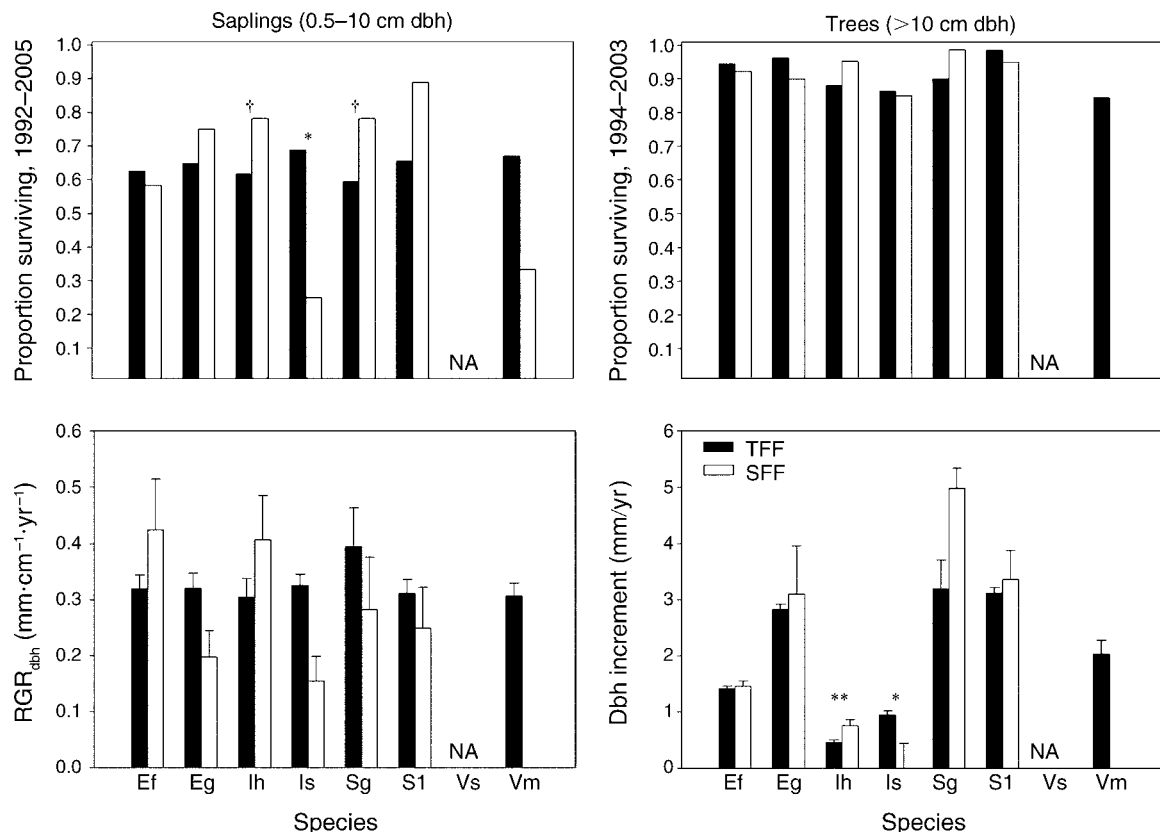


FIG. 2. Survival and growth of saplings (>150 cm tall, <10 cm dbh, beginning at 1.5 cm for growth) and trees (dbh ≥ 10 cm) for four congeneric species pairs in seasonally flooded (open bars) or terra firme (solid bars) habitats. Survival is shown as the proportion of stems surviving from 1995 to 2003 (trees) or 2005 (saplings). Growth of all saplings surviving from 2001 to 2005 was calculated as relative diameter growth (RGR), to account for the positive relationship between dbh and dbh increment found for these species in this size class. For adults, we report annual dbh increment for trees surviving from 1995 to 2003. Shown are the mean growth rates and standard errors. For each species, significant effects of habitat, following logistic regression (survival) or ANCOVA (growth), with neighborhood basal area as a covariate, are indicated as follows: $\dagger P < 0.10$; $*P < 0.05$; $**P < 0.01$. Sample sizes are indicated in Table 1; for *V. surinamensis*, insufficient individuals were available to test these effects (NA). See Fig. 1 for species names.

