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Are Plant Populations Seed Limited? A Critique and Meta-Analysis of Seed Addition Experiments

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ABSTRACT: We examine the relative importance of processes that underlie plant population abundance and distribution. Two opposing views dominate the field. One posits that the ability to establish at a site is determined by the availability of suitable microsites (establishment limitation), while the second asserts that recruitment is limited by the availability of seeds (seed limitation). An underlying problem is that establishment and seed limitation are typically viewed as mutually exclusive. We conducted a meta-analysis of seed addition experiments to assess the relative strength of establishment and seed limitation to seedling recruitment. We asked (1) To what degree are populations seed and establishment limited? (2) Under what conditions (e.g., habitats and life-history traits) are species more or less limited by each? (3) How can seed addition studies be better designed to enhance our understanding of plant recruitment? We found that, in keeping with previous studies, most species are seed limited. However, the effects of seed addition are typically small, and most added seeds fail to recruit to the seedling stage. As a result, establishment limitation is stronger than seed limitation. Seed limitation was greater for large-seeded species, species in disturbed microsites, and species with relatively short-lived seed banks. Most seed addition experiments cannot assess the relationship between number of seeds added and number of subsequent recruits. This shortcoming can be overcome by increasing the number and range of seed addition treatments.

Keywords: seed limitation, establishment limitation, meta-analysis, seed addition, seed mass.

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Identifying mechanisms that determine the abundance and distribution of plant and animal populations is a central challenge of ecology (Tilman 1997; Levine and Rees 2002; Osenberg et al. 2002; Coomes and Grubb 2003; Turnbull et al. 2005). The failure of a species to recruit at a given site can result from processes that occur at practically any life-history stage and include propagule production and transportation, competition, predation, and herbivory. Despite this range of disparate processes and stages, several of the best-known models of species coexistence are focused on propagule availability in space or time (Sale 1982; Tilman 1994; Hurt and Pacala 1995; Pacala and Levin 1997; Coomes and Grubb 2003). These models are bolstered by empirical studies across diverse systems, demonstrating that early life-history events (e.g., during the transition from seed to seedling or from larva to juvenile fish) can be bottlenecks for recruitment (Persson and Greenberg 1990; Chambers and MacMahon 1994; Fenner 2000; Doherty 2002). Indeed, there is growing consensus that processes underlying mortality at early stages in the life cycle may disproportionately influence the structure, dynamics, and species composition of communities. This consensus is particularly evident in studies of plant communities. Two processes thought to limit plant recruitment at early stages in the plant life cycle are seed limitation and establishment limitation.

Seed-limited populations have fewer individuals than possible because seeds fail to arrive at saturating densities at all potential recruitment sites (Eriksson and Ehrlén 1992; Nathan and Muller-Landau 2000; Turnbull et al. 2000; Svenning and Wright 2005). Seed limitation can be partitioned into two processes that restrict the ability of seeds to reach recruitment sites: (1) "source limitation," that is, not enough seeds are produced to saturate potential recruitment sites even if the seeds could reach all sites, and (2) "dispersal limitation," that is, not enough seeds reach all recruitment sites, even though enough are produced to saturate sites (Clark et al. 1998; Schupp et al. 2002).

"Establishment limitation" (also called microsite limitation) occurs when plant population size is constrained by the number and quality of available sites for establishment, not by the number of seeds (Clark et al. 1998; Nathan and Muller-Landau 2000). Establishment limitation can be partitioned into several processes that occur between seed deposition and recruitment into the adult population (Clark et al. 1998; Muller-Landau et al. 2002). In this article, we focus on seedling recruitment, because it represents a key stage of establishment limitation. Specifically, we examine the time between seed arrival at the soil surface and the census of seedlings after the first season of growth. Establishment limitation is thus determined by factors that constrain the recruitment of new individuals into the seedling population, regardless of the number of seeds that arrive at a site. Seed and establishment limitation are analogous to supply limitation and postsettlement mortality, as developed in the literature on reef fish ecology (Schmitt et al. 1999; Doherty 2002; Osenberg et al. 2002).

Because both seed and establishment limitation can limit plant recruitment, both are likely to influence the abundance and distribution of species (Hubbell et al. 1999; Juenger and Bergelson 2000; Zobel et al. 2000; Dalling and Hubbell 2002; Levine and Rees 2002). At issue is their relative importance. At stake are competing theories of community composition (Coomes and Grubb 2003; Turnbull et al. 2005). If establishment limitation dominates, then the abundance and distribution of a species is readily framed as an issue of competitive ability, regeneration niches, and the relative abundance and quality of microsites (Grubb 1977; Turnbull et al. 2000; Muller-Landau et al. 2002; Pearson et al. 2002). If seed limitation dominates, then the abundance and distribution of a species are better viewed in the context of a lottery system, where few sites are "won" by the best possible competitor and most are won "by default"—recruits are drawn at random from the seeds that happen to arrive at a site (Cornell and Lawton 1992; Hubbell 2001; see also Sale 1982). Thus, empirical studies on the relative importance of seed and establishment limitation can guide theoretical models of community dynamics.

