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Flower and Seed Production, Seedling Dynamics, and Tree Life Cycles

*S. Joseph Wright, Osvaldo Calderón, Andrés Hernández, and Helene C. Muller-Landau**

ABSTRACT. We present highlights derived from 36 years of weekly observations of flower and seed production and 25 years of annual observations of seedling dynamics at Barro Colorado Island (BCI), Panama. Highlights concern levels and causes of spatial, temporal, and interspecific variation in flower production, seed production, seed dispersal, and seedling recruitment, growth, and survival as well as the consequences for plant regeneration and diversity. Full tree life cycles are assembled by combining seed production, seedling dynamics, and observations of larger plants from the 50-ha Forest Dynamics Plot and are used to evaluate the costs of dioecy, lifetime insights from functional traits, and interspecific variation in the impact of lianas among host tree species. A variety of results demonstrate the importance of long-term observations to understand forest dynamics and responses to rising atmospheric carbon dioxide concentrations and a changing climate.

Keywords: flower phenology; flower production; fruit production; seed dispersal; seed limitation; seed production; seedling growth; seedling survival; trade-offs; tree life cycles

Plant species richness in humid tropical forests is unmatched at spatial scales relevant to trees (Wilson et al., 2012). The 605 tree species recorded from a single hectare of humid tropical forest in Ecuador exceeds the 543 tree species recorded across the entire Temperate Broadleaf and Mixed Forest Biome of North America (Balslev et al., 1998; Cazzolla Gatti et al., 2022). These numbers challenge ecological theory. How can hundreds of tree species coexist in sympatry in humid tropical forests? To address this and related questions, S.J.W. resolved to close tree life cycles by documenting seed production and seedling dynamics as Steve Hubbell and Robin Foster conducted the first census of trees larger than 1 cm in diameter at breast height (dbh) in the Barro Colorado Island (BCI) 50-ha plot.

A surprising number of mechanisms hypothesized to enable plant species coexistence concern early regeneration. These include the regeneration niche, enemies, competition-colonization, tolerance-fecundity, forest architecture, and storage hypotheses. Briefly, the regeneration niche hypothesis posits species-specific requirements that deaths of established plants alter creating a temporally shifting mosaic of sites suitable for regeneration by different species (Grubb, 1977; Hartshorn, 1978). The enemy hypothesis posits species-specific pathogens and herbivores that congregate at adult plants preventing successful regeneration of conspecifics, thereby opening space for other species (Janzen, 1970; Connell, 1971; Smith, 2022). The competition-colonization hypothesis posits a trade-off

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between competitive and dispersal abilities, with inferior competitors colonizing disturbed sites before superior competitors arrive (Tilman, 1994). The tolerance-fecundity hypothesis posits a seed size-seed number trade-off with large-seeded species better able to survive hazards while small-seeded species reach more sites (Muller-Landau, 2010). The forest architecture hypothesis posits a trade-off between recruitment rates and maximum size, with smaller statured species having larger recruitment rates per unit basal area (Kohyama, 1993). The storage hypothesis posits a long-lived life stage that ensures population continuity and interspecific, temporal asynchrony in reproduction that increases competition between conspecifics during the early stages of regeneration (Chesson, 2018). We started in 1987 and have now documented more than 5,500,000 seeds and nearly 100,000 seedling recruits enabling tests of these hypotheses.

Additional objectives were to accumulate weekly observations of flower and seed production and leaf fall over a temporal scale sufficient to observe rare events. Weekly observations accumulated over decades of natural climate variation enable discrimination of proximate cues hypothesized to initiate flower production and leaf fall. Rare events that might recur and be better documented and understood include a community-wide failure of fruit production that led to famine among frugivores and granivores in 1970–1971 (Foster, 1982). A final objective became apparent as time passed, atmospheric carbon dioxide (CO_2) concentrations continued to rise, climate change began in earnest, and our long-term observations detected changing levels of production at species-, lifeform-, and community-wide scales. The accumulated data now enable tests of hypotheses concerning species coexistence and proximate phenological cues, evaluation of long-term change, and, when combined with data on later life stages from censuses of the 50-ha plot, construction of full life cycles. Highlights follow.

METHODS AND CAVEATS

Methods are described in detail in cited publications. Briefly, we quantify flower and seed production through weekly censuses of 200 0.5-m^2 traps located randomly near preexisting trails in the BCI 50-ha plot and woody seedling dynamics through annual censuses of 600 1-m^2 plots associated with the seed traps (Fig. 1). These censuses began in January 1987 and 1994, respectively, with the seedling census only being possible after Nancy Garwood learned to identify all BCI seedlings (Garwood, 2009). We added another 50 sets of seed traps and seedling plots in natural treefall gaps between 2002 and 2004, traps that continue to be censused today. We censused another 200 seed traps colocated with the original traps for two years (2013 and 2014) to quantify spatial variation in seed production at the distance between traps and seedling plots (Detto et al., 2019). Finally, we quantified flower and fruit production since November 1985 with the same methods albeit fewer and smaller traps (59 0.25-m^2 traps) at Poacher's Peninsula, approximately 1.5 km south of the Forest Dynamics Plot (FDP). From the start, the litter trap censuses included all plant species, not just trees, and the seedling censuses included all woody plants, enabling insights regarding lianas as well as trees (e.g., Wright et al., 2004). COVID-19 interrupted the 2020 seedling census but not the trap censuses. We therefore report results through 2019 for seedlings and through 2021 for flowers and fruit.