DISCUSSION

Habitat preferences for seasonally flooded and terra firme habitats

We found strong evidence for contrasting habitat preferences between species pairs in all four genera (Table 1). Because the torus translation model compares relative densities of species, species could potentially exhibit positive associations in one habitat without a corresponding negative association with the other habitat if densities between habitat types differ (Harms et al. 2001). In our study, though, congener pairs show reversed patterns of both a strong positive association with either seasonally flooded forest or terra firme forest and the corresponding negative association with the other habitat type, indicating specialized ecological sorting. If we interpret the strength of these associations as a correlate of distribution restriction to one habitat or the other, then it appears that terra firme forest specialists such as *E. grandiflora* and *V. michelii* are less

likely to be found in seasonally flooded forest than vice versa for their congeners (Table 1). This pattern suggests that intolerance of terra firme forest species to seasonally flooded forest conditions may be a stronger constraint on distribution than limitations of terra firme conditions for species associated with seasonally flooded forest (Duivenvoorden 1995, Parolin 2001, Lopez and Kursar 2003).

Consistent strong habitat discrimination was found in all eight species for stems ≥ 10 cm dbh, yet there are differences among genera in the developmental stage at which habitat associations became apparent (Table 1, Fig. 1). Within *Iryanthera* and *Symphonia*, strong contrasting associations of the species pairs were observed beginning at the sapling stage, and these associations strengthened for the tree stage. Neither species of *Eperua* was significantly associated with seasonally flooded forest at the sapling stage, but *E. falcata* was significantly and positively associated with seasonally flooded forest at the tree stage, and trees of *E.*