The most direct means of testing the relative importance of seed and establishment limitation is to conduct seed addition experiments (Turnbull et al. 2000, 2005; Muller-Landau et al. 2002). Seeds are added to plots, and the numbers of seedlings that emerge are compared to those in control plots to which no seeds have been added. If no increase in seedling density is observed after seed addition, one can conclude that recruitment opportunities for that species are not seed limited. Instead, the number of microsites available or the suitability of those sites for seedlings limits recruitment, and establishment limitation is more important for that species. If, on the other hand, an increase in seedling density is observed after seed addition, one can conclude that limitations on species presence or abundance are at least partially attributable to seed availability (although its importance relative to factors that limit recruitment at later life-history stages cannot be evaluated without longer-term study). Such experiments, by decreasing the extent of seed limitation and isolating the emergence and early postemergence stages of establishment limitation, offer a conservative estimate of the strength of establishment limitation relative to seed limitation in plant populations. The relative importance of establishment limitation would be expected to increase if additional mortality at later life-history stages were included.

The difficulty in interpreting results of seed addition experiments lies in situations in which seed limitation is detected (i.e., one finds a statistically detectable increase in seedlings after seed addition). In large part, interpretation depends on how the experiment was framed. If the underlying goal was to determine why a given species does not occur at a particular site, then even a single seedling demonstrates seed limitation. This goal is common among seed addition studies based on small plots; the response they document is local and the number of seedlings largely irrelevant (assuming that enough survive to establish a population). If, on the other hand, the underlying goal was to determine factors limiting population size or density, the number of seedlings becomes key to disentangling the relative strengths of seed and establishment limitation. In this scenario, detection of seed limitation is largely irrelevant; attention should focus on the magnitude of response rather than its presence or absence.

The magnitude of seed limitation is rarely considered in seed addition studies. For example, a review of seed addition experiments concluded that as many as 50% of all plant populations are seed limited (Turnbull et al. 2000). However, seed limitation was depicted dichotomously: either seed availability limited plant population size (i.e., there was a significant effect of seed augmentation) or it did not (i.e., the resulting P value was >0.05). A central theme of this article is that seed limitation is a continuous variable, potentially varying widely among species, habitats, life forms, plant characteristics, and seed sizes. Using P values to infer seed limitation not only dichotomizes this continuous scale but also confuses a statistical view of significance with the more appropriate biological view of overall effect (e.g., Osenberg et al. 1997). Indeed, effect sizes and P values derived from null hypothesis tests can give very different results (Osenberg et al. 2002).

Viewing seed limitation as a continuous variable provides a framework for evaluating the relative strength of seed and establishment limitation. In particular, one can

view seed and establishment limitation as being inversely related, occupying opposite ends of a gradient (Muller-Landau et al. 2002). By quantifying the position of a plant population along this gradient, one can judge the relative strength of seed and establishment limitation and determine the magnitude of each. For example, if 100 seeds are added to a plot and result in 100 emerged seedlings, the proportion of emerged seedlings to sown seeds is 1, and the population is strongly seed limited. If, on the other hand, 100 seeds are added and no new seedlings emerge, the proportion of additional emerged seedlings to added seeds is 0, and the population is strongly establishment limited, with no evidence of seed limitation. More typical and revealing are situations in which the proportion of added seeds that emerge is intermediate, indicating that populations are simultaneously limited by two factors but probably to different degrees.

We present a meta-analysis of seed augmentation experiments, with the goal of teasing apart the relative strengths of seed and establishment limitation for seedling recruitment. Because our focus is on factors that limit population size and density, we develop an effect size measure based on per seed return (i.e., change in seedling density/density of augmented seeds). We also use a second effect size to examine the absolute extent by which plant populations and species distributions are seed limited (i.e., the change in seedling density without correction for augmentation level). We then examine variation among studies in effect sizes to determine differences among them in the magnitude of seed and establishment limitation. We have three objectives. The first is to examine the degree to which plant populations are seed and establishment limited. The second is to determine under what conditions we might expect plant species to be most seed limited. Specifically, we test how life form, habitat, dispersal mode, plant characteristics, reproductive characteristics, seed bank persistence and density, and species origin (native or exotic) influence the degree of seed and establishment limitation. We evaluate the suggestion that seed limitation is more common in early successional habitats (Turnbull et al. 2000) by examining studies in which seeds were sown into disturbed and undisturbed plots, and we determine whether the positive relationship between seed limitation and seed size observed by Moles and Westoby (2002) is maintained when the magnitude of effect is considered. Our third objective is to use our results to inform future studies based on seed addition. Specifically, our examination of this literature revealed shortcomings of common experimental designs that greatly limit the interpretation of seed addition experiments. Thus, we conclude by suggesting improvements for the design of future studies.

Methods

Database

We searched for published studies in which seeds had been experimentally added to plots, regardless of why they had been added. We used a recent review of seed augmentation experiments (Turnbull et al. 2000) as our main source of references, but we also searched *Web of Science* (Thomson ISI 2004) for all articles published by the summer of 2004 that cited this review or included the keywords "seed sowing," "seed limitation," "seed augmentation," "germination," "seed introduction," or "seedling recruitment." When necessary, we contacted authors for information. In the process, we learned of several unpublished studies, which we included with permission.

Many studies were not included in our analysis because they failed to meet one or more of the following criteria. (1) Experiments were conducted in natural or seminatural settings (e.g., not in greenhouses). (2) Estimates of seedling emergence/early postemergence establishment for a single plant species for both treatment (seeds added) and control plots (no seeds added) were available. The only exceptions were studies that introduced seeds of species absent from the study site. We included these studies lacking true control plots if the author explicitly stated that the species was not present in nearby sites. In these cases, seedling emergence under ambient conditions (control) was assumed to be zero. (3) Sample sizes, replication, means, and variance were appropriately reported (i.e., no pseudoreplication) or were made available by authors.