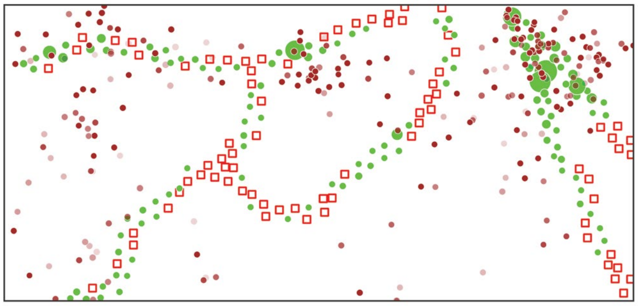

FIGURE 1. The 50-ha plot (1 km by 0.5 km) with potentially reproductive individuals of *Beilschmedia tovarensis* (formerly *B. pendula*) (brown) and seed traps that did (green) and did not (red) capture *B. tovarensis* seeds. The size of the green symbols indicates the number of seeds captured in 35 years, which ranges from 1 to 542 seeds per trap (2,824 total seeds). Seeds are large (6.8 g fresh mass), estimated mean dispersal distance is 4.8 m (Muller-Landau et al., 2008), and 78 out of 200 traps failed to capture a single seed in 35 years. The opacity of the brown symbols indicates the number of five-year censuses when trees were alive and larger than the reproductive size threshold of 20 cm dbh between 1985 and 2015. The lightest and darkest opacity correspond to 1 and 7 censuses, respectively. Traps are located at 13.5-m intervals on alternating sides and 4 to 10 m from 2.7 km of preexisting trails. The median distance between a trap and its nearest neighbor is 18 m.

There are four caveats. The smallest diaspore reliably captured in seed traps has a mean dry mass of 95 µg and belongs to *Alseis blackiana*. At least 35 woody BCI species have smaller diaspores (Garwood, 2024) that pass through the 1-mm trap mesh and are omitted from analyses of seed production. A second caveat concerns identifications of seeds in the genera *Anthurium*, *Ficus*, *Inga*, and *Philodendron*. Fruit are identified to species, but seeds, except for *Inga marginata*, are identified only to genus. A third caveat concerns seedling identifications, which are corrected on rare occasions as seedlings mature and leaf form changes. A small percentage of seedlings that die in their first year will have been misidentified. Finally, several cryptic species have been separated in recent years, including one after we captured unknown seeds (*Mascagnia ovatifolia*). Fortunately, in all cases except *Mascagnia*, the newly separated species is rare.

