

Ecological and environmental factors constrain sprouting ability in tropical trees

Carl F. Salk · Sean M. McMahon

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Abstract Most theories of forest biodiversity focus on the role of seed dispersal and seedling establishment in forest regeneration. In many ecosystems, however, sprouting by damaged stems determines which species occupies a site. Damaged trees can quickly recover from disturbance and out-compete seedlings. Links among species' traits, environmental conditions and sprouting could offer insight into species' resilience to changes in climate, land use, and disturbance. Using data for 25 Neotropical tree species at two sites with contrasting rainfall and soil, we tested hypotheses on how four functional traits (seed mass, leaf mass per area, wood density and nitrogen fixation) influence species' sprouting responses to disturbance and how these relationships are mediated by a tree's environmental context. Most species sprouted in response to cutting, and many species' sprouting rates differed significantly between sites. Individual traits showed no direct correlation with sprouting. However, interactions among traits and site variables did affect sprouting rates. Many species showed increased

sprouting in the higher-quality site. Most nitrogen-fixing species showed the opposite trend, sprouting more frequently where resources are scarce. This study highlights the use of functional traits as a proxy for life histories, and demonstrates the importance of environmental effects on demography.

Keywords Functional traits · Disturbance · Damage · Panama · *Prorena*

Introduction

Sprouting is a dominant means of tropical forest regeneration following catastrophic damage (Vandermeer et al. 1995; Van Bloem et al. 2006). However, many theories of forest biodiversity focus on seed dispersal and species turnover (Janzen 1970; Connell 1971; Grubb 1977), overlooking the role of vegetative regrowth following disturbance. Regrowth from roots or stumps of damaged trees is a demographic shortcut that allows many species to regenerate following disturbance more quickly than by seed (Dietze and Clark 2008). Understanding what types of trees are likely to sprout is of fundamental importance to forest ecology. This study aims to better understand the ecological role of sprouting in tropical forests with two interrelated goals: (1) placing sprouting in a larger ecological context of life-history strategies, and (2) testing the environmental dependence of sprouting rates.

While sprouting rates are known to differ among different types of ecosystems (Vesk and Westoby 2004), surprisingly little work has been done to quantify the sprouting ability of individual species under contrasting climatic conditions. Previous studies of sprouting by tropical forest trees have been largely limited to surveys of

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C. F. Salk (✉)
Department of Biology, Duke University, Durham,
NC 27708, USA
e-mail: cfs14@duke.edu

S. M. McMahon
Smithsonian Environmental Research Center,
Edgewater, MD 21037, USA

sprout prevalence and survival in mature forests (e.g., Paciorek et al. 2000; Putz and Brokaw 1989). No previous study that we are aware of has examined sprouting in contrasting environments for a phylogenetically broad suite of tropical tree species.

Because traits of direct ecological importance are difficult to measure (e.g., drought or shade tolerance), we take a functional trait approach to assessing sprouting patterns. Functional traits are an accessible proxy for life history strategies in ecological studies (Ackerly and Cornwell 2007). They can represent latent ecological traits of interest, such as shade tolerance or dispersal ability, that are difficult and time consuming to measure directly. In this study we focus on four key functional traits that are proxies for different ecological strategies: leaf mass per area (LMA), wood density (WD), seed mass (SM), and nitrogen-fixing ability (NF). LMA is positively associated with shade tolerance (Westoby et al. 2002). WD is a good measure of structural damage resistance (Muller-Landau 2004). SM is inversely related to dispersal ability (Augsburger and Franson 1987), and NF is an obvious advantage in nutrient-poor sites (Wright et al. 2001).

