

Seed limitation and the coexistence of pioneer tree species

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Abstract

Seed limitation, defined as the failure of seeds to arrive at sites favorable for recruitment, may be a critical force structuring plant communities. When seed limitation is strong, interspecific competition is reduced, and competitive exclusion may be slowed to the extent that diversity can be maintained through speciation and migration. In mature tropical forests, seed limitation may be especially important in determining the recruitment patterns of pioneer tree species. These species depend on dispersal to infrequent and ephemeral tree fall gaps for successful seedling establishment. Despite this requirement, pioneers show wide variation in the life-history traits that affect dispersal ability. Here we use seed trap data for pioneers from the 50 ha forest dynamics plot on Barro Colorado Island (BCI), Panama to show that seed limitation has a significant effect on seedling recruitment patterns. We then assess whether the effects of limited dispersal in space can be offset by prolonged dispersal in time through the accumulation of a persistent soil seed bank. Using a simulation model we show that variation in dispersal in space may have surprisingly little effect on overall seedling recruitment rates. This is because there is a trade-off between the number of gaps colonized and recruit density per gap. While long-term seed persistence increases the fraction of gaps colonized, it cannot fully compensate for limited dispersal in space and carries a substantial fitness cost resulting from increased generation time.

Introduction

Most mechanisms thought to contribute to the maintenance of species diversity (e.g., niche differentiation, competition, and density dependence) are predicated on the recruitment of individuals into the community. The first step in the recruitment process is the arrival of a viable seed at a site suitable for seedling establishment. The probability of successful arrival is fundamentally constrained by the resources available to a plant's reproduction, and is further influenced by a suite of adaptive compromises that determine the size and number of seeds produced, and the resources allocated to ensure seed dispersal (Muller-Landau, chapter xxx). The consequence of these constraints on recruitment is 'seed limitation'. This has been defined as the failure of seeds to arrive at sites favourable for recruitment as a consequence of either limited seed production, or limited dispersal of the seeds produced (Nathan & Muller-Landau 2000). At the population level, seed limitation potentially restricts rates of population spread,

opportunities for the colonization of patches of new suitable habitat, and influences population genetic structure (Wright 1969, Hanski 2001, Muller-Landau et al. 2003).

At the community level, theoretical work has shown that strong seed limitation can promote species coexistence by greatly slowing competitive exclusion (Tilman 1994, Hurtt & Pacala 1995). This is because when plants are seed limited recruitment sites are frequently won not by the strongest competitor in the community (Kitajima and Poorter, chapter xxx), but by the best competitor among the restricted set of species that arrives at that site. If competitive exclusion can be slowed sufficiently then diversity might be maintained as species loss is balanced through speciation and migration into the local community (Hubbell 2001). Most evidence for seed limitation comes from analyses of seed captures in temperate forests. These studies indicate that even in stands containing high conspecific adult densities much of soil surface fails to receive seeds of any one species. While this limitation was due primarily to limited seed dispersal, variance in the reproductive output of individual trees and temporal variation in seed production also contribute to the observed seed limitation (Clark et al. 1998, 1999, McEuen & Curran 2004, Clark et al. 2004).

Here we present evidence for seed limitation in tropical pioneer species. Pioneers face particular challenges to maintaining populations in mature forest. The traits that allow these species to achieve high growth rates in the juvenile phase also restrict their initial recruitment to light gaps (Schnitzer et al., chapter xxx). In most forests, these sites are formed predominantly by treefalls and landslides, and typically occur at low densities (< 2 % of the landscape/year; Uhl & Murphy 1981, Brokaw 1982a, Lieberman et al. 1990). The rarity of these disturbances and the short duration for which these sites are available for colonization therefore suggests that recruitment of pioneer species could be strongly limited by their ability to disperse.

If the need to regenerate in gaps is a strong selective force shaping pioneer life-histories then we might expect that traits influencing dispersal would differ between shade-tolerant and pioneer species. Although pioneers are noted for their small seed size and high fecundity (Swaine and Whitmore 1988), seed mass and reproductive output still varies over four orders of magnitude among coexisting pioneer species (Dalling et al. 2002, Dalling and Burslem 2005). As a consequence, pioneer species may vary in the degree of seed limitation that they experience, or may have developed other mechanisms that offset the effects of seed limitation to increase the probability of colonization success. Two potential mechanisms are: 1) non-random (directed) dispersal to gaps; and 2) long-term persistence of seeds in soil seed banks. Evidence for directed dispersal to gaps in tropical forests is limited (Wenny 2001), but may be important for wind-dispersed species (Loiselle et al. 1996). In contrast, seed persistence is common among pioneers (e.g. Hopkins and Graham 1987, Dalling et al. 1997), although the contribution these seeds make to gap colonization and net reproductive output has rarely been quantified (Murray 1988).

In this chapter we use the pioneer tree species of Barro Colorado Island, Panama, as a case study. We use seed trap data to estimate components of seed limitation, and to

generate parameters for models of seed dispersal. We provide evidence that spatial variation in annual seed rain can help explain patterns of seedling recruitment for some pioneers but not for others. We explore whether long-term persistence of seeds in the soil seed bank can compensate for limited dispersal in space, and finally, we briefly review evidence for the operation of other mechanisms that can promote coexistence among these species.