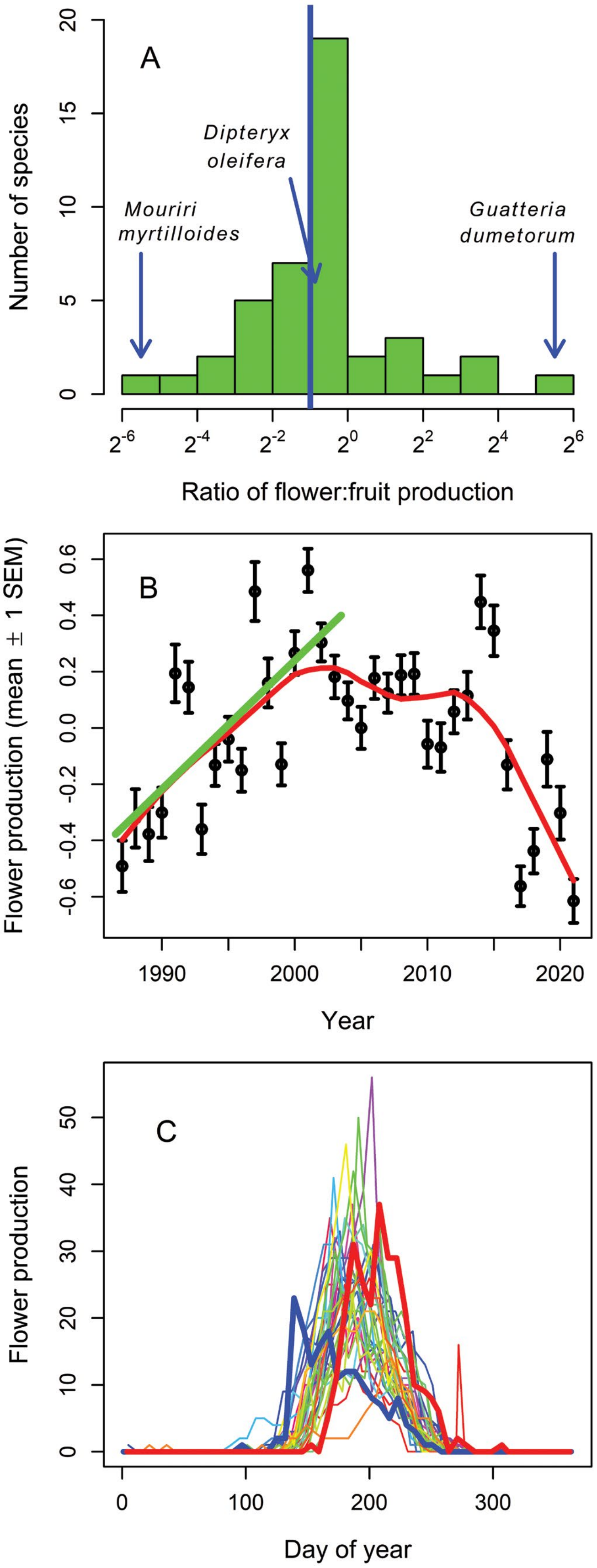

FIGURE 2. Flower production and phenology. (**A**) The ratio of flower-to-fruit dry mass production. Flower production exceeds 50% of fruit production to the right of the blue vertical line. Most *Mouriri myrtilloides* but few large, fleshy *Guatteria dumetorum* flowers develop into fruit. *Dipteryx oleifera* has the largest fruit production of any species (181 kg ha^{-1} yr^{-1}). The 44 species were captured as both flowers and fruit 300 or more times in 36 years at Poacher's Peninsula. (**B**) Mean flower production (±1 SE) for 128 species and 35 years combining 50-ha and Poacher's Peninsula data. Production increased from 1987 to 2003 ($p < 0.001$, green line) but the increase did not persist. The red line is Friedman's super smoother. Units for production are standard normal deviates to place the 128 species on a common scale (see Wright and Calderon, 2006). Each species was present in 500 or more trap-census combinations. (**C**) Weekly flower production for *D. oleifera* at the 50-ha plot. Colored lines represent 35 years. The heavy blue and red lines represent the year of earliest (1991) and latest (2015) mean flowering dates, respectively. Units for production are the number of traps with *D. oleifera* flowers each week.

FLOWER PRODUCTION AND PHENOLOGY

Tropical forest plants allocate more resources to flowers and pollination than is generally realized. At the species level, flower dry mass production exceeds 50% of fruit dry mass production for 28 of 44 well-sampled species (Fig. 2A), with fruit production defined broadly to include immature and mature fruit, seeds, capsules, bracts, and other fruit fragments that arrive in the litter traps. Fruit and flowers consumed in the canopy are missed. At the community level, flower production (709 kg ha^{-1} yr^{-1}) averages 70% of broadly defined fruit production (1,001 kg ha^{-1} yr^{-1}). Flower production also accounts for 4.2% of aboveground wood and fine litter production combined, which averages 17 Mg ha^{-1} yr^{-1} on BCI (Muller-Landau et al., 2024). Total aboveground net primary production (ANPP) includes consumption by heterotrophs in addition to aboveground wood and fine litter production. The nectar, pollen, and resins consumed by bees account for 3.2% of ANPP on BCI (Roubik, 1993), which exceeds the 2% of ANPP consumed by frugivores on BCI (Leigh and Windsor, 1982). Flower biomass production plus the nectar, pollen, and resins consumed by bees account for approximately 7.4% of ANPP. Given the direct consequences of pollination for fitness, this massive investment in flowers should not surprise.

Because of its direct link to fitness, reproduction is expected to increase if availability of a previously limiting resource increases. Thus, we expect flower production to rise with atmospheric CO_2 concentrations if carbon was previously limiting. Flower production increased significantly between 1987 and 2003 as atmospheric CO_2 rose from 349 to 376 ppm (Wright and Calderón, 2006) and continued to rise for selected life forms through 2014 (Pau et al., 2013, 2018). Figure 2B extends this record to 2021 when atmospheric CO$_2$ reached 416 ppm. The 17-year increase (1987–2003) is clear but is followed by 12 years of variable but consistently high production (2004–2015), and after 2016, is followed by lower production not seen since the 1980s. The relationship between flower production and atmospheric CO$_2$ has not withstood the test of time. Is the stress of increasing temperatures prevailing over the benefits of increasing CO$_2$? Future research will explore other factors that might limit flower production.