Our study is organized around a set of hypotheses about how traits, site, and their interactions mediate sprouting behavior. Central to these hypotheses is the recognition that sprouting ability has costs. While these costs apparently derive from maintenance requirements of dormant buds, they are poorly understood. However, the fact that not all woody plants are able to sprout suggests that these costs are real (Vesk and Westoby 2004). We predict a tradeoff between a fast-growing, far-seeding lifestyle and persistence via sprouting, analogous to the colonization–competition tradeoff (Tilman 1994). This drives the expectation that LMA, SM and WD will all be positively correlated with species' sprouting rates. Alternatively, SM may be negatively correlated with sprouting due to a seeding/sprouting investment tradeoff, and sprouting may be less useful in species with dense wood if they are more damage resistant. We also predict that environmental conditions will affect sprouting rates; specifically, that species will consistently sprout better at the less stressful site. Trait-by-site interactions are expected to play a further role in sprouting rates. As noted above, increased LMA, WD and NF are useful adaptations to various stresses. Thus, we expect these traits to help offset the cost of maintaining dormant buds (Vesk and Westoby 2004), and be more positively related to sprouting rates at the dry site than at the wet site. If sprouting involves a demographic tradeoff with seeding (Pate et al. 1990), we expect species adapted to invest in greater SM to be more negatively affected by stressful dry conditions.