Are tropical pioneers seed limited?

The best evidence for seed limitation (the failure of seeds to arrive at a site over time) comes from long-term studies of seed capture rates. On BCI, an on-going study with two hundred 0.5 m² seed traps placed in the 50 ha Forest Dynamics Plot has shown that, on average, 88 % of pioneer and shade-tolerant tree species fail to disperse a single seed *to any given* trap over ten years, and that *no seeds at all* were collected in any of the 200 traps for > 50 species during the same period (Hubbell et al. 1999, Harms et al. 2000). These analyses also show that all pioneer species on BCI are also seed limited based on annual trap data (Table 1) and would therefore fail to disperse seeds to all parts of every gap that forms each year. Seed limitation for some pioneers remains remarkably high over much longer periods, suggesting their seed rain only reaches a small fraction of new gap sites (Dalling et al. 2002).

Seed limitation can arise because an insufficient number of seeds are produced, defined as '*source limitation*', or because seeds are non-randomly dispersed across the landscape, defined as '*dispersal limitation*' (Clark et al. 1998). When seed trap data are available, the degree to which a tree population is source limited can be evaluated by randomly 'redistributing' the total seed count among all the traps used in the study. Source limitation is then defined as the proportion of traps that are still expected to fail to capture a single seed (Table 1). Differences in source limitation among species are the consequence of variation in adult population density, adult size at reproduction, and mean seed mass. Once source limitation has been calculated, dispersal limitation can be determined as the measure of how the proportion of traps receiving seeds is further reduced above and beyond constraints due to source limitation. Dispersal limitation is calculated as $1 - (\text{proportion of traps receiving seeds}) / (1 - \text{source limitation})$. Dispersal limitation can be expected to be high for species with high seed production and short dispersal distances or with highly clumped dispersal.

Among the BCI pioneers, three species (*Alchornea*, *Alseis* and *Luehea*) effectively escape source limitation in a given year, with sufficient seed production at the population level that seeds could theoretically reach ≥ 99 % of sites (Table 1). In contrast, none of the species escape dispersal limitation and thus seed limitation, such that seeds of even the best-dispersed species, *Luehea*, reached only 76 % of traps. Differences between species with wind versus animal-vectored seed dispersal are clear. While seeds of the five wind dispersed species reached between 10 and 76 % of traps, seeds of animal dispersed species only managed to reach from 4-8 % of traps. This difference reflects the more aggregated pattern of animal seed dispersal in which seeds are often defecated together in

clumps at dining roosts, sleeping roosts and latrine sites (e.g. Schupp et al. 2002, Wehncke et al. 2003). The species exhibiting the strongest seed limitation, however, was *Croton billbergianus*, a sub-canopy tree with ballistic dispersal (Table 1). This is one of the most abundant pioneers on BCI, and illustrates how pioneers can apparently recruit successfully despite extreme seed and source limitation.

Do pioneer recruitment patterns reflect seed limitation?

Measures of seed limitation, based on captures of single seeds to traps, represent minimal dispersal rates from which recruitment could theoretically occur. However, probabilities of seed survival to germination, and of seedling survival to emergence and establishment can be very low, even when conditions for recruitment are favorable (Harms et al. 2000). Furthermore, seedling emergence and establishment probabilities are strongly seed-size dependent (Dalling & Hubbell 2002), and are affected by leaf litter density and other microsite conditions within gaps (Brandani et al. 1988, Vázquez-Yanes et al. 1990, Molofsky & Augspurger 1992). Initially high seed densities on the soil surface may also be greatly reduced by a variety of animals (Levings & Franks 1982, Kaspari 1993, Carson et al., chapter xxx), while fungal pathogens may prevent seeds accumulating in the soil (Alvarez-Buylla & Martínez-Ramos 1990, Dalling et al. 1998a). As a consequence, seedling recruitment may be largely uncoupled from seed abundance, or at least reflect an interaction between seed abundance and substrate favorability, as been found in a north temperate forest community (LePage et al. 2000).

To determine the relationship between seed abundance and seedling recruitment, Dalling et al. (2002) compared predicted seed rain densities to observed seedling recruitment patterns in natural tree fall gaps. Seed rain densities in gaps were predicted using data on seed captures to traps in conjunction with information on the size and location of potential seed sources to parameterize a seed dispersal model (for more information on this approach see Ribbens et al. 1994, Clark et al. 1998, Nathan & Muller-Landau 2000). We have confidence in the seed rain predictions for wind and ballistically dispersed species, as fits of predicted against actual seed counts in traps were good ($r^2 = 0.49-0.87$; $n=6$ species). However, predictions for animal dispersed species may be poor because model fits were weak for these species ($r^2 = 0.11-0.44$; $n=7$ species; Dalling et al. 2002). The low predictive power of dispersal models for animal-dispersed species using seed trap data is consistent with observations that large birds and mammals frequently carry seeds several hundred meters and that seeds are often secondarily dispersed from initial aggregations (e.g. Clark et al. 1998, Wehncke et al. 2003).