Weekly flower production combined with daily meteorology provides an opportunity to explore the proximate cues that initiate flower production. With few exceptions, lowland tropical flowers live a single day (Primack, 1985), so flower captures represent the timing of flowering well. Hypothesized proximate cues include daylength, cool temperatures, and increases in moisture or light availability (reviewed by Van Schaik et al., 1993). Strong seasonal correlations among these cues (Yang et al., 2021) make it difficult to distinguish among the possibilities. In addition, hypotheses are vague (e.g., increasing moisture availability cues flowering) and do not specify durations or thresholds, whether rates of change or absolute levels are important, and whether preconditioning (akin to winter vernalization at higher latitudes) is necessary.

We systematically recast these vague hypotheses as models whose parameters capture duration, thresholds, lags, and preconditioning to predict the probability of flowering for each day of the year. We then evaluated predicted probabilities against observed flowering times (Zimmerman et al., 2007; Chen et al., 2018; Wright and Calderón, 2018; Wright et al., 2019). As an example, Figure 2C presents weekly flower captures for 35 years for the canopy tree *Dipteryx oleifera*, with the year of earliest (1991) and latest (2015) flowering highlighted. The sudden onset of flowering is typical of most species and occurred 41 days earlier in 1991 than in 2015 for *D. oleifera*. This interannual variation in flowering times combined with interannual variation in hypothesized environmental cures enables discrimination among the hypothesized proximate cues. Attributes of the dry-season insolation peak had the greatest support to be the phenological cues for flowering in *D. oleifera* and many other BCI species (Wright and Calderón, 2018). A new analysis integrates preconditioning (e.g., by drought before increasing moisture availability becomes an effective cue) and successfully identified thresholds, durations, and lags previously determined experimentally for two BCI species (Wright et al., 2019). This new analysis promises further insights into flower phenology.

Seed Production and Dispersal

Mature fruit production measured by litter traps averages 895 kg ha^{-1} yr^{-1} on BCI. Frugivores have been estimated to consume another 114 to 136 kg of fruit ha^{-1} yr^{-1} (Leigh, 1999; Muller-Landau and Hardesty, 2005), and immature fruit contributes another 121 kg ha^{-1} yr^{-1} (Jackson et al., 2022). Mature fruit production is highly seasonal, peaking between January and April, when ample sunlight favors productivity, and bottoming out between October and December after many months of cloudy, low-light conditions (Fig. 3A; Wright and van Schaik, 1994; Detto et al., 2018). One keystone species, *D. oleifera*, contributes 69% of community-wide fruit production in January and February. When *D. oleifera* has a poor year, five consecutive months of food scarcity can precipitate famine among frugivores and granivores (Fig. 3A; Foster, 1982, Wright et al., 1999). Interannual variation in seed production is high both within species (Wright et al., 2005) and at the community level (Wright and Calderón, 2006). Overall, seed production is higher in sunny El Niño years and lower in cloudy La Niña years (Wright and Calderón, 2006; Detto et al., 2019).

Community-wide seed production averaged 887 seeds m^{-2} yr^{-1} on the 50-ha plot for seeds larger than 95 µg between January 1986 and December 2021. This astonishing number is consistent with a 300-fold increase in seed production from boreal to humid tropical forests (Journé et al., 2022). Six species with tiny seeds (<0.01 g) account for 53% of the seeds captured (Fig. 3C, right axis). The trade-off between seed size and seed number (Muller-Landau et al., 2008; Qiu et al., 2022), combined with the highly skewed species abundance distributions of woody plants, means that many species are rare in the seed rain. This sets the stage for seed limitation in many species, where seed limitation is defined as the failure of seeds to arrive in suitable regeneration sites (e.g., the 78 red traps in Fig. 1; Muller-Landau et al., 2002).

Seed limitation will reduce the potential for species to coexist through habitat specialization when species fail to arrive in optimal habitats (Hurtt and Pacala, 1995). Hubbell et al. (1999) used the first 10 years of seed captures to evaluate potential seed limitation for free-standing woody species. Figures 3B,C extend figure 4 of Hubbell et al. (1999) to 35 years and by adding climbers. Just eight species reached all 200 traps in 35 years, including six wind-dispersed species with tiny seeds (<0.01 g) and two animal-dispersed species with much larger seeds that happen to be the most abundant canopy and understory tree species (*Trichilia tuberculata* and *Faramea occidentale*, respectively). The number of species arriving at individual traps averaged 13 for the first year and rose steadily to 96 after 35 years (Fig. 3B). In contrast, 50-ha plot censuses have recorded 489 climbing and free-standing woody species (Condit et al., 2019; Schnitzer et al., 2021). Seed limitation is widespread even after 35 years. Seed addition experiments demonstrate that the failure of seeds to arrive limits seedling recruitment at BCI (Svenning and Wright, 2005). Muller-Landau et al. (2002, 2008) and Dalling et al. (2002) provide additional insight into the causes and consequences of seed limitation at BCI.