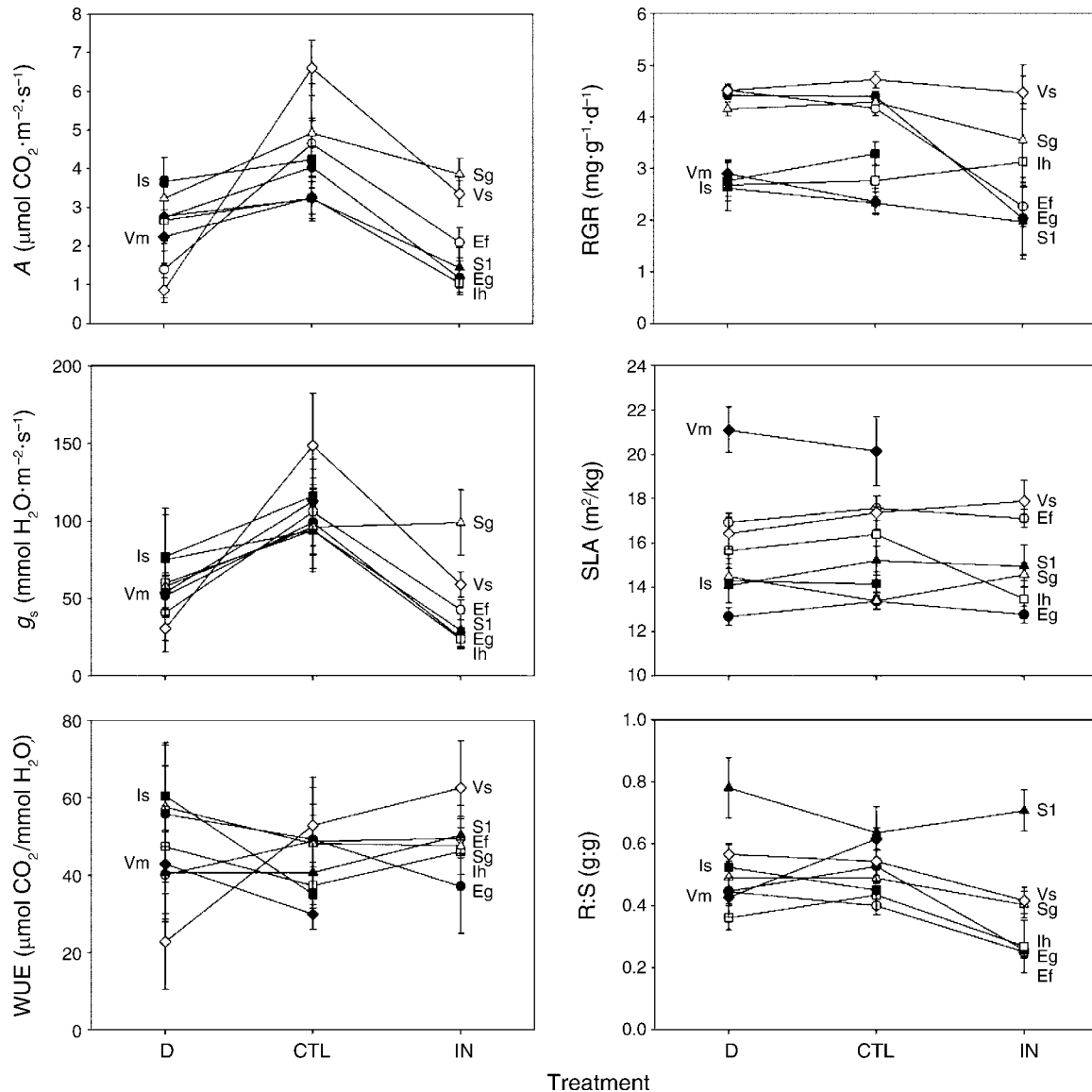


FIG. 3. Juvenile morphological and physiological traits under controlled (CTL) conditions of drought (D) and inundation (IN). Each panel shows the mean trait value (\pm SE) for 6–10 individuals grown from 18 to 22 months of age. Trait values (y-axis) are: A , carbon assimilation; g_s , stomatal conductance; WUE, water use efficiency; RGR, relative growth rate; SLA, specific leaf area; and R:S, root:shoot ratio. Open and closed symbols indicate species associated with seasonally flooded or terra firme forests, respectively. Each of the four genera is indicated with a different symbol, with species abbreviations (see Fig. 1) adjacent in each panel for clarity. Results for statistical tests for effects of treatments on the different species are presented in Appendix B: Table B1.

grandiflora were found almost exclusively in terra firme forest (Table 1). Russo et al. (2005) report a similar pattern in the 50-ha Malaysian Lambir plot, with species diversity decreasing between dbh classes because of losses of species on soil types with which they were not significantly associated. Coupled with low survival rates and reduced performance exhibited by juveniles of *I. sagotiana*, *S. sp. 1*, and *V. michelii* in simulated inundation treatments (Fig. 3), this suggests that associations in *Virola* and *Eperua* occur because of

differential performance at some point between the sapling and adult tree stage.

Alternative explanations for correlations of distributions with habitats involve ecological processes that we did not study explicitly. First, seed dispersal may be constrained for these species by a lack of dispersal agents or limited colonization sites (Condit et al. 2000). Dispersal limitation may be particularly pronounced for autochorous *Eperua*, because unlike the other three genera that are dispersed by bats and terrestrial rodents