Next, Dalling et al. (2002) compared the ability of models with and without parameters for estimated seed rain to predict observed seedling abundance in the gaps. In the first (null) model, the number of seedling recruits per species in a gap was assumed to be proportional to the area potentially colonizable to seedlings. The expected seedling number per gap in this model was calculated by dividing the total seedling number per species in all gaps by the total area of all gaps. In subsequent models, seedling abundance was fitted as either a linear or non-linear (i.e. density-dependent) function of the

predicted seed rain to the gap. Models were compared using the Akaike Information Criterion (for more details see Dalling et al. 2002).

Comparison of the models showed that the abundance of seed rain did affect the probability of seedling recruitment, at least for some pioneers. Overall, models incorporating seed rain improved predictions of seedling recruitment over the null model for 8 of 14 pioneer species. Variation in how well recruitment models fit the seedling abundance data in part reflected the fit of dispersal functions, but also reflected the commonness of adult trees in the plot, and the proximity of seed sources to gaps (Fig. 1). Large *Jacaranda* trees are common in the plot, and most gaps contain at least a few seedlings of this species. In contrast, the fit for a rarer species, *Cordia*, reflects the presence of a single gap with high estimated seed rain. For *Croton*, another common pioneer species, the recruitment model fitted surprisingly poorly despite a high confidence in the dispersal function. *Croton* seeds are ballistically dispersed, land close to the plant and may be secondarily dispersed a few meters more by ants. For three gaps that lacked adult *Croton* trees within 30 m, seedling recruit abundance was an order of magnitude higher than estimated annual seed rain (Fig. 1). For this species we suspect that seedling recruitment may reflect many years of accumulation of viable seeds in the seed bank.

Can long-term seed persistence compensate for limited dispersal in space?

In addition to annual seed rain, recruitment patterns may also reflect contributions from seeds that persist for many years in the soil. Although most pioneers are known to form soil seed banks (e.g. Guevara Sada & Gómez-Pompa 1972, Putz & Appanah 1987), little is known about the time scale of seed persistence for tropical pioneers, or the relative contributions of buried seeds versus seed rain for recruitment in gaps. Direct studies of seed persistence in the soil have used mesh bags to bury seeds several centimeters below the soil surface. These studies show that the majority of pioneer species retain some seed viability over two years (e.g., Perez-Nasser & Vázquez-Yanes 1986, Hopkins & Graham 1987, Dalling et al. 1997). Comparisons of annual seed rain inputs with soil seed bank densities in Costa Rican cloud forest also suggests that seed persistence over five years or more is common (Murray & Garcia 2002). On BCI, direct measurements of seed age using ^{14}C dating of seeds sieved from the soil has shown that viable seeds of three of the larger seeded pioneer species with thick seed coats (*Trema micrantha*, *Zanthoxylum eckmannii* and *Croton bilbergianus*) buried at depths of < 3 cm below the soil surface can be > 30 years old (J. Dalling and T. Brown, unpublished data).

In situ studies of seed persistence in the soil, however, may over-estimate the contribution of the seed bank to seedling recruitment. This is because probabilities of successfully ‘entering’ and ‘leaving’ the seed bank are quite low (Williams-Linera 1990, Kennedy & Swaine 1992, Dalling & Hubbell 2002). Seeds dispersed onto the soil surface are especially susceptible to seed predation. Rates of seed removal by ants (and rodents for larger seeds) are very high in lowland tropical forests (e.g. Horvitz & Schemske 1986, Alvarez-Buylla & Martínez-Ramos 1990, Kaspari 1993, Fornara & Dalling 2005), with

most seeds likely to be consumed (Levey & Byrne 1993). These high initial predation rates may explain the large discrepancy between estimated seed rain and soil seed bank densities. For two small-seeded pioneer species on BCI, *Cecropia insignis* and *Miconia argentea*, only 2 % and 23 % respectively of annual seed rain became incorporated into the seed bank (Dalling et al. 1998a).

Evidently, a direct evaluation of the contribution of persistent seeds to pioneer recruitment success would be difficult because this would require long-term data on seed survivorship and fate. We therefore built a spatially explicit simulation model to examine the potential consequences of seed persistence for recruitment success, and the interactions between persistence and other life-history traits. The model allows us to simulate seed dispersal, gap formation, and recruitment for a 1000m X 500m area. We used the model to explore the impact on recruitment success and population growth rate of species-specific parameters for fecundity, dispersal, seed persistence, and germination rates in gaps. Although seed burial experiments and ¹⁴C dating studies have provided estimates of seed longevity, the exact survivorship curves for buried seeds are not adequately known. In the simulations described here we derived hypothetical seed survivorship curves whose functional form was based on a model used to describe the loss of viability of seeds stored in constant conditions (Ellis and Roberts 1980, see also Lonsdale 1988). This model assumes that seed mortality is normally distributed in time, and yields a type I survivorship curve, in which survivorship rate decreases with seed age. Here we use the model to explore how traits for dispersal and persistence interact to affect recruitment by comparing three hypothetical species with contrasting dispersal characteristics and by varying seed persistence from <1 year to about 20 years. Adult densities, fecundities, adult mortality rates, probabilities of incorporation into seed banks, and rates of germination in gaps also affect recruitment rates and were therefore kept constant in these simulations.