Contagious seed dispersal refers to the tendency for some sites to receive many dispersed seeds, while other sites receive few. Heterogeneity in canopy height contributes to contagious dispersal with 72% fewer seeds arriving in newly formed canopy gaps than in nongap sites (Puerto-Piñera et al., 2013). Canopy gaps also affect the species composition of arriving seeds. Few

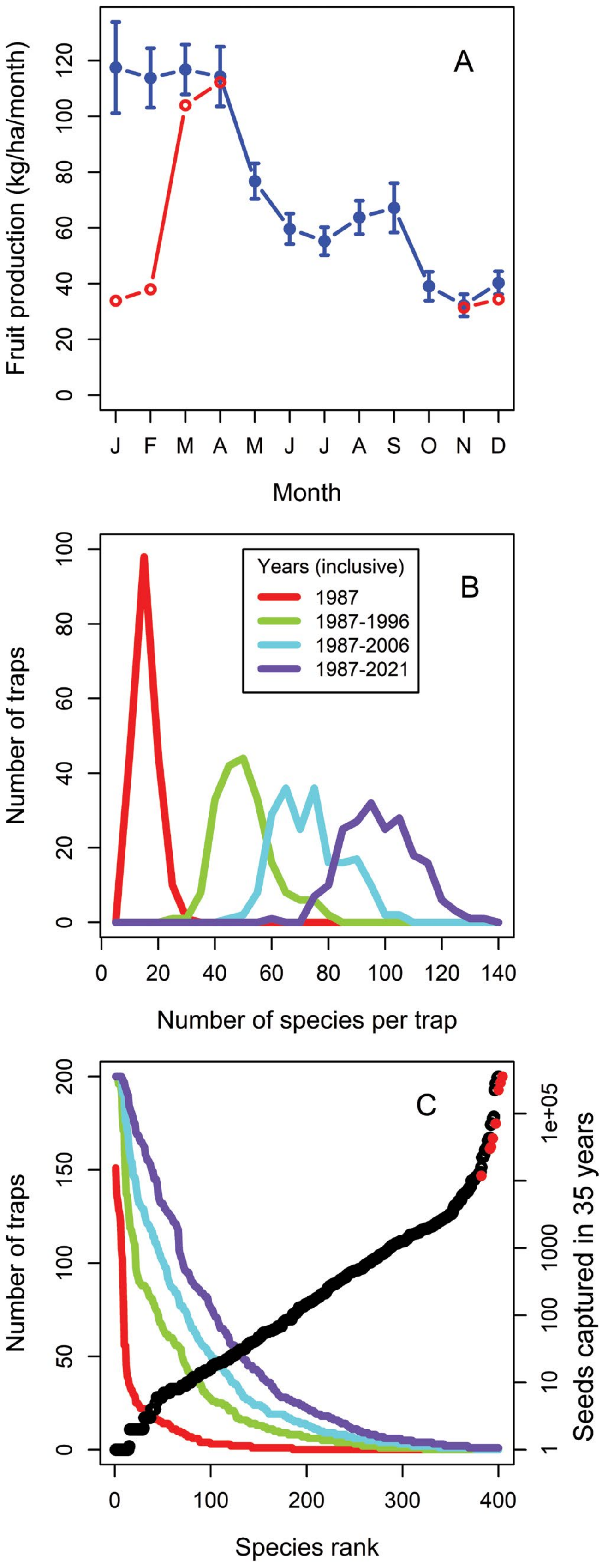

FIGURE 3. Fruit production and seed arrival. (**A**) Community-wide monthly fruit production (mean dry mass ± 1 SE) over 36 years at Poacher's Peninsula. The red line excludes D. *oleifera*, which accounts for 69% of fruit dry mass production in January and February. Intact fruit, seeds, capsules, and fruit damaged by animals are included. Immature fruit are excluded. (**B**) Histograms of the number of traps that captured seeds of different numbers of species over one (red), 10 (green), 20 (blue), and 35 (purple) years. The legend in panel b also applies to panel c. Panels b and c are for the 50-ha plot. (**C**) Species ranked by the number of traps where their seeds arrived over one (red), 10 (green), 20 (blue), and 35 (purple) years and ranked inversely by the number of seeds captured in all 200 traps over 35 years (black symbols and right axis). The red symbols represent eight species that reached all 200 traps in 35 years. The horizontal axis excludes another 85 species recorded in stem censuses of the 50-ha plot but not as seeds.

large-seeded species arrive in gaps, presumably because frugivores lack perches. In contrast, wind-dispersed species dominate seed arrival in gaps even though the number of wind-dispersed seeds arriving in gaps is reduced relative to undisturbed understory. Statistically significant interspecific associations in seed arrival characterize 10.8% of species pairs, are more likely for species with similar fruiting times and for animal- than wind-dispersed species, and persist through seedling recruitment (Wright et al., 2016).