When studies monitored plots for more than 1 year, we restricted our analyses to the end of the first growing season. The sole exception to this rule was the inclusion of the study by Edwards and Crawley (1999), which quantified seedling density after 15 months (450 days). Thus, our effect sizes apply only to first-season seedlings. The period of time between seed sowing and first-season seedling censuses varied among studies (ranging from 14 to 450 days, with a mean of 292 days); we assumed that investigators censused first-season seedlings at the most appropriate time for each species.

From all studies that met our criteria, we extracted (1) mean density and variance of recruited seedlings in treatment and control plots, (2) number of replicate plots, (3) number of seeds added in each plot, and (4) grouping variables thought to influence the degree of seed limitation. Grouping variables included characteristics of the study site (habitat and geographical zone), characteristics of the focal species (plant life form, maximum plant height, plant longevity, seed mass, average fecundity, dispersal mechanism, presence/absence of seed bank, seed bank density, seed bank longevity, time to first flowering, and/or seedling growth rate), and characteristics of the experimental treat-

ments (removal of vegetation, sterilization of soil, or turnover of the soil; table 1). These environmental and plant characteristics potentially influence seedling emergence and, presumably, the strength of seed limitation (Turnbull et al. 2000). If studies did not provide information on grouping variables, we gathered these data from outside references whenever possible (Grime et al. 1988; Thompson et al. 1997; Royal Botanic Gardens 2002; Moles et al. 2004; USDA NRCS 2004; University of York 2005).

Meta-Analysis

Meta-analysis involves two key steps. First, results of each study are used to calculate a biologically relevant effect size, often a measure of the disparity of responses between a control and a treatment group (Osenberg et al. 1999). Second, effect sizes are statistically summarized to estimate a weighted average for the sample of studies (average effect size) and to test hypotheses (e.g., Gurevitch et al. 1992).

Definition of Effect Sizes and Weighting Factors. Although we considered several potential measures of effect size for seed limitation, we chose the metric that most closely matched our question of interest and the design of the seed-sowing experiments (app. A, in the online edition of the *American Naturalist,* provides a theoretical discussion and empirical evaluation of alternative effect size metrics). Our metric of seed limitation, the per seed response, was the difference between seedling densities in treatment and control plots, standardized by the number of seeds added to treatment plots,

$$E_i = \frac{R_{\text{exp},i} - R_{\text{cont},i}}{A_i}, \tag{1}$$

where E_i is the effect size, $R_{\text{exp},i}$ is the average density of recruits (seedlings) in experimental plots, $R_{\text{cont},i}$ is the average density of recruits in control plots, and A_i is the density of seeds added to treatment (seed augmentation) plots in the ith study. The density A_i varied by more than an order of magnitude among studies and necessitated the standardization in equation (1). Our effect size can be interpreted as the number of recruits obtained per sown seed. In theory, E should vary between 0 and 1, unless density effects are so strong that total recruitment is reduced by the addition of more seeds (i.e., if there is overcompensation). Because recruit densities are estimated and background seed rain is an uncontrolled variable, estimated effect sizes also could be <0 or >1 because of sampling error.

Meta-analysis combines effect sizes obtained from a collection of studies, giving greater weight to studies with higher precision. In general,

$$\overline{E} = \frac{\sum_{i=1}^n w_i E_i}{\sum_{i=1}^n w_i}, \tag{2}$$

where $\overline{E}$ is the average effect size and w_i is the weight associated with the ith effect size. Parametric approaches use weights that are inversely related to the variance in effect size for a given study (Rosenberg et al. 2000). In our data set, however, many studies had small numbers of replicate plots and sown seeds, which often resulted in no emergence ($R_{\text{exp}} = R_{\text{cont}} = 0$), a variance of 0, and a weight of infinity. For this reason, using the inverse of variance as the weight was impractical and likely not a good reflection of precision. Therefore, we used a weighted resampling procedure (with replacement) in MetaWin 2.0 (Rosenberg et al. 2000). Weights were based on the total number of seeds added to augmentation plots (across all replicates), which we assumed was approximately proportional to the precision of the estimated effect sizes; that is, we assumed that effect sizes were better estimated when more seeds were added and therefore the number of potential recruits was greater. Because we did not take a parametric approach based on true variance estimates, we could not subdivide within- and among-study sources of variation. Thus, we used

$$w_i = \sum_{x=1}^{X_i} N_{i,x}, \tag{3}$$

where $N_{i,x}$ is the number of seeds added to the xth replicate of the augmented treatment and X_i is the number of replicates in study i.

Some plant species were used in more than one study or were added at more than one seed density within a single study. To prevent species that were used in multiple studies from carrying more weight in the calculation of average effect sizes, we first estimated the effect size from each study and then averaged these effect sizes for each species, using equations (2) and (3) and the resampling procedure in MetaWin 2.0 (Rosenberg et al. 2000). We then derived a pooled weighting term reflecting that the averaged effect size was based on several studies (all with different levels of augmentation and replication),

$$w_j = \frac{K_j^2}{\sum_{i=1}^{K_j} (1/\sum_{x=1}^{X_{j,i}} N_{j,i,x})}, \tag{4}$$

where K_j is the number of effect sizes being pooled for species j, $N_{j,i,x}$ is the number of seeds added to the xth replicate of the ith study for species j, and $X_{j,i}$ is the number