Materials and methods

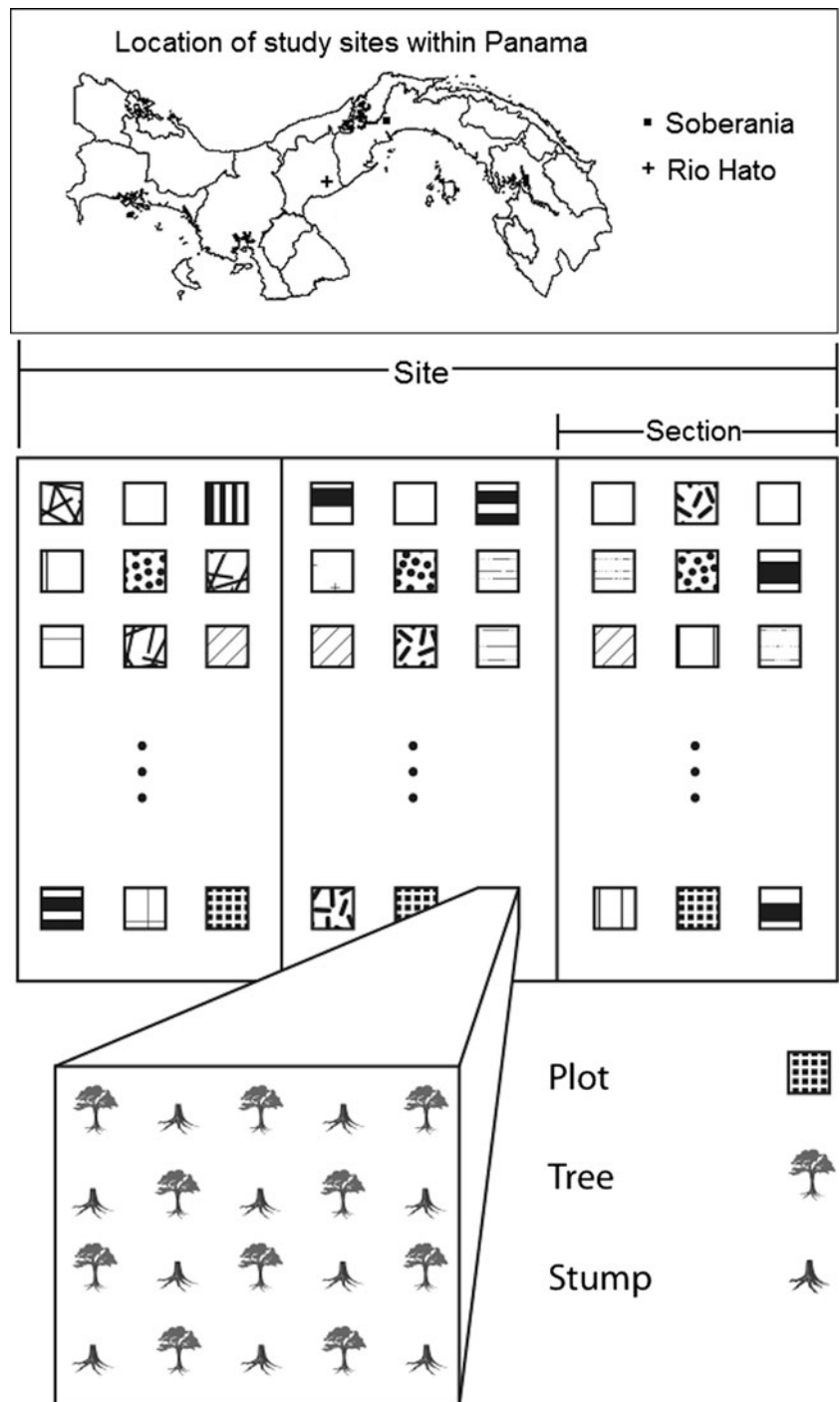
Study sites and data collection

Sprouting data was collected at two sites in central Panama, Soberania National Park (SNP), and Rio Hato (RH) (Fig. 1). Both plantations were established by a reforestation study known as PRORENA (PROyecto de REforestación con especies NATivas). The Soberania plantation is in an area of seasonally dry tropical forest with an annual rainfall of about 2,100 mm and a yearly dry season averaging 4.1 months (Craven et al. 2007). Rio Hato is much drier with about 1,100 mm of rain per year and a dry season lasting 6.7 months on average. Soil nutrient levels are consistently lower at Rio Hato than at Soberania. A detailed description of the sites can be found in Craven et al. (2007).

In 2003, vegetation was cleared from the sites and 25 species of mostly native trees were planted as part of a reforestation study by PRORENA staff. Each site was split into three sections, in which three plots of each species were planted, for a total of 18 plots per species (see diagram in Fig. 1). In each plot, 20 greenhouse-germinated seedlings were planted in a 5×4 grid with about 3 m between adjacent plants. Seedlings used at both sites were germinated from seeds collected from the same parent trees. Plantations were regularly cleared of weeds following planting. About 2 years after planting, all stands were thinned such that all surviving trees in excess of ten per plot were cut a few cm above ground level (for a total of $J = 450$ plots, and $N = 3,474$ surviving plants). The height of the plants at cutting varied among species, but was generally between 1 and 5 m, depending on growth rate. The stumps were left intact and sprouts were not cut. In February 2007, each cut stump in the two plantations was visited and scored for the presence or absence of sprouts. Because the demographic advantage of sprouting comes from the regrowth of a tree from a root system that would otherwise die, the number of sprouts from each stump is less important than the presence of any sprouts at all, so this was not counted.

The plantation setting is ideal for this experiment as it allows all species to be subject to the same treatments in similar numbers. Sprouting responses in this setting may differ from a naturally established forest for reasons such as the relatively high light and low competition in a plantation. However, there is an inherent tradeoff between the realism of a forest and the practical advantages of controlled treatments and large sample size in a plantation. The cost of our setting is that trees were cut rather than snapped or knocked down by wind or other trees, and they may react to this damage

Fig. 1 Locations within Panama of the study sites (Rio Hato and Soberania) and the layout of the PROENA forestry trial plantations used in this study. Each site was divided into three sections, each of which contained 75 plots that were planted with 20 seedlings of a single species at a spacing of ~3 m. About 18 months following planting, the surviving trees were thinned so that ten plants remained per plot



differently than they would in natural forests. Damaged trees that sprout are typically snapped at the lower trunk, or have much of their root system tipped out of the ground (Dietze and Clark 2008). While the cutting imposed in our study did not exactly simulate either of these scenarios, it is qualitatively most like a snapped stem, since only belowground reserves are available for reallocation.

Compilation of species' functional traits

We assimilated data on the leaf mass per area (LMA), wood density (WD), seed mass (SM), and nitrogen fixing ability (NF) of the study species from a variety of published sources [see the Electronic supplementary material (ESM), Table A1]. Literature data on LMA were incomplete, so some species' values were measured from leaf

specimens collected at the study sites. All data were converted into common units for analysis.

Model development and statistical analysis

The data are spread across nested levels (plots and species). Before we developed a model with covariates, we tested whether these higher-level groupings were different by fitting an “unconditional model” (McMahon and Diez 2007). There was significant variance across plots and across species, so we constructed a generalized linear mixed model using the lme4 package (version 0.999375-32) in R (R Core Development Team 2009) to estimate the sprouting of an individual given a suite of functional trait variables and the site at which the plots were established (Rio Hato or Soberania). Site (S) was treated as a binary covariate and included as a main effect and an interaction term (an ANCOVA model). We included all functional traits [seed mass (SM), wood density (WD), leaf mass per area (LMA), and nitrogen-fixing status (NF)] in a main effect model and as an interaction term. Model selection began with all saturated third-order (three-variable) interactions among species-level variables (SM, WD, LMA, and NF), which were then pruned based on parameter significance and the deviance information criterion (DIC).