Dispersal functions were chosen to match those of two pioneer species on BCI – *Croton bilbergianus* [Euphorbiaceae], with ballistically dispersed seeds and an *aggregated* dispersal kernel (median dispersal distance=2.2m), and *Jacaranda copaia* [Bignoniaceae], with wind dispersed seeds and relatively *widespread* dispersal (median=21.2m) (Fig. 2). To investigate gap colonization under these contrasting dispersal scenarios, we simulated gap formation and closure based on empirical data from the BCI 50 ha plot, maintaining about 5% of the forest area under gaps at all times. Gap sizes varied from 25m² through 625m², with the size distribution of gaps declining as a power law of gap size (Hubbell et al. 1999, Schnitzer et al. 2000).

We found that gap colonization rates were substantially lower under aggregated dispersal (such as in *Croton*), compared to widespread dispersal (such as in *Jacaranda*). Under widespread dispersal, increasing seed persistence resulted in a rapid increase in gap colonization, but it tended to asymptote at longer seed persistence. Under highly aggregated dispersal as in *Croton*, the functional form of the relationship between seed persistence and gap colonization success was similar to that of *Jacaranda* but the initial increase was shallower and it did not saturate over the time-scale of our simulations (Fig. 3). Gap colonization success was, however, far lower under aggregated dispersal and

seed persistence alone could not compensate for limited dispersal (Fig. 3). Although aggregated seed dispersal results in lower gap colonization rates, overall seedling recruitment rates can still match those for more widely dispersing species if high-density clumps of seeds encounter gaps at a sufficient rate. We examined recruitment success by computing total life-time reproduction of individuals under the two dispersal scenarios for different levels of seed persistence. Since adult densities and fecundities were considered equal for the two species, the same numbers of seeds were dispersed each year by each species in our model, and the same per-seed recruitment probabilities were applied in gaps. Results from our simulations show that long-term mean recruitment rates increased with an increase in seed persistence but surprisingly, were statistically indistinguishable between the two dispersal scenarios at all levels of seed persistence considered (Fig. 4). Increasing seed persistence in the soil seed bank thus led to a general increase in long-term mean recruitment rates independent of dispersal.

Recruitment rates were, however, much more variable from year to year under aggregated dispersal compared to widespread dispersal (Fig. 4). This was due to the differences in spatial variation in seed densities between the two dispersal scenarios. Distributions of seed densities in quadrats were much more skewed for aggregated dispersal compared to widespread dispersal, so although recruitment rates were often low with aggregated dispersal, pulses of high recruitment were observed when light gaps occurred in quadrats with high densities of seeds. Increased spatial variation in seed densities therefore led to greater inter-annual fluctuations in recruitment, but as our simulations also show, long-term mean recruitment rates were similar for the two dispersal scenarios. This illustrates one potential way in which recruitment success can be equalized for species with different life histories, but also underlines the importance of spatial and temporal scales in understanding coexistence among pioneer species.

Seed limitation in context

We have drawn attention to how the frequency and nature of gap disturbances could drive the evolution of pioneer species life histories and to the potential importance of seed limitation for their coexistence. However, while steady-state seed limitation can help maintain diversity, species may occasionally escape seed limitation when individuals become sufficiently abundant to saturate recruitment sites. For pioneers, which generally occur at low adult population densities, escaping seed limitation is probably rare except perhaps when windstorms or landslides open large areas that favor the recruitment of one or a few species. Shade-tolerant trees with seedlings that persist for years in the forest understory, may more frequently overcome recruitment limitation. Wright (2002) describes the case of *Trichilia tuberculata*, a relatively large-seeded strongly shade-tolerant tree species that in years of heavy seed set recruits seedlings into the majority of seedling plots monitored. Density-dependent mortality is important in regulating population growth in these species, both in temperate and tropical forest (Harms et al. 2000, HilleRisLambers et al. 2002, Carson et al., chapter xxx).

Initial gap colonization patterns are also unlikely to be the sole determinant of adult distribution patterns. Variation in gap characteristics, coupled with constraints imposed on the ability of species to simultaneously disperse and establish at recruitment sites also provides opportunities for species to coexist through niche differentiation (Kitajima and Poorter, chapter xxx). The substantial variation in seed mass among pioneers reflects this constraint (Muller-Landau, chapter xxx). Larger seeded pioneers are able to establish at a wider range of microsites than small seeded species, while small-seeded species reach more of the rare microsites they need because of their greater fecundity (Dalling et al. 1998b, Dalling & Hubbell 2002). A similar colonization-establishment trade-off also operates for temperate grassland pioneer communities (Turnbull et al. 2005).

A second axis of niche differentiation is important for pioneer species once seedlings outgrow their seed reserves. Growth rates of seedlings a few months old are uncorrelated with seed mass but strongly positively correlated with mortality rate. This correlation reflects two general trade-offs: firstly, between investment in growth versus defence against herbivores (Kitajima 1994, Dalling et al. 1998b, Dalling & Hubbell 2002), and secondly between growth and susceptibility to drought-related mortality during the dry season (Pearson et al. 2003). Fast-growing species are therefore less likely to survive in gaps but more likely to reach reproductive size before a gap closes and may potentially shade-out slower growing competitors. Fast-growing species are also known to require larger gap sizes (Brokaw 1987), which may reflect greater opportunities to escape herbivory when growth rates are high.