Table 1: Comparison of seed limitation (per seed response) by grouping variables for undisturbed treatments, disturbed treatments, and the effect of disturbance on seed limitation

Grouping variables	Undisturbed (E_U)			Disturbed (E_D)			Disturbance (ΔE)			Description
	Q or R^2	df	P	Q or R^2	df	P	Q or R^2	df	P	
Categorical:										
Habitat[a]	10.149	2	.176	12.350	2	.146	1.986	1	.392	Habitat in which the study was conducted (intertidal, grassland, or forest)
Geographic zone[a]	.342	1	.538	2.530	1	.413	1.088	1	.514	Zone where study was conducted (midlatitudes or subtropical)
Dispersal mode[b]	1.415	4	.727	2.746	3	.788	5.269	2	.246	Typical method of seed dispersal (unassisted, ballistic, wind, water, or animal)
Plant life form[a]	1.354	3	.687	9.365	3	.407	3.629	3	.683	Tree, perennial herb, annual herb, or perennial grass
Existence of seed bank[b]	.815	1	.245	.642	1	.645	5.438	1	.075	"Seed bank" defined as seeds remaining in the ground for longer than 1 year
Plant longevity[a]	.012	1	.914	6.081	1	.191	1.609	1	.426	Perennial or annual
Plant life span[c]	.845	3	.729	3.555	2	.560	5.840	2	.219	<1, 1–10, 11–100, >100 years
Seed origin[a]	10.604	1	.005	3.093	1	.359	.079	1	.868	Native or exotic
Seed presence[a]	7.777	1	.007	.986	1	.610	.167	1	.807	"Seed addition" refers to the sowing of seeds in microhabitats where the species is known to be present; "introduction" is the sowing of seeds of a species that may be native but is not present at the time of sowing
Seed size category[b]	9.915	5	.044	66.407	5	.002	33.926	5	.010	Seed mass categories: 0–.20, .21–.50, .51–1.0, 1.01–2.00, 2.01–10.0, >10.01 mg
Continuous:										
Seed augmentation density (seeds m^{-2})[a]	-5.754×10^{-3}	126	.687	2.403×10^{-2}	92	.074	2.150×10^{-2}	74	.092	Density of seeds sown in treatment plots
Duration of study (days)[a]	-4.348×10^{-4}	126	.05	6.617×10^{-5}	92	.838	-1.782×10^{-5}	74	.446	Days for which seeds were monitored for recruitment in studies
Maximum plant height (m)[b]	2.110×10^{-2}	119	.304	-1.473×10^{-2}	86	.503	1.312×10^{-3}	70	.962	
Seedling growth rate (day^{-1})[c]	-7.384×10^{-1}	36	.262	-1.565×10^{-1}	21	.607	-2.667×10^{-3}	19	.990	
Average first flowering (years)[c]	-1.815×10^{-2}	22	.606	-2.287×10^{-2}	16	.844	-9.346×10^{-3}	15	.811	Age at which plants typically flower for the first time
Average fecundity (seeds plant^{-1})[c]	4.178×10^{-3}	74	.760	-2.409×10^{-2}	62	.276	-1.391×10^{-2}	54	.424	
Average seed bank density (seeds m^{-2})[c]	-2.138×10^{-2}	73	.313	-5.563×10^{-5}	50	.999	3.011×10^{-4}	43	.992	
Average seed bank longevity (years)[c]	-1.160×10^{-2}	38	.092	-6.682×10^{-3}	23	.640	-1.586×10^{-3}	21	.885	Number of years that seeds remain viable in the seed bank
Seed mass (mg)[b]	2.477×10^{-2}	120	.049	1.71×10^{-2}	84	.325	1.157×10^{-2}	70	.360	

Note: The test statistics are Q for categorical variables and R^2 for continuous variables (see "Summary Analyses"). All randomization tests were two sided, and therefore a P value of .025 indicates statistical significance at the 5% level. Footnotes indicate where data for the grouping variable were collected.

[a] Original article.

[b] Data extracted from original articles when possible but often supplemented by external sources.

[c] External sources.

of replicates in the ith study for species j. When sample sizes are equal, equation (4) reduces to $K_j X_j N_j$, or total augmentation across all studies for species j, which is comparable to the weighting term given in equation (3).

Absolute response effect size. Although E_i (eq. [1]) is the most appropriate effect size, given the available data (app. A), we also calculate the absolute response of the population to seed addition to better examine the degree by which seed limitation and establishment limitation limit the absolute extent of plant populations. The absolute response measures the absolute change in recruitment (seedling density) between the augmented (experimental) and control treatments,

$$E_{\text{abs},i} = (R_{\text{exp},i} - R_{\text{cont},i}), \qquad (5)$$

where $R_{\text{exp},i}$ and $R_{\text{cont},i}$ are the average densities of recruits in the experimental and control plots, respectively, in the ith study (see app. A for further discussion).