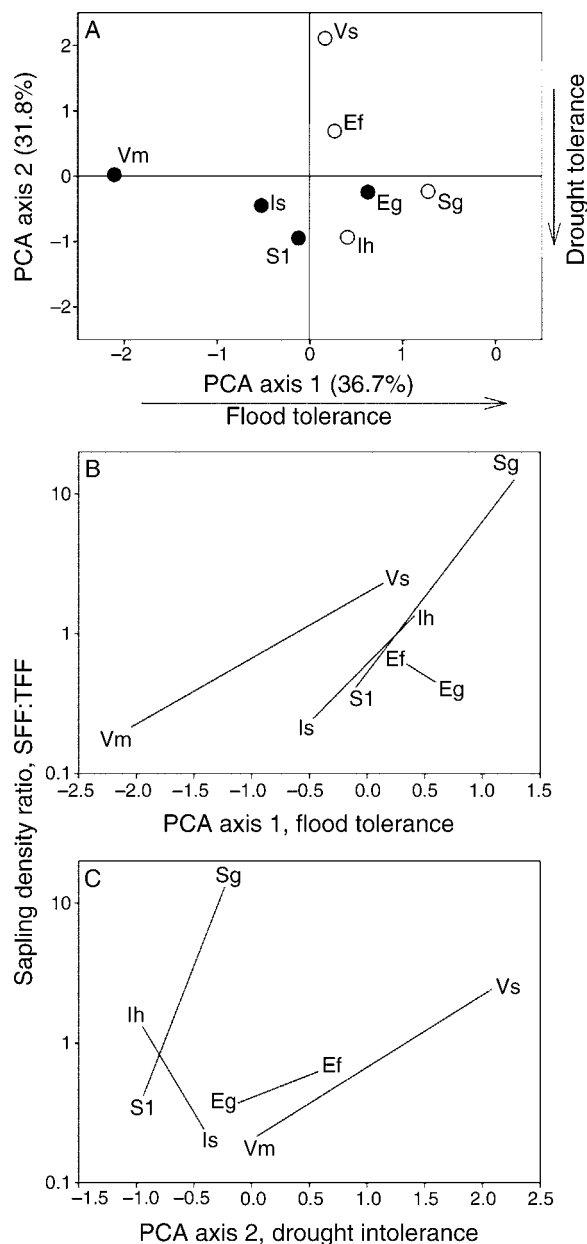


FIG. 4. Juvenile response to experimentally controlled conditions of water stress, and its relationship to sapling densities in seasonally flooded (SFF) vs. terra firme (TFF) forest habitats. (A) Results of a principal components analysis for juvenile morphological and physiological traits under controlled conditions of drought and water stress. Shown are four congeneric species pairs with contrasting associations with either seasonally flooded (open circles) or terra firme (solid circles) habitats. PCA Axis 1 represents flood tolerance, with strong positive loadings for the response ratio of relative growth rate and photosynthetic capacity to inundation. PCA Axis 2 represents drought intolerance, with a strong negative loading for the response ratio of photosynthetic capacity to drought. Labels adjacent to each symbol are abbreviations for species epithets (see Fig. 1). See Appendix B for a full description of methods and PCA axis loadings. (B, C) The ratio of the mean densities (stems/ha) in 2005 across all undisturbed permanent plots at Paracou, French Guiana,

(*Symphonia*) or birds and primates (*Virola*, *Iryanthera*), seeds of *Eperua* are dispersed by explosive pod dehiscence, with median distances of <20 m in *E. falcata* (Forget 1989) and <10 m in the very large seeded *E. grandiflora* (Forget 1992). This might limit seeds to habitats where adults are found. However, dispersal limitation would predict similar distributions of saplings and trees, contrary to our observations (Table 1).

A second alternative is that germination may be inhibited by conditions in seasonally flooded or terra firme forest. For example, species that do not occur in seasonally flooded forest have been found to have lower germination rates under inundated conditions in both Amazonian river floodplains and Guiana Shield forests (ter Steege 1994, Parolin et al. 2004). Seedlings of all eight species have been observed to germinate in both flooded and terra firme forest, though the rates of germination have not been studied explicitly (*C. Baraloto, personal observation*). Selective filtering during germination may contribute to the observed habitat associations at the sapling stage, but cannot explain the strengthening of these associations between sapling and tree stages (Fig. 1).

A third alternative is that species distributions are constrained by herbivore or pathogen pressure (Gilbert et al. 1994, Fine et al. 2004). A characterization of these pressures for a large number of stems for multiple species would be a useful contribution for future research.