Conclusions

We proposed that seed limitation should be particularly strong for pioneer species given their low population densities and the infrequency with which their recruitment sites become available. Evidence from seed trap data from BCI shows that seed limitation is strong for most pioneers, with only a few wind-dispersed species producing sufficient seeds that are widely enough dispersed to reach >90 % of seed traps over two consecutive years of seed production. Long-term persistence of viable seeds in the soil seed bank can help compensate for strong seed limitation, but as our simulations show, gap colonization rates are still poor with aggregated dispersal. Further, theoretical studies seem to indicate that long-term seed persistence is unlikely to be selected for in perennial species due to the fitness cost incurred by extended generation time (Rees 1994). Nevertheless, there is direct evidence that seeds of some tropical pioneer species remain viable for decades in the soil seed bank. It is therefore unclear whether long-term seed persistence is a significant axis of niche differentiation among tropical pioneer species. Species with strong seed limitation are nevertheless successful in the BCI forest. The most seed-limited species, *Croton billbergianus*, with low fecundity and short-distance dispersal has among the highest population density in this functional group. The ability for larger-seeded pioneers to maintain populations in this forest indicates that post-dispersal processes must be important in determining recruitment patterns. We have shown that seedling distribution patterns reflect seed dispersal patterns for some species but have not examined the legacy left by dispersal on adult distribution patterns. Future work now

awaits the development of a complete recruitment model for pioneers that includes dispersal, seed persistence and the growth and mortality of seedlings to adulthood. This will provide the framework now needed to explore how variation in seed production, dispersal, and persistence affect species coexistence.

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FIGURE LEGENDS:

Figure 1. Plots of seedling number per gap against the expected seed rain to each gap (log scale) for three pioneer species *Cordia alliodora*, *Jacaranda copaia* and *Croton billbergianus*. Seedling data are from complete censuses of 36 tree fall gaps on the BCI 50 ha plot (Dalling et al. 1998b). Seed rain to gap was estimated using a seed dispersal model (Dalling et al. 2002). The fitted curve represents the density-independent expectation for seedling number per gap, where seedling number is proportional to the expected seed rain times the seed-seedling transition probability (calculated from all 36 gaps combined). Redrawn from Dalling et al. (2002).

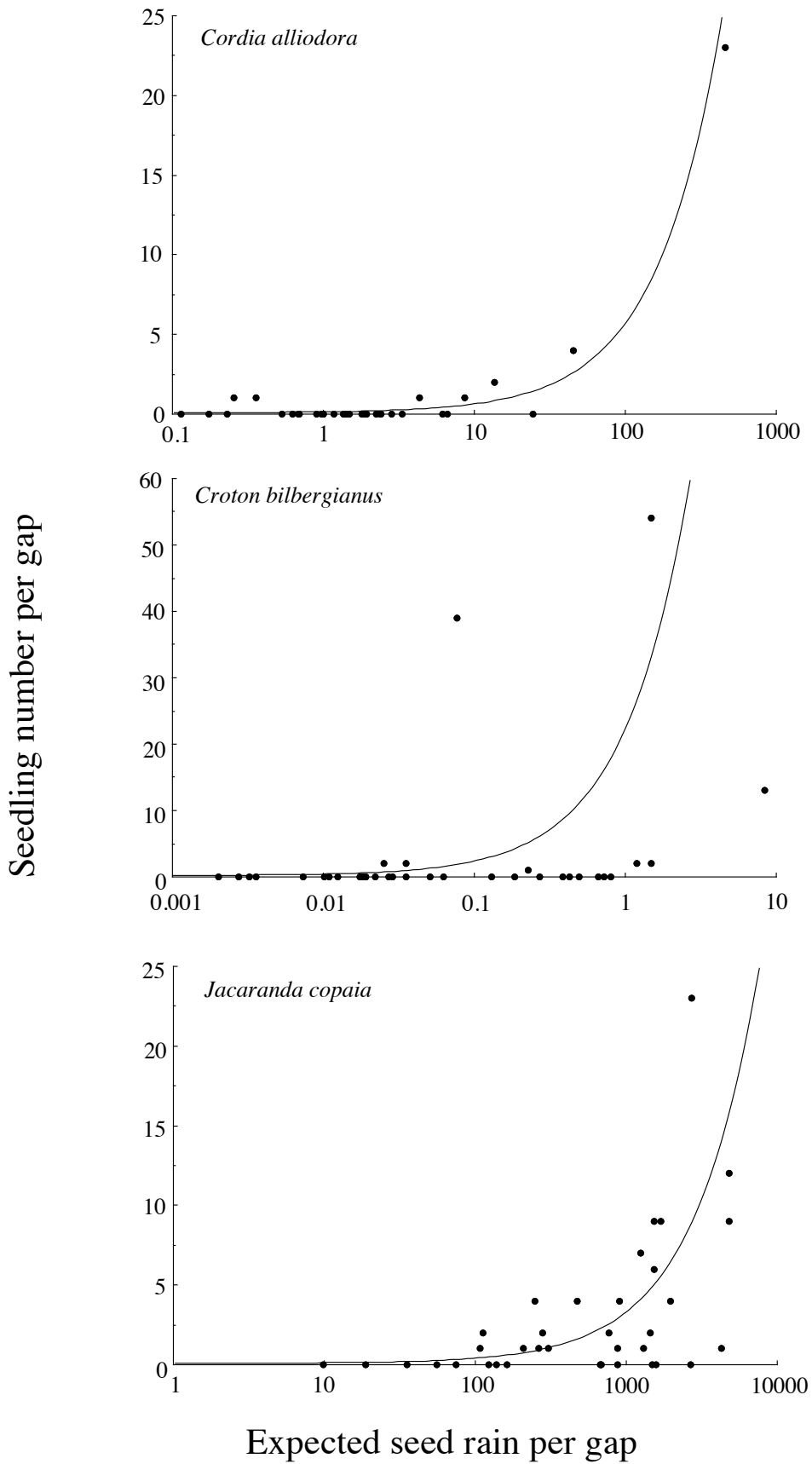
Figure 2. Cumulative probability density curves for the two-parameter 2Dt dispersal function for *Croton billbergianus* ($p=0.73$, $u=2.9$) and *Jacaranda copaia* ($p=0.81$, $u=328.8$). In *Croton* 99.9% of the seeds fall within 194m of the parent tree, while that distance for *Jacaranda* is over 1000m. Dispersal parameter estimates from Dalling et al. (2002).