Summary Analyses. Studies were conducted under disturbed or undisturbed conditions and sometimes in both disturbed and undisturbed conditions. Therefore, we distinguish three types of effects: E_D, E_U, and ΔE. Disturbed conditions were created by removing vegetation or litter, turning the soil, or physically manipulating the plot in some other way. We took two approaches to analyzing these data. First, we examined patterns of seed limitation separately for seed augmentations done in disturbed and undisturbed settings. This yielded effect sizes in disturbed plots ($E_{D,i}$; i.e., seed limitation in disturbed plots for species i) and effect sizes in undisturbed plots ($E_{U,i}$). We then explored the relationships between the magnitude of seed limitation (i.e., using either $E_{D,i}$ or $E_{U,i}$) and the grouping variables (e.g., growth form or seed mass for species i), by examining the heterogeneity of effect sizes using Q statistics, which are essentially weighted sums of squares after a χ^2 distribution. The corresponding P value indicates whether the variance among effect sizes is greater than expected from chance. Weighted effect sizes and bias-corrected 95% confidence intervals (CIs) of seed limitation (eq. [1]) were estimated for categorical grouping variables using resampling methods with 10,000 iterations in MetaWin 2.0 (Rosenberg et al. 2000). For continuous grouping variables, we conducted weighted linear regressions to determine whether plant characteristics explained variation in the effect size of seed limitation. After examining plots of residuals, we used a logarithmic transformation on several of the plant characteristics to satisfy the assumptions of normality and homoscedasticity. We then regressed the plant characteristic against our estimate of effect size ($E_{D,i}$ or $E_{U,i}$), using randomization tests with 10,000 iterations to conduct significance tests. Regressions

were done with the R language (R Development Core Team 2005).

Because the species and studies in the disturbed and undisturbed data sets differed, it is problematic to infer the effect of disturbance on seed limitation by comparing the distributions of E_D and E_U. Instead, we took a second approach to directly evaluate the effect of disturbance on seed limitation. We used only the studies in which seeds of a single species were sown in both undisturbed and disturbed plots, and we defined the effect of disturbance on seed limitation for species i as

$$\Delta E_i = E_{D,i} - E_{U,i}, \qquad (6)$$

where $E_{D,i}$ and $E_{U,i}$ were calculated with equation (1). Note that ΔE will be negative if seed limitation is more severe in undisturbed plots and positive if seed limitation is more severe in disturbed plots. If seed limitation is independent of disturbance regime (i.e., equal in disturbed and undisturbed plots), then $\Delta E = 0$. Thus, ΔE can be small (close to 0) for a particular species even when seed limitation is strong (but comparable in magnitude) in the disturbed and undisturbed plots. In such a case, other characteristics of the plot or the species (but not disturbance per se) determine the magnitude of seed limitation.

To derive an appropriate weighting term for ΔE, we assumed that

$$\text{Var}(\Delta E_i) = \text{Var}(E_{D,i}) + \text{Var}(E_{U,i})$$
$$= \frac{c}{N_{D,i}} + \frac{c}{N_{U,i}} = \frac{c(N_{D,i} + N_{U,i})}{N_{D,i} N_{U,i}}, \qquad (7)$$

where c is a scaling term that relates the number of seeds sown and the resulting variances and $N_{D,i}$ and $N_{U,i}$ are the total numbers of seeds sown in the disturbed and undisturbed augmentation treatments for study i, respectively. Because parametric weighting factors should be inversely related to the variances, we defined a weighting term that was inversely proportional to the presumed variance (eq. [7]),

$$w_{\Delta,i} \frac{N_{D,i} N_{U,i}}{N_{D,i} + N_{U,i}}, \qquad (8)$$

where $w_{\Delta,i}$ is the weighting given to ΔE_i.

As described above, species that occurred more than once in the data set were combined into a single pooled effect size, and the pooled weighting term described above (eq. [3]) was calculated. A cumulative disturbed effect size was calculated in MetaWin 2.0, and differences in seed limitation among grouping variables were evaluated. Disturbed plots were considered significantly more (or less)

seed limited than undisturbed plots if the 95% CIs on ΔE did not overlap 0.

Results

Studies reported in 43 publications met all criteria for inclusion, yielding 798 effect sizes based on 159 species in 49 families. The most common reasons for exclusion of a study were lack of control plots and presence of multiple species of seeds sown together in treatment plots. Other studies were excluded because establishment or survival was not recorded until after the first growing season.

Seed Limitation in Undisturbed Plots

In most undisturbed environments tested, plant species were seed limited; adding seeds to a plot generally resulted in more seedlings than in plots where no seeds were added (fig. 1*A*). However, the average effect of seed limitation was small, with only 15 out of 100 seeds emerging as seedlings ($\overline{E}_U = 0.15$, 95% CI $= 0.111–0.195$). Assuming an inverse relationship between seed limitation and establishment limitation, this effect size indicates that establishment limitation, calculated as $1 - E$, more strongly limits emergence of seedlings than does seed limitation (0.85 vs. 0.15). Effect sizes of seed limitation for all species were relatively low: 68% of species had $E < 0.25$, 20% had $0.25 < E < 0.50$, and only 12% had $E > 0.50$ (app. B in the online edition of the *American Naturalist*).

Of the habitat and life-history characteristics that we examined, only seed origin, seed size, seed presence (seed augmentation vs. seed introduction), and the average seed bank longevity explained a significant portion of variation in seed limitation effect size (table 1; fig. 1*A*). Exotic species were more seed limited than native species ($P = .019$; fig. 1*A*). Similarly, native species that were introduced into an area where they naturally occurred but were not present during the study were more seed limited than native species whose seed densities were augmented by the researcher (table 1). There was an inverse relationship between the longevity of the seed bank and the strength of seed limitation ($P = .012$): species with seed banks of short duration were more seed limited than those with seed banks of longer duration (table 1). The strength of seed limitation was also significantly different among groups of species with different seed masses ($P = .002$; fig. 1*A*): species with larger seeds were more seed limited. Regression analysis identified a marginally significant positive relationship between seed mass and the degree of seed limitation, with a 3% increase in seed limitation per milligram increase in seed mass ($P = .049$; fig. 2*A*). The species with the largest seed (200 mg) was approximately 20 times more seed limited than the species with the smallest seed (0.02 mg).