Mapped trees and traps enable estimation of seed dispersal distances (Fig. 1). Inverse models specify functional relationships between seed numbers (fecundity) and tree size (dbh) and between seed arrival probability and tree-to-trap distances and compare observed numbers of seeds to summed probabilities that seeds arrive from each potential mother for each trap (Ribbens et al., 1994). Jones and Muller-Landau (2008) validated dispersal distances estimated using inverse models by genotyping mothers and trapped seeds to obtain known dispersal distances. Numbers of seeds estimated to arrive in tree-fall gaps explain the relative abundances of seedling recruits, demonstrating seed limitation across 14 light-demanding tree species (Dalling et al., 2002). Seed mass alone explained 45% of interspecific variation in fecundity across 41 species, and seed mass, dispersal syndrome, and maximum height explained 28% of interspecific variation in dispersal distances, providing hope for trait-based generalization and modeling of seed dispersal (Muller-Landau et al., 2008). Increasingly sophisticated mechanistic models of seed dispersal have also advanced our understanding of seed arrival patterns, especially for seeds dispersed by wind (Wright et al., 2008; Augspurger, 2024) and for seeds dispersed by animals (Beckman et al., 2024).

SEEDLING RECRUITMENT AND DYNAMICS

Hundreds of shade-tolerant species have recalcitrant seeds that germinate quickly, lack a seed bank, and must regenerate from a persistent seedling bank in humid tropical forests (Garwood, 1989, 2024). Seedling bank dynamics affect plant diversity and species composition (e.g., Green et al., 2014). Nonetheless, few tropical forest studies track seedlings from initial recruitment (e.g., Metz et al., 2008; Norden et al., 2009; Xu et al., 2019; Martini et al., 2022) and just one has incorporated seedling age into analyses of dynamics (Record et al., 2016).

With 25 years of annual seedling censuses and contemporaneous seed production, we can answer fundamental questions about the seedling bank for the first time. There is 10,000-fold variation among species in the number of seeds required to produce one first-year recruit, with values ranging up to 81,000:1 and 65,000:1 for *Hieronyma alchorneoides* and *Alseis blackiana*, respectively (Fig. 4A; also see Terborgh et al., 2014). This establishment limitation will exacerbate widespread seed limitation (Fig. 3B,C; Muller-Landau et al., 2002). After establishment, the seedling bank remains a risky place. Community-wide mortality is 54% yr^{-1} in the first year and still averages 8% yr^{-1} for 20- to 24-year-old seedlings (Fig. 4B). Growth is slow with frequent setbacks, and median heights first reach 20 and 50 cm when seedlings are 8 and 22 years old, respectively (Fig. 4C).

Three trade-offs are evident in the seedling bank. The familiar survival-growth trade-off is particularly strong among seedlings, with species tending to have high survival and slow growth rates or vice versa. Surprisingly, lianas and trees fall along the same survival-growth trade-off relationship, with seedlings of several liana species (e.g., *Abuta racemosa* and *Maripa panamensis*) having survival and height growth rates characteristic of the most shade-tolerant tree species (Gilbert et al., 2006). In a second shade-drought trade-off, shade-tolerant species tend to be drought sensitive and vice versa (Kupers et al., 2019b). In a