Figure 3. The percentage (± 1 standard deviation) of gaps that receive at least 1 seed/m² of gap area (mean density). Under aggregated dispersal gap colonization rates remain poor even if seeds are able to persist for a long time. Simulations were carried out on a 1000m X 500m grid area with 5mX5m quadrats. Seeds were dispersed from 50 randomly distributed adult trees, each dispersing about 8600 seeds per year. The total number of canopy gaps simulated was 419, over 60% of which were $\leq 50\text{m}^2$ in area, while 3 gaps were about 650m^2 in area.

Figure 4. Long-term, plot-wide mean (\pm standard error) net reproductive rate at different levels of seed persistence for two different dispersal scenarios. The values are the number of germinating seedlings per adult trees during its lifetime. Adult density and seed production parameters are the same as those used in Fig. 3. The per-seed probability of germination and establishment (seedling recruitment) was set to about 0.03 for both dispersal types. Mean seedling recruitment rates increase with seed persistence, but are evidently not different between the two dispersal scenarios. Inter-annual fluctuations are, however, greater under aggregated dispersal.

Table 1: Estimated median dispersal distances, fecundity and seed, source, and dispersal limitation for pioneer species varying in dispersal mode, seed mass, and abundance on the BCI 50 ha forest dynamics plot. For each species, n is the number of reproductive-sized individuals in the plot. Seed, source and dispersal limitation are defined in the text, and are mean captures to two hundred 0.5 m² traps calculated over twelve years. Mean values for limitation metrics are presented for one or two consecutive years. Seed bank data provides the longest reported period of seed persistence in the soil. Data are presented for 11 of 24 pioneer taxa commonly encountered in treefall gaps on BCI (Dalling et al. 1998), and for which sufficient seed captures to traps allow dispersal parameters to be calculated. Data from Dalling et al. (1997, 2002) and Dalling and Brown, unpublished data.

| | Seed mass (mg) | n | Median Dispersal (m) | Fecundity Seeds/cm ² | Seed bank years | Seed limitation | | Source limitation | | Dispersal limitation | |
|--------------------------------|----------------|------|----------------------|---------------------------------|-----------------|-----------------|------|-------------------|-------|----------------------|------|
| | | | | | | 1 yr | 2 yr | 1 yr | 2 yr | 1 yr | 2 yr |
| Wind dispersal: | | | | | | | | | | | |
| <i>Alseis blackiana</i> | 0.1 | 784 | 3.2 | 907.2 | <2 | 0.68 | 0.47 | <0.01 | <0.01 | 0.68 | 0.47 |
| <i>Cordia alliodora</i> | 12.5 | 54 | 7.0 | 18.1 | 0 | 0.90 | 0.86 | 0.41 | 0.16 | 0.82 | 0.83 |
| <i>Jacaranda copaia</i> | 4.7 | 193 | 21.2 | 67.3 | <2 | 0.39 | 0.03 | 0.22 | <0.01 | 0.25 | 0.03 |
| <i>Luehea seemannii</i> | 1.9 | 64 | 8.2 | 273.7 | <2 | 0.24 | 0.06 | <0.01 | <0.01 | 0.26 | 0.06 |
| <i>Terminalia amazonia</i> | 3.8 | 20 | 83.1 | 61.3 | N/A | 0.29 | 0.10 | 0.10 | 0.01 | 0.21 | 0.09 |
| Animal dispersal: | | | | | | | | | | | |
| <i>Alchornea costaricensis</i> | 38.5 | 135 | 1.3 | 33.5 | N/A | 0.96 | 0.93 | 0.01 | <0.01 | 0.96 | 0.93 |
| <i>Apeiba aspera</i> | 14.2 | 141 | 3.2 | 7.8 | >2 | 0.96 | 0.94 | 0.19 | 0.04 | 0.95 | 0.94 |
| <i>Cecropia insignis</i> | 0.5 | 182 | 0.8 | 225.6 | <2 | 0.93 | 0.89 | 0.23 | 0.17 | 0.77 | 0.73 |
| <i>Palicourea guianensis</i> | 14.3 | 1055 | 5.6 | 50.5 | N/A | 0.95 | 0.91 | 0.74 | 0.55 | 0.52 | 0.67 |
| <i>Zanthoxylum</i> spp. | 11-36 | 108 | 0.8 | 22.7 | >30 | 0.92 | 0.86 | 0.50 | 0.25 | 0.70 | 0.81 |
| Ballistic dispersal: | | | | | | | | | | | |
| <i>Croton bilbergianus</i> | 24.0 | 367 | 2.2 | 2.6 | >40 | 0.99 | 0.99 | 0.94 | 0.89 | 0.41 | 0.61 |