Differential performance in seasonally flooded tropical forests

Whereas randomization tests such as the torus translation method improve the interpretation of habitat associations, they still provide only correlative evidence for habitat specialization (Potts et al. 2002). One means by which such small-scale plot patterns can be confirmed is provided by consistent associations across sites separated by hundreds of kilometers, the data for which are currently lacking for this and many tropical forest sites (but see Fine et al. 2005). Alternatively, corroboration of these results may be achieved by evidence for better performance of species in the habitat with which they are positively associated, or by species outperforming all potential competitors in this "home" habitat (Valladares et al. 2000, Russo et al. 2005). We found the strongest evidence for performance that corroborated patterns of habitat association within *Iryanthera*, with congeners showing differential sapling survival and tree growth that matched habitat associations. A similar pattern was observed in *S. globulifera* but not its congener (Fig. 2).

← between seasonally flooded (water table never descends below 1 m depth) and terra firme habitats, of saplings (0.5 cm < dbh < 10 cm), plotted against the first two principal components axes. Note the log scale of the y-axes. Lines connect congeneric species pairs.

Alternative explanations for differential performance incorporate factors other than seasonal water stress. For example, seasonally flooded forests may provide a refuge from competitive interactions because in addition to fewer species they generally have fewer stems (Fig. 1), lower basal area (Prance 1979, Koponen et al. 2004), and higher understory light levels (Baraloto et al. 2005). Therefore, it has been suggested that tree species found primarily in seasonally flooded forest may simply be outcompeted in all other areas by those species that are intolerant of seasonal inundation (Duivenvoorden 1995, Lopez and Kursar 2003). In the Paracou forest, for example, seasonally flooded habitats tend to have lower basal area (Salvado 2002), and thus stems may experience lower competition for both above- and belowground resources in addition to conditions of inundation or reduced drought stress. We attempted to account for this in our models of performance by including an individually based spatially explicit index of neighborhood basal area (Gourlet-Fleury and Houllier 2000). However, both seasonally flooded and terra firme forest species showed similar reductions in performance with increasing neighborhood basal area, suggesting that species associated with seasonally flooded forest are not restricted in distribution because they are inferior competitors in areas with higher competition.

Contrary to predictions, we found no performance differences between habitats at the sapling or adult stage within *Eperua* and *Virola* (Fig. 2). Despite the intensity of our sampling in both space and time, we may have failed to detect performance differences for at least two reasons. First, we may have failed to describe accurately the factors responsible for performance differences. Indeed, even the models with significant effects explained <5% of the variation in growth or survival, suggesting that performance is affected by factors other than the discrete habitat difference or covariate we studied. We attempted to account for differences in local competition, but herbivore and pathogen pressure, for example, may vary both within and among discrete habitat types (Fine et al. 2006).

Another limitation in the analysis of performance across habitats is that significant habitat associations often preclude sufficient sample size to test for differential performance. The models we used to analyze habitat effects on growth and survival approached the limitations of parametric analyses because we had few individuals in both habitats (see also Russo et al. 2005). An alternative to achieve sufficient sample sizes across habitats would be via reciprocal transplant studies (Fine et al. 2004, Palmiotto et al. 2004, Baltzer et al. 2005, Baraloto et al. 2005). However, such manipulations for long-lived large organisms such as trees are always restricted to seedlings for practical reasons, and performance at one developmental stage may not be correlated with that of another stage (C. Baraloto and L. Blanc, unpublished data).

Morphological and physiological adaptations to inundation and drought

A third means by which habitat specialization can be addressed is via differentiation in traits that are hypothesized to confer fitness in different habitats (e.g., Cavender-Bares et al. 2004). Specialization may be correlated with particular suites of traits, such as high osmotic adjustment in dry environments, or with trait plasticity across environmental conditions, such as stomatal closure in response to shade or drought (Chapin et al. 1993). In both cases, specialization to seasonally flooded or terra firme forest would not necessarily require trait divergence because similar suites of traits or plastic responses may be predicted as a general response to both types of water stress (Lopez and Kursar 2003).