After selecting an optimal model, we sampled each coefficient 1,000 times from a normal distribution with a mean and standard error derived from the coefficient estimates (as demonstrated in Gelman and Hill 2007). These draws were combined with the species random error and used to create simulated probabilities of sprouting for each species at each subsequent site (also following Gelman and Hill 2007). This allowed us to compare how site influenced the probability of sprouting across all species.

Results

Overall, 55% of stumps had living sprouts in February 2007, about 18 months after the trees were cut. In agreement with our expectations, sprouting probability was higher at SNP ($p < 0.05$), although this effect was slight. Most species showed some difference in their sprouting rates between the two sites (Fig. 2). The direction of these differences was species specific, with some species sprouting more in SNP while others showed the opposite pattern. Sprouting rates of individual species ranged from negligible (e.g., *Ochroma pyramidale*) to nearly 100% (e.g., *Spondias mombin*; Fig. 2). No functional traits had a direct effect on sprouting rate. Nitrogen fixers had a near-identical sprouting rate (54%) to nonfixers (55%). However, while most species showed higher sprouting probabilities in Soberania, nitrogen fixers showed the

reverse. Non-nitrogen fixers that showed a large difference between sprouting at the two sites tended to have higher LMA (Table 1).

The main effects model included all predictor variables. Only site difference showed strong differences in sprouting probability ($p = 0.039$; DIC = 3216; ESM Table A2; Spiegelhalter et al. 2002). However, when all interaction terms were included in the model, all trait:site interactions had $p < 0.05$. Ultimately, all interaction terms that reduced DIC were retained in the model (Table 2).

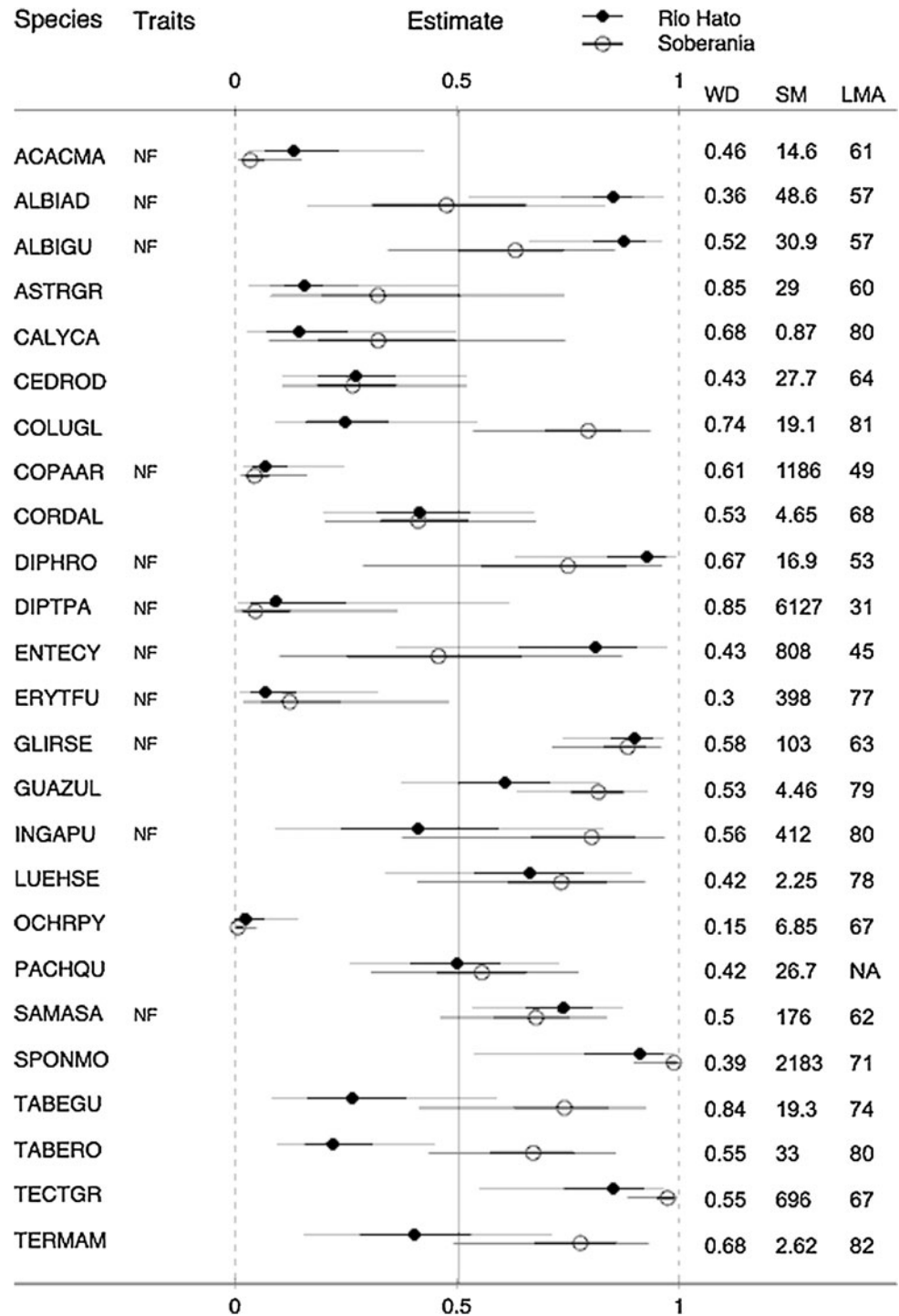
Functional traits were useful indicators of sprouting only when considered in an environmental context (Table 2; Fig. 3). Interactions among traits, as well as between traits and site, were critical when estimating sprouting. Increases in each continuous trait (LMA, SM and WD) were correlated with increased sprouting in the moister site relative to the dry site. This is contrary to our expectations for all traits except LMA. Species that fix nitrogen (NF) sprouted more readily at the drier site. This indicates a possible link between the ability to fix nitrogen and response to damage under nutrient or moisture stress. Other important interactions that did not involve site were relationships between species traits, like seed mass and nitrogen fixation ($p < 0.05$), and seed mass and wood density ($p < 0.1$). Both of these interactions were negative. The negative interaction between seed mass and nitrogen fixation shows that plants with large seeds tended to have high sprouting levels unless they were nitrogen fixers, in which case they had low levels. Likewise, high wood density was positively related to sprouting for small-seeded species, and negatively for large seeds.