To examine the possibility that study design influenced the magnitude of seed limitation, we also regressed E_U against duration of study and seed augmentation density (but see Osenberg et al. 1999). Neither of these factors significantly influenced E_U (table 1).

Seed Limitation in Disturbed Plots

Plant species were also significantly seed limited in disturbed plots, with an effect size comparable to that obtained in the undisturbed plots ($\overline{E}_D = 0.14$, 95% CI $= 0.102–0.180$), indicating that 14 out of every 100 seeds sown in disturbed plots typically emerged as seedlings. This effect represents the average number of seedlings that emerged per seed added in disturbed plots but not the direct effect of disturbance on seed limitation. As in the analysis with undisturbed plots, the small effect size suggests that establishment limitation limits emergence of seedlings more strongly than does seed limitation (0.86 vs. 0.14). Effect sizes for all species were relatively low (81% with $E < 0.25$, 11% with $0.25 < E < 0.50$, and 8% with $E > 0.50$; fig. 1*B*; app. B).

We found no significant differences in the effect size of seed limitation among most of the plant and habitat grouping variables that we investigated for studies using disturbed plots (table 1; fig. 1*B*). Again, the strength of seed limitation was significantly different among groups of species with different seed masses ($P < .001$; fig. 1*B*). This difference was driven by the difference between seeds weighing less than 0.2 mg and those weighing between 1 and 2 mg (fig. 1*B*); however, when seed size was regressed against seed limitation, the slope of the linear regression was not significantly different from 0 ($P = .325$; fig. 2*B*).

Neither the level of seed augmentation nor the duration of study significantly influenced the effect size in disturbed plots. This result is the opposite of what would be expected on the basis of density-dependent seed survival (Poulsen et al. 2007) and suggests that another factor was correlated with sowing density (e.g., seed mass).

Effect of Disturbance

Disturbance had a significant positive effect on seedling emergence (i.e., disturbance increased the magnitude of seed limitation). A direct comparison of seed limitation in disturbed and undisturbed plots from the same studies ($N = 75$ studies with disturbed and undisturbed treatments) revealed that disturbance resulted in ~10 more emerged seedlings per 100 seeds sown relative to undisturbed plots ($\Delta\overline{E} = 0.10$, 95% CI $= 0.073–0.132$).