We found inconsistent evidence for suites of traits associated with distributions restricted to seasonally flooded or terra firme forest. Three of the species that were strongly associated with seasonally flooded forest (*V. surinamensis*, *S. globulifera*, and *E. falcata*) shared a similar characteristic of high photosynthetic capacity and relatively high specific leaf area, but the other, *I. hostmanii*, did not share these traits (Fig. 3). This result is concordant with other trait screenings of tropical tree species associated with seasonally flooded forest, in which no consistent trait differences were associated with flood tolerance (Lopez and Kursar 1999, 2003, Parolin 2001).

We did not observe some leaf morphological responses reported to be shared between inundated plants and plants subjected to drought, including leaf shedding and the production of thicker and/or smaller leaves (ter Steege 1994, Lopez and Kursar 2003, Parolin et al. 2004). However, five of the eight species (but only one of four congener pairs) showed similar reductions in leaf gas exchange (A and g_s) in response to inundation and drought (Fig. 3). The main effect of flooding on plant growth is the deprivation of oxygen for the root system (Mendelssohn and Burdick 1988, Kozłowski 1997), which strongly and rapidly affects carbon and energy metabolism (Kozłowski 1997, Mitsch and Gosselink 2000, Kozłowski and Pallardy 2002). Decreases in both leaf transpiration (and stomatal conductance) and carbon assimilation have been observed in tree seedlings that survive after a few days of anoxia (Mendelssohn and Burdick 1988, ter Steege 1994, Kozłowski 1997, Lopez and Kursar 1999, 2003, Parolin 2001). Mielke et al. (2003) suggest that such adaptations are mainly related to stomatal closure rather than to any damage to the photosynthetic apparatus, which is consistent here with the increase in water use efficiency for these species, except *E. grandiflora*. The main effect of soil drought on plant functioning is the regulation of leaf gas exchange through stomatal closure, as exhibited by most tropical trees (Meinzer et al. 1993, Hogan et al. 1995, Bonal and Guehl 2001). The mechanisms underlying stomatal response to drought remain unclear, even though both hydraulic and metabolic root-to-shoot signals have been described to induce stomatal closure under drought

stress (see recent reviews in Kozłowski and Pallardy 2002, Chaves et al. 2003). The two species in our experiment that did not survive long-term inundation, *I. sagotiana* and *V. michelii*, were able to maintain photosynthetic rates under drought with some stomatal regulation (Fig. 3). Only one of their congeners, *V. surinamensis*, showed any other distinct morphological difference in response to experimental inundation (i.e., the development of lenticels and adventitious roots). These plastic responses have been suggested to contribute to the maintenance of stomatal conductance under waterlogged conditions (Mitsch and Gosselink 2000, Parolin 2001, Lopez and Kursar 2003, Parolin et al. 2004). Similar morphological responses were observed in *S. globulifera*, which actually maintained high stomatal conductance and had no significant reduction in photosynthetic rate under experimental flooding (Fig. 3).

The PCA analysis integrated information on suites of traits with physiological response to drought and inundation. Rather than indicating a trade-off between drought tolerance and flood tolerance (which would be represented by a positive relationship in Fig. 4A), the PCA axes separate at least three groups of species. The three species least tolerant of the inundation treatment (*V. michelii*, *I. sagotiana*, and *S. sp. 1*) have negative values for PCA Axis 1; these same species show negative associations with seasonally flooded forest and positive associations with terra firme forest (Table 1). Three other species (*I. hostmanii*, *E. grandiflora*, and *S. globulifera*) exhibited tolerance of both drought and inundation, with positive values of PCA Axis 1 and negative values of PCA Axis 2. *Virola surinamensis* and *E. falcata* tolerated experimental inundation but not drought.

We note, however, that the PCA axes represent only proxies for flood and drought tolerance. In our experiment, plants were maintained under inundation for 16 weeks until harvest, a situation that would occur only in extreme years in a small proportion of seasonally flooded habitats at Paracou (Salvado 2002). The fitness of these plants will depend not only on their ability to survive such extreme conditions, but also on their performance during drier periods when soils are not inundated. The magnitude of performance reduction during waterlogging treatment may not reflect the ability to recover; for example, no correlation exists between the response ratios of seedling height after 18 weeks of treatment and following 12 weeks of recovery, for control vs. waterlogged seedlings of six Amazonian várzea species (Parolin 2001).