Discussion

The objective of this study was to look for ecological correlates and the environmental dependence of sprouting rates. This was done for a diverse group of 25 Neotropical tree species. Species' overall sprouting rates ranged from almost never to nearly always. The variation among species was not random. Much of the species-specific pattern in sprouting can be explained by interactions among different ecological traits. For example, large seed size correlates with high sprouting probabilities in non-nitrogen fixers, with the opposite pattern seen in legumes. Aggregated across species, sprouting rates were only slightly higher in a moist, nutrient-rich site than in a very dry, low-nutrient plantation. However, over a third of the tree species showed substantial differences in sprouting rates between the two sites. The direction and magnitude of this effect varied greatly among species (Fig. 2).

To our knowledge, this is the first study to quantify sprouting responses in distinct environmental conditions

Fig. 2 Simulated results from the final functional relationship between covariates and the probability of resprouting at two sites in Panama. Data for Rio Hato and Soberania are indicated with *open and closed symbols*, respectively. Species random effects are included as fixed coefficients in the calculation. Values are simulated from draws of the mean and standard deviations of all coefficients and then run through the linear model (see “Methods”). Median, 25/75, and 5/95 percent quantiles are shown as *dots, thick, and thin lines*, respectively. Nitrogen fixing (NF) is indicated. Species traits for wood density (WD, g/cm³), seed mass (SM, mg), and leaf mass per area (LMA, g/cm²)



for a broad suite of tree species. Previous studies of environmental effects on woody plant sprouting have generally looked at a single species or genus, or have compared different species growing at different sites. For instance, Kabeya et al. (2003) found that *Quercus crispula* seedlings sprouted more in high-light than in shady environments. In a summary of 12 studies, Everham et al. (1996) concluded that community-level sprouting rates

were higher following catastrophic disturbance in wetter sites (but see Busby et al. 2010). However, these studies did not match species across sites, so it is not possible to conclude whether wet sites promote more sprouting, or if wet-site species are better sprouters. In a study of several species in the genus *Piper*, Lasso et al. (2009) found that pioneer species were more likely to sprout in high than in low light. This is of particular relevance to successional