We found no significant differences in the effect size of seed limitation among most of the plant and habitat grouping variables that we investigated, with the exception
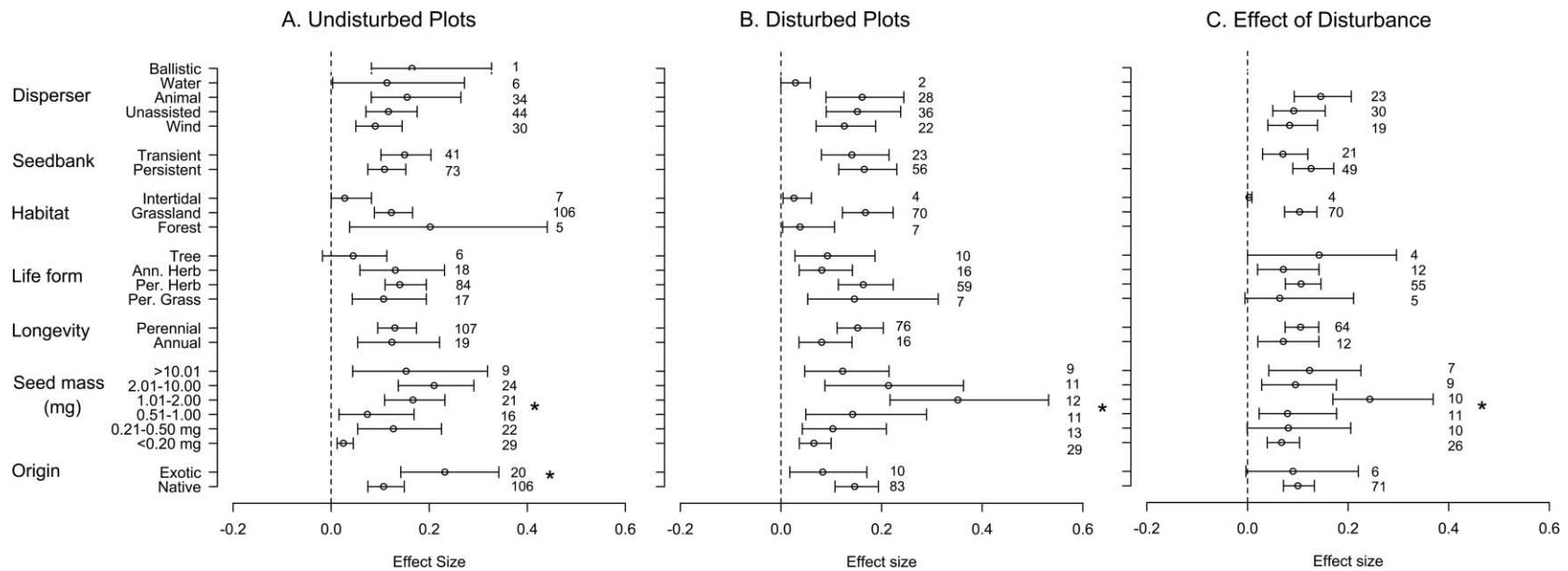
Figure 1: Seed limitation for undisturbed plots ($\overline{E}_U$, A) and disturbed plots ($\overline{E}_D$, B) and the effect of disturbance on seed limitation ($\Delta\overline{E}$, C) for each of the categorical grouping variables examined. Randomization tests were used to examine differences in effect size within the grouping variable clusters on the Y-axis; significant heterogeneity ($P < .05$) among factors within a grouping variable (e.g., tree, perennial herb, annual herb, and perennial grass within life form) is indicated by an asterisk and suggests significant differences in the effect size of seed limitation among the factors. Bars give bias-corrected bootstrapped 95% confidence intervals (CIs). The number of species included in the analyses for each of the factors within a grouping variable is listed to the right of the CI bars. Native and exotic species have significantly different effect sizes despite having overlapping CIs. This is because significance tests were carried out with randomization tests, while CIs were estimated with resampling (see "Methods").
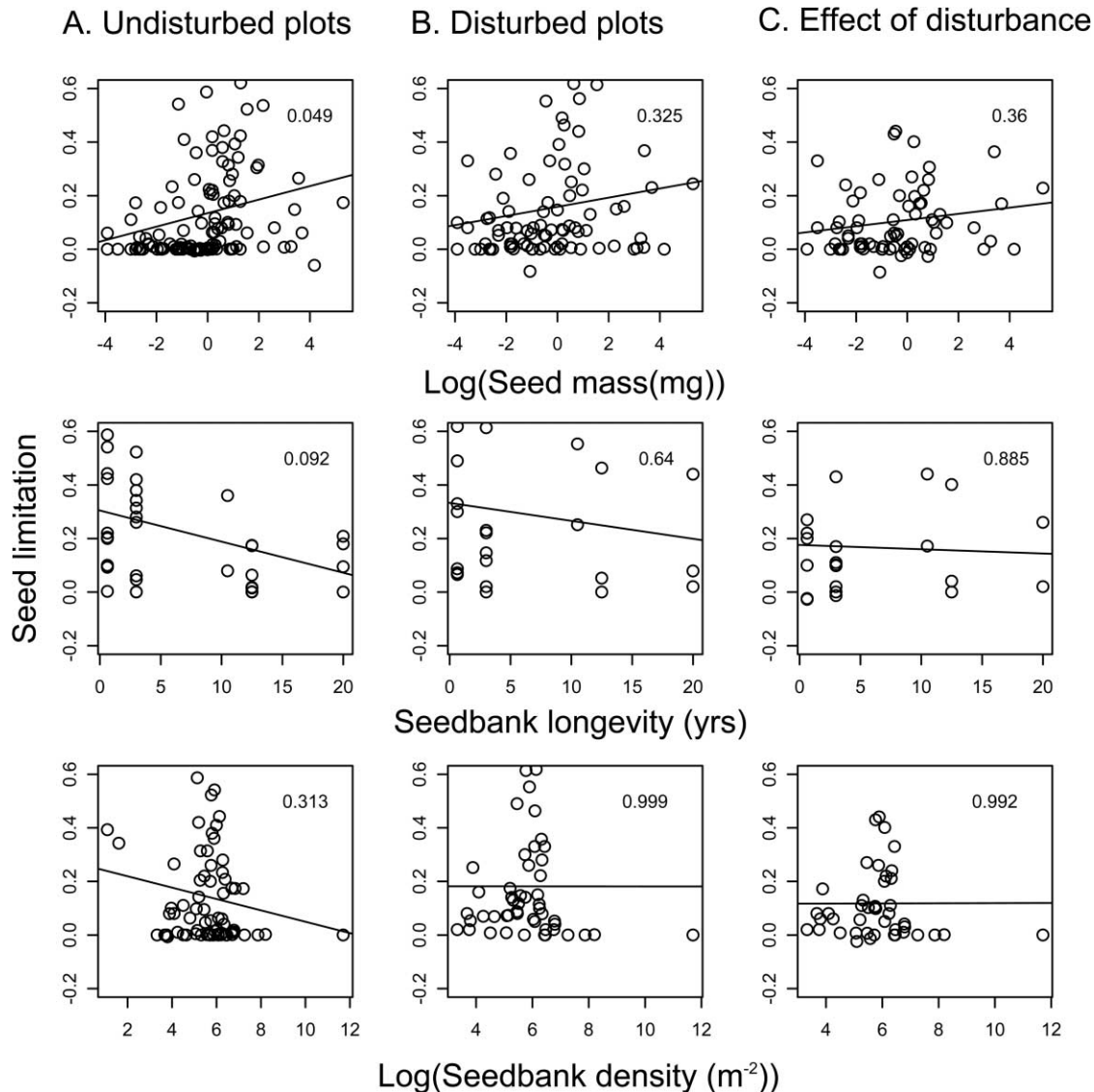
Figure 2: Seed limitation for undisturbed plots ($\overline{E}_U$, A) and disturbed plots ($\overline{E}_D$, B) and the effect of disturbance on seed limitation ($\Delta\overline{E}$, C) in relationship to seed mass, seed bank longevity, and average seed bank density. The fitted lines represent weighted regressions to determine whether plant characteristics explain variation in the effect size of seed limitation. Note that seed mass and average seed bank density are on a $\log_{10}$ scale. The *P* value indicating the significance of the regression is shown in the upper right-hand corner of each plot.

of species with different seed masses (table 1; fig. 1*C*). The strength of seed limitation was significantly different among groups of species with different seed masses ($P = .011$; fig. 1*C*).