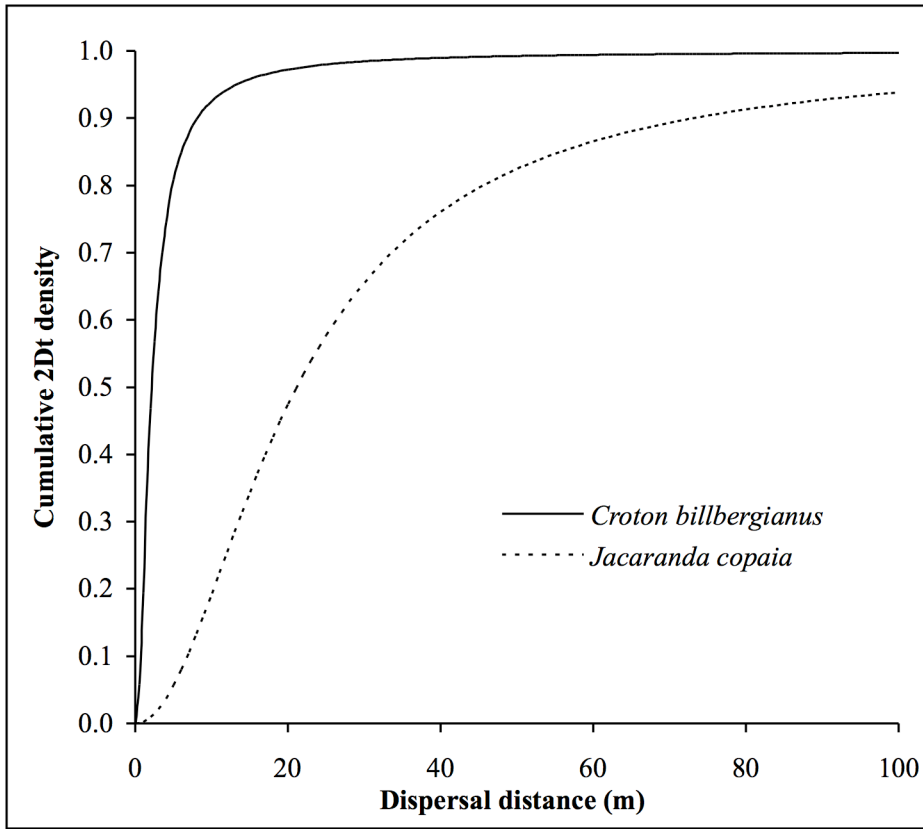


Fig. 2

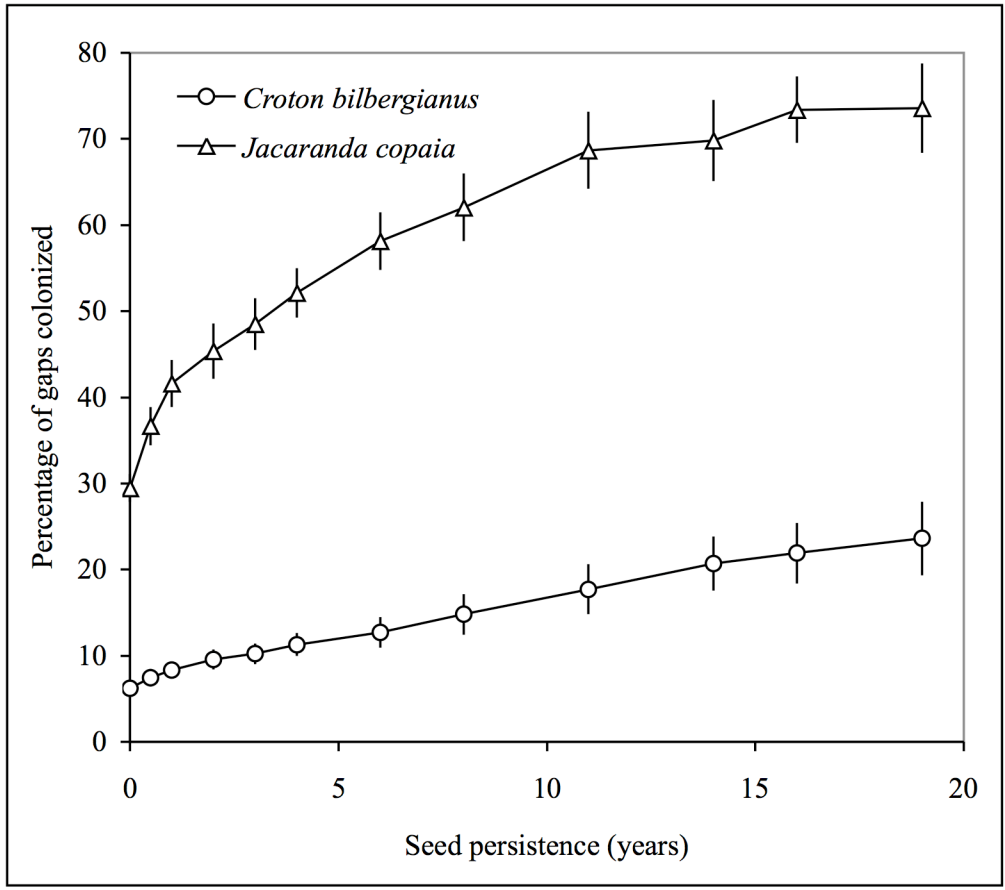