Table 1 Summary statistics for a saturated model of sprouting rate predictors with plot and species-level random effects and second-level interaction terms

Parameter	Coefficient (β)	Standard error	<i>p</i> value
Intercept	0.297	0.600	
Wood density (WD)	3.035	2.428	
Seed mass (SM)	0.197	0.206	
Leaf mass/area (LMA)	587.241	462.487	
Nitrogen fixation (NF)	0.769	1.105	
Site (S)	0.303	0.190	
WD:SM	-2.045	1.471	
WD:LMA	1324.584	2322.823	
WD:NF	8.265	6.624	
WD:S	3.336	1.278	**
SM:LMA	-84.271	355.897	
SM:NF	-1.155	0.758	
SM:S	0.370	0.113	**
LMA:NF	-566.207	1712.762	
LMA:S	934.106	216.357	***
NF:S	-1.063	0.508	*

DIC = 3,152

*** *p* < 0.001** *p* < 0.01* *p* < 0.05**Table 2** Summary statistics for the best model of sprouting rate predictors, including plot and species-level random effects and second-level interaction terms that were used in the results and analysis

Parameter	Coefficient (β)	Standard error	<i>p</i> value
Intercept	0.455	0.400	
Wood density (WD)	3.642	2.272	
Seed mass (SM)	0.134	0.187	
Leaf mass/area (LMA)	341.434	423.496	
Nitrogen fixation (NF)	0.505	0.949	
Site (S)	0.308	0.190	
WD:SM	-2.494	1.408	.
WD:NF	8.944	6.477	
WD:S	3.356	1.277	**
SM:NF	-0.892	0.398	*
SM:S	0.367	0.112	**
LMA:S	929.701	215.996	***
NF:S	-1.056	0.507	*

DIC = 3,154

*** *p* < 0.001** *p* < 0.01* *p* < 0.05. *p* < 0.1

environments, and emphasizes both the importance and constraints of the consistently high light levels throughout our study sites.

Past studies have suggested that shade-intolerant species may not store sufficient carbohydrate reserves below-ground to produce viable sprouts (Pate et al. 1990). We found no evidence of such a limitation. Species' sprouting rates had no direct relation to SM, LMA or WD, all of which are positively related to shade tolerance at different life stages (Poorter and Markesteijn 2008; Poorter et al. 2008). It is still possible that this storage trade-off does affect some extremely fast-growing, light-demanding species. Indeed, the fastest growing species in this study, *Ochroma pyramidale*, almost never sprouted following cutting.

Although these sites differ strongly in environment and sprouting patterns, the generalization of our results is limited by the multiple environmental factors, principally soil nutrients and rainfall, which differ between our two study sites. Because the labor-intensive plantation layout was not replicated at sites with different combinations of fertility and precipitation, we cannot determine how these two factors would independently affect sprouting rates of different functional groups. However, because some of the plant traits we studied are adapted to either drought or nutrient limitation, it is possible to infer some likely causes of the patterns that we observed from basic plant biology and previous studies. In the following discussion, it is important to bear in mind that these relationships are generalizations, not directly tested mechanisms. It is also important to remember that sprouting is only one of several important demographic junctures in a tree's life. This study cannot detect adaptations that trade off with other demographic processes. While these patterns are not complete explanations of species' sprouting behavior, they still provide valuable insights into tradeoffs involving sprouting.

Nitrogen fixation

It is tempting to attribute the pattern of N-fixing plants sprouting more than non-N-fixing plants at the drier, infertile site to the ability of these species to overcome nutrient limitation. Previous studies have clearly shown that the advantage of nitrogen fixation is greatest at the least favorable (e.g., dry or nutrient-poor) sites (Wright et al. 2001). This could explain the increased sprouting of legumes relative to non-legumes at the dry site. However, it still doesn't explain why plants of a given species would do better at the unfavorable site than at the favorable location. It is possible that pathogens or insect pests play a role in this pattern, as both of these agents tend to be drought sensitive (Givnish 1999). If nitrogen-rich legumes are a tempting target for insects or pathogens, the dry conditions at the Rio Hato site may help these plants resist attack.