In addition, we characterized drought tolerance based largely on response ratios for RGR or leaf gas exchange between two discrete treatments (control vs. drought) defined on the basis of volumetric water content during the experiment ($0.10 \text{ m}^3/\text{m}^3$ water per cubic meter of soil for at least four weeks, see Appendix B). An alternative definition of drought tolerance is the water potential at which stomata begin to close. For example, *E. falcata* has been characterized elsewhere as relatively drought

tolerant because it maintains leaf gas exchange until soil moisture drops below the $0.10 \text{ m}^3/\text{m}^3$ level, where it closes stomata completely and thus exhibits a drastic reduction in leaf gas exchange; in contrast, *V. michelii* might be characterized as even less tolerant of drought because it begins to close stomata at higher soil moisture fractions although the magnitude of this reduction is not as severe (Bonal and Guehl 2001). In fact, fitness for juveniles in seasonally flooded forest may require a combination of tolerance to both drought and inundation, as Lopez and Kursar (2003) suggest, because sandy seasonally flooded forest soils can have volumetric water reduced below $0.10 \text{ m}^3/\text{m}^3$ at the soil surface during extreme dry seasons (D. Bonal, *unpublished data*).

Convincing evidence for ecological filtering among these species was provided by the associations between the magnitude of habitat specialization, measured as a demographic response ratio, and the differential responses of morphology and physiology to experimental treatments, measured by the principal components analysis. Here we found patterns of experimental response that were strikingly consistent with species distributions (Fig. 4B, C). Noteworthy among these congeneric contrasts is the evidence for the distinction of a new species of *Symphonia*, based on significant differences from the described *S. globulifera* in distribution, performance, and morphological and physiological traits. *Symphonia* sp. 1 has been accepted as a distinct morphotaxon for more than a decade based on smaller flower size, smooth bark, and adventitious roots but no pneumatophores, in addition to a distribution limited to terra firme forest (D. Sabatier, *personal communication*). Degen et al. (2004) reported that this "ecotype" showed no differences from *S. globulifera* in three microsatellite markers, citing also sampling by Dick et al. (2003) at the Paracou site. However, their study distinguished individuals using adult leaf size, which has been found to be highly variable within both of these morphotaxa (C. Baraloto, *unpublished data*). We believe that further studies on the genetic differences between these taxa, including assays for non-neutral markers and description of quantitative traits, will be necessary to resolve this species complex. If these two morphotaxa are indeed a single species, our results for this pair represent an even more conservative test of habitat differentiation.

The consistency of response to experimental water stress treatments and habitat preferences that we observed in four phylogenetically distant angiosperm genera suggests that specialization to seasonally flooded forest must have evolved repeatedly several times (Terborgh and Andresen 1998). We propose that adaptive radiation in many other tropical tree genera may lead to species filtering along soil hydrological gradients, providing a significant contribution to regional tree diversity. These effects may be even more pronounced in the western Amazon regions where the genera studied here are more diverse (ter Steege et al. 2000). Associations with seasonally flooded forest are

currently being described within *Sterculia* (Sterculiaceae), *Pachira* (Bombacaceae), *Pterocarpus* (Papilionaceae), *Protium* (Burseraceae), *Diospyros* (Ebenaceae), *Licania* (Chrysobalanaceae), *Parkia* and *Inga* (Mimosaceae), *Eschweilera*, *Lecythis*, and *Gustavia* (Lecythidaceae), *Carapa* (Meliaceae), and *Caryocar* (Caryocaraceae) (Koponen et al. 2004; C. Baraloto, unpublished data). Further experimental manipulation of these species, including the measure of other traits such as hydraulic conductance, will provide an understanding of how adaptive trait divergence may lead to speciation events and coexistence in this diverse plant community.

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APPENDIX A

A modification of the torus translation method to test for habitat associations (*Ecological Archives* E088-029-A1).

APPENDIX B

Juvenile traits in response to drought and inundation (*Ecological Archives* E088-029-A2).