Fig. 3

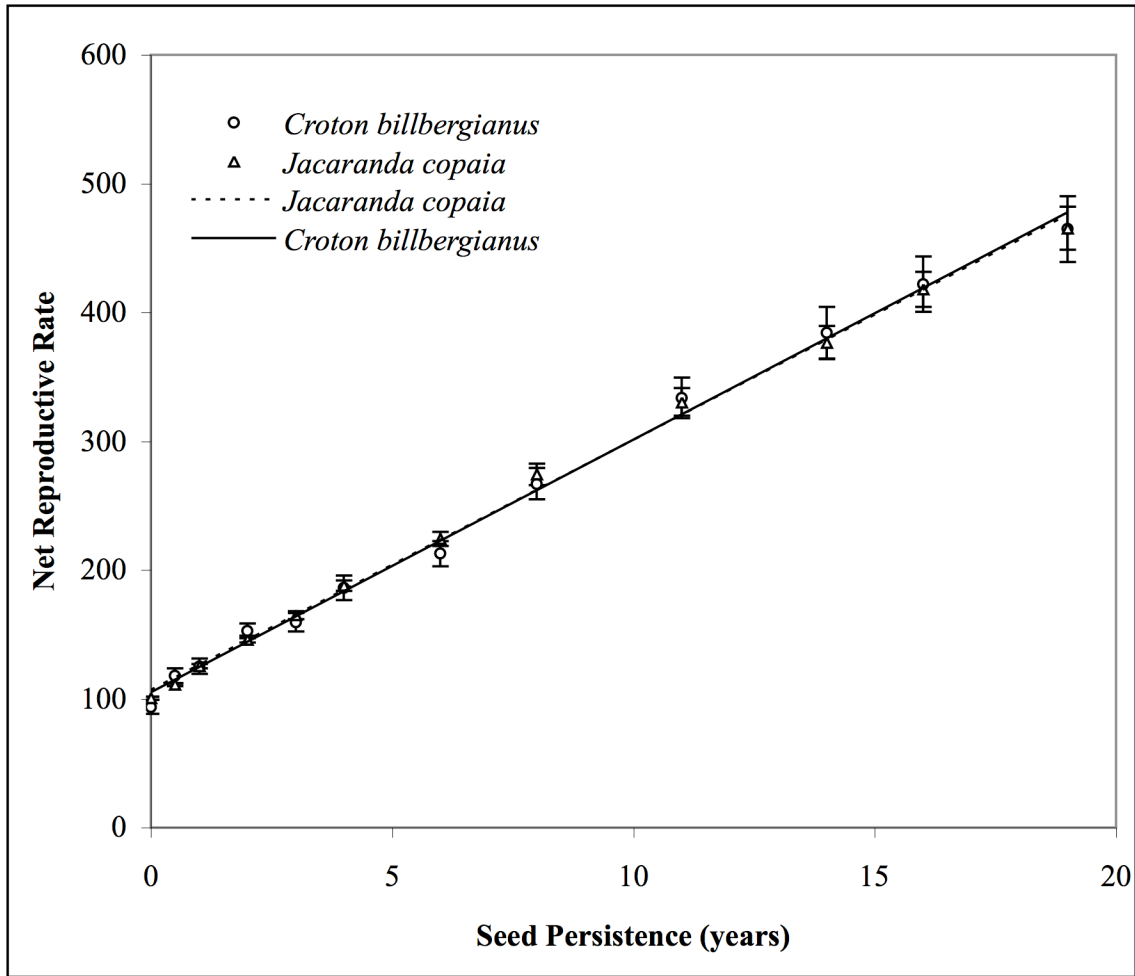


Fig. 4