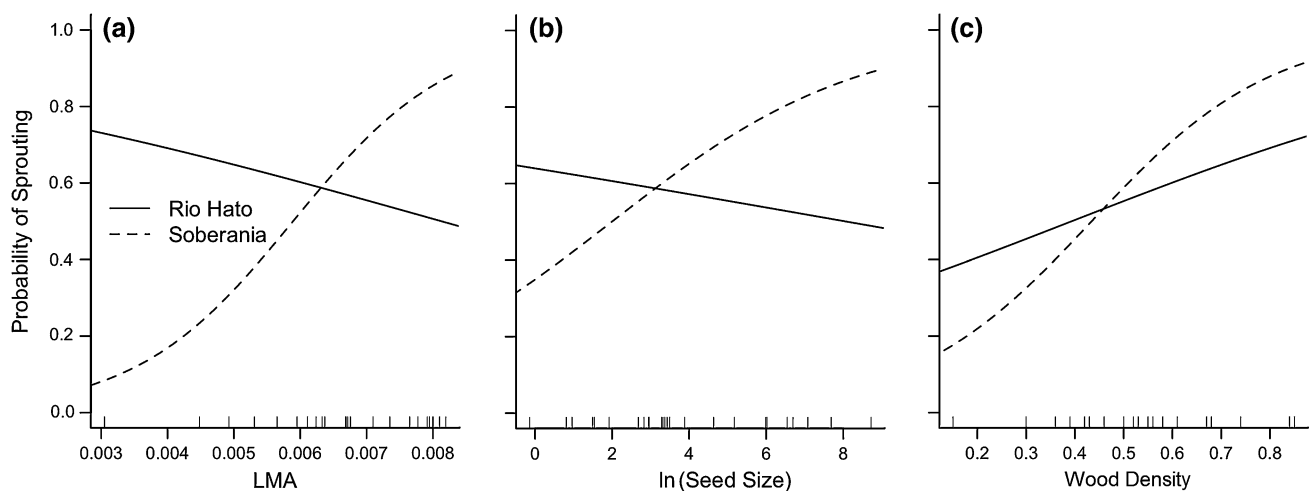


Fig. 3a–c Predicted relationships between three functional traits and site for stump sprouting of 25 species in two sites. Traits shown are **a** leaf mass per area (g/cm^2), **b** log-transformed seed mass (mg), and **c** wood density (g/cm^3). Predictions were generated assuming that all

other variables are at their means. Data for three functional traits are indicated along the x-axes, whose limits span the range of observed values for the 25 species

Leaf mass/area

High leaf mass per area is associated with long-lived, well-defended leaves, drought tolerance, and slower-growing plants (Westoby et al. 2002). Within a small area of uniform Mediterranean climate, Paula and Pausas (2006) found that nonresprouting species had a higher LMA and were more resistant to drought. It is possible that being freed from drought stress allows high-LMA species to redirect resources in a way that favors sprouting, consistent with our finding of high-LMA species having an increasing advantage in the wet site.

Wood density

Wood density is positively associated with slow growth, mechanical durability, drought tolerance and fungal pathogen resistance (Muller-Landau 2004; Poorter and Markesteijn 2008). Our finding that denser wood is correlated with better sprouting at the wet/fertile site relative to the dry/infertile site may be due to the increasing prevalence of pathogens at wetter tropical sites (Givnish 1999).

SM

Increased seed mass is correlated with decreased dispersal distance (Augspurger and Franson 1987). Sprouting is a demographic alternative to seed production and dispersal in disturbed environments, so it is reasonable to expect some sort of tradeoff between these two strategies. Thus, a more stressful environment may disproportionately affect the sprouting ability of larger seeded species, explaining our

finding that large-seeded species sprout less at the dry, infertile site.

This paper has documented environmental influences on sprouting rates and has shown that functional traits can be used to coherently group species in terms of their sprouting responses. While these relationships are complex, they are not intractable. Our results reiterate the need to think of forest demography as a high-dimensional process in which many traits of each species simultaneously interact with one another and their environment. Models that can untangle complicated responses of multiple species at appropriate scales will elucidate the drivers of community dynamics. Future research into forest response to environmental variation should focus on these traits instead of allowing poorly quantified designations like “shade tolerance” to drive analysis.

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