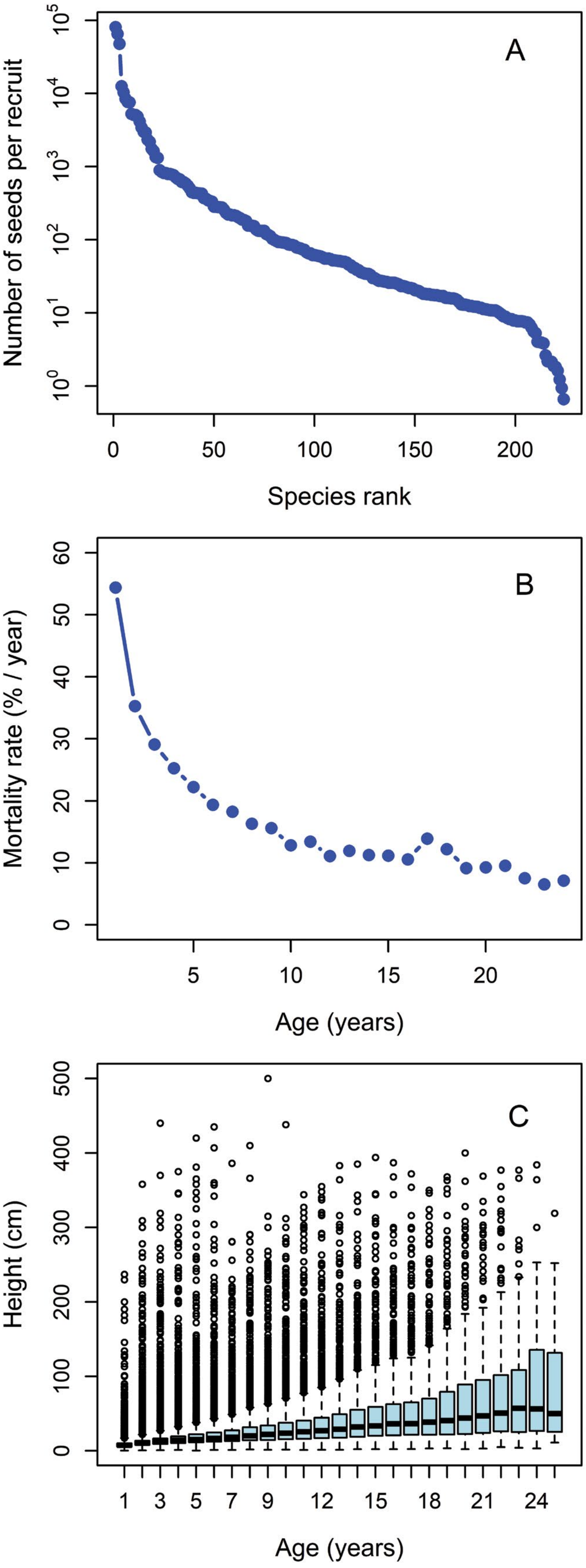

FIGURE 4. Seedling recruitment and dynamics in the 50-ha plot. (**A**) Species ranked by the number of seeds required to produce one seedling recruit. Species in the descending tail above rank 200 are mostly small shrubs shorter than the traps whose seeds are therefore underrepresented. Each species had seeds captured in 10 or more of the 200 traps. (**B**) The community-wide seedling mortality rate declines with seedling age. Rapid deaths of light-demanding species contribute to the rapid initial decline. A consistent, gradual decline with age characterizes shade-tolerant species. (**C**) Bar-and-whisker plot of seedling height versus seedling age. Black horizontal bars represent medians, boxes represent the interquartile range (IQR, 25th to 75th percentile), whiskers extend 1.5 IQRs beyond boxes, and points represent seedlings outside the whiskers. Seedlings that grew to be more than 5 m tall are not shown but contributed to medians and IQRs.

third stature-fecundity trade-off, large-statured tree species tend to produce few seeds and recruits per unit basal area and vice versa (Rüger et al., 2018). These trade-offs contribute to species coexistence by stabilizing niche differences (Detto et al., 2021) as well as by reducing fitness differences (Chesson, 2018).

Conspecific negative density dependence (CNDD) is particularly strong among seedlings. The negative effect of neighbors for survival of focal seedlings is 10 times stronger (per standard deviation of density) for conspecific seedling neighbors than for larger conspecific and all heterospecific neighbors (Lebrija-Trejos et al., 2014). Seedling root systems and canopies rarely come into contact on BCI (Svenning et al., 2008). Thus, the negative effects of conspecific seedlings cannot be explained by resource competition but, instead, are most likely due to pathogens (e.g., Mangan et al., 2010). Seedling–seedling CNDD is stronger in species with smaller seeds, in years with lower seed production, and in wetter years (Wright et al., 2005; Lebrija-Trejos et al., 2016, 2023). Seedling–seedling CNDD is statistically significant but not as strong in other tropical forests perhaps because sample sizes are smaller in other studies and analytical methods differ (e.g., Metz et al., 2010; Martini et al., 2022). CNDD contributes to species coexistence by stabilizing populations (Chesson, 2018), CNDD is stronger in early than later life stages (Green et al., 2014; Zhu et al., 2015), and strong CNDD early in life affects the diversity and abundance of tropical trees (e.g., Comita et al., 2010; Mangan et al., 2010; Bagchi et al., 2014). Future cross-site studies using a common analysis and studies of pathogen–seedling interactions will elucidate the generality and mechanism of seedling–seedling CNDD.

Seedlings have small, shallow root systems, and we predicted survival and growth would track temporal and spatial variation in dry-season severity and soil moisture availability. This prediction was not realized. Just 1 of 63 seedling species had significantly slower growth and just 4 had significantly lower survival at lower soil moisture availability across spatial and temporal variation spanning our 200 stations and 20 years, respectively (Kupers et al., 2019a). During a severe dry season, seedlings maintained low rates of stomatal conductance (11 to 26 mmol m^{-2} s^{-1}) and photosynthesis (0.8 to 1.1 μmol m^{-2} s^{-1}) even as mean predawn and midday leaf water potentials fell to −2.0 and −3.0 MPa, respectively (Engelbrecht et al., 2002). Seedlings of many BCI species are surprisingly well buffered against seasonal drought even during exceptionally dry years.

Interannual variation can contribute to stabilizing species coexistence through the storage effect. The storage effect requires a long-lived life stage so that generations overlap and asynchronous variation in recruitment across species so that conspecific recruits interact more frequently than heterospecific recruits. Trees fulfill both requirements. Interannual variation in recruitment is large (Metz et al., 2008) and asynchronous across species, which increases conspecific relative to heterospecific interactions among recruits (Usinowicz et al., 2012). At higher latitudes, shorter growing seasons constrain the seasonal timing of reproduction imposing greater recruitment synchrony across species. This increases the ratio of conspecific-to-heterospecific interactions among recruits at higher latitudes and decreases the potential contribution of the storage effect by 0.25% for each degree of latitude that a forest is located further from the equator (Usinowicz et al., 2017). The storage effect combined with strong CNDD among recruits (see previous two paragraphs; Milici and Comita, 2024) contributes to stabilizing coexistence of tropical tree species.

Full Life Cycles

We combined seed production, seedling demography, small sapling demography (>20-cm tall and <1 cm dbh; Comita et al., 2024), reproductive size thresholds (Wright et al., 2015), and 50-ha plot censuses (Condit et al., 2019) to complete tree life cycles and address three questions. Functional traits are promising predictors of life histories. Many studies link traits and demographic rates; however, analyses have evaluated single life stages and predictive power is often low. In a full life-cycle analysis, trait-demography relationships at one life stage were often absent and sometimes offset at other life stages (Visser et al., 2016). Robust links between traits and life histories will require understanding trait-demography relationships across all life stages.

Lianas are structural parasites of trees and reduce tree growth, survival, and fecundity. We evaluated the importance of these effects for host tree fitness, and variation in fitness consequences among tree species, using a full life-cycle analysis and integrating additional data on the growth, survival, and reproduction of liana-infested trees (Visser et al., 2018b). Lianas substantially reduced host tree fitness, with the largest impact from reduced survival, and more modest impacts from reduced growth and reproduction. Light-demanding hosts suffered the largest decreases in fitness, because of larger reductions in survival. Previous literature found that light-demanding tree species had a lower prevalence of liana infestation and hypothesized that light-demanding species were able to avoid liana infestation (e.g., Putz, 1984). The new findings demonstrate that survival bias explains the lower prevalence of liana infestation observed for light-demanding trees (Visser et al., 2018a).

Dioecy imposes a demographic disadvantage—just half of adults produce seeds—that must be offset by a compensatory advantage for dioecious and hermaphroditic species to coexist (Bawa, 1980). Increased outcrossing and genetic variation is unlikely to provide the advantage because hermaphroditic species also have efficient outbreeding mechanisms (Bawa, 1974). In a full life-cycle analysis, increased seed production provided the compensatory advantage, resulting in no net costs of dioecy (Bruijning et al., 2017). Foregoing the large costs of pollen and male flower production (Fig. 2A) enables increased seed production by dioecious females.

CONCLUSIONS

The novel insights presented here (e.g., Figs. 2, 3B,C, 4) are enabled by enormous sample sizes accumulated over 36 years of weekly flower, fruit, and seed production censuses and 25 years of annual seedling censuses. Nonetheless, sample sizes remain small for species that produce small numbers of large seeds and for the many rare species. The median height of 24-year-old seedlings is still only 50 cm (Fig. 4C), and the effective sample size is only 25 or 36 years for analyses of interannual variation. Although this is the longest continuous record of flower and seed production and seedling dynamics for any tropical forest, its duration remains short relative to the 60- to 80-year period of the Atlantic Multidecadal Oscillation, which plays an important role in driving climate variability in this region (Elder et al., 2014).These are compelling reasons to continue this work.

As atmospheric CO_2 concentrations rise and global climate change takes hold, responses at these sensitive life stages will help determine the species composition, structure, and dynamics of future tropical forests. Flower production, seed production, and seedling recruitment all vary widely among years, variation explained in part by climate. Temporal trends observed earlier in the record have not remained consistent to the present day (e.g., Wright and Calderón, 2006; Fig. 2B), highlighting the dangers of extrapolation from phenomenological models. Mechanistic models offer an alternative pathway for prediction, and our data have been used to develop a substantially improved recruitment scheme for vegetation dynamic models that project future tropical forest carbon budgets (Hanbury-Brown et al., 2022), but these models are no substitute for observations. Ongoing, long-term observational studies are crucial in a changing world.

Because forests differ in their climate drivers, dynamics, and responses to global change, broader insight requires data from multiple sites. Our methods have been adopted at multiple additional sites, including 26 sites in the ForestGEO network (see table S6 in Anderson-Teixeira et al., 2014). Multisite studies have already enabled generalization beyond BCI (e.g., Metz et al., 2008; Usinowicz et al., 2017), and we hope to see many more multisite long-term studies in the future.

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