Absolute Response Effect Size

The absolute population size of emerged seedlings increased with seed augmentation. The average increase in population size was greater in disturbed environments ($\overline{E}_{abs,D} = 1,412.7$, 95% CI = 768.246–2,704.661) than in undisturbed environments ($\overline{E}_{abs,U} = 658.2$, 95% CI = 348.629–1,177.679). Disturbance also had a positive effect on seedling emergence ($\Delta\overline{E}_{abs} = 1,172.1$, 95% CI = 667.834–2,045.675).

The absolute response was influenced by the seed augmentation density, with the number of emerged seedlings increasing significantly with the density of seed augmentation in disturbed plots ($E_{abs,D}$; table 2). Similarly, the increase in the number of emerged seedlings with in-

Table 2: Comparison of seed limitation (absolute response) by grouping variables for undisturbed treatments, disturbed treatments, and the effect of disturbance on seed limitation

Grouping variables	Undisturbed ($E_{abs, U}$)			Disturbed ($E_{abs, D}$)			Disturbance (ΔE_{abs})			Description
	Q or R^2	df	P	Q or R^2	df	P	Q or R^2	df	P	
Categorical:										
Habitat[a]	1.314	2	.393	3.467	2	.197	23.883	1	.050	Habitat in which the study was conducted (intertidal, grassland, or forest)
Geographic zone[a]	1.761	1	.085	4.593	1	.109	1.559	1	.121	Zone where study was conducted (midlatitudes or subtropical)
Dispersal mode[b]	6.195	4	.621	4.832	3	.532	2.734	2	.473	Typical method of seed dispersal (unassisted, ballistic, wind, water, or animal)
Plant life form[a]	11.927	3	.285	11.698	3	.324	8.092	3	.226	Tree, perennial herb, annual herb, or perennial grass
Existence of seed bank[b]	15.727	1	.058	2.955	1	.355	.529	1	.653	"Seed bank" defined as seeds remaining in the ground for longer than 1 year
Plant longevity[a]	6.422	1	.209	9.423	1	.162	6.728	1	.120	Perennial or annual
Plant life span[c]	82.347	3	.088	11.448	2	.195	6.170	2	.158	<1, 1–10, 11–100, >100 years
Seed origin[a]	3.053	1	.498	2.803	1	.159	2.175	1	.108	Native or exotic
Seed presence[a]	.378	1	<.962	.711	1	.561	.508	1	.469	"Seed addition" refers to the sowing of seeds in microhabitats where the species is known to be present; "introduction" is the sowing of seeds of a species that may be native but is not present at the time of sowing
Seed size category[b]	19.526	5	.362	10.299	5	.641	7.043	5	.546	Seed mass categories: 0–.20, .21–.50, .51–1.0, 1.01–2.00, 2.01–10.0, >10.01 mg
Continuous:										
Seed augmentation density (seeds m^{-2})[a]	175.485	126	.039	494.252	92	.012	412.711	74	.038	Density of seeds sown in treatment plots
Duration of study (days)[a]	−3.777	126	.005	−8.870	92	.036	−6.148	74	.033	Days for which seeds were monitored for recruitment in studies
Maximum plant height (m)[b]	−124.799	119	.301	−482.732	86	.092	−427.478	70	.126	
Seedling growth rate (day^{-1})[c]	−5,196.236	36	.076	−452.965	21	.808	−197.931	19	.917	
Average first flowering (years)[c]	−209.715	22	.414	−457.751	16	.776	−497.532	15	.379	Age at which plants typically flower for the first time
Average fecundity (seeds plant^{-1})[c]	85.744	74	.403	225.028	62	.388	193.522	54	.416	
Average seed bank density (seeds m^{-2})[c]	60.187	73	.618	514.754	50	.232	281.927	43	.390	
Average seed bank longevity (years)[c]	−34.677	38	.201	−71.397	23	.45	−27.086	21	.816	Number of years that seeds remain viable in the seed bank
Seed mass (mg)[b]	9.221	120	.909	−206.275	84	.34	−150.727	70	.343	

Note: The test statistics are Q for categorical variables and R^2 for continuous variables (see "Summary Analyses"). All randomization tests were two sided, and therefore a P value of .025 indicates statistical significance at the 5% level. Footnotes indicate where data for the grouping variable were collected.

[a] Original article.

[b] Data extracted from original articles when possible, but often supplemented by external sources.

[c] External sources.

creased seed augmentation density was marginally significant for both undisturbed plots $E_{abs, U}$ and the effect of disturbance (ΔE_{abs}; table 2). It is likely, therefore, that the absolute response is influenced largely by the study design (degree of augmentation) and not the biology of the system. Whereas the per seed response (E) varied significantly with several grouping variables (table 1), the absolute seed response varied significantly only with grouping variables related to the study design (seed augmentation density and duration of study; table 2).

Discussion

Recent reviews on seed limitation have employed a "vote-counting" approach, in which plant populations were deemed either seed limited or not seed limited (Turnbull et al. 2000; Moles and Westoby 2002). They concluded that most plant species were seed limited. Using an approach based on magnitude of response, we also found that plants were generally seed limited, as indicated by an average effect size greater than 0. However, a statistically detectable pattern of seed limitation is not necessarily biologically important. The average effect sizes for seed limitation were usually small, averaging ~0.14–0.15, with ~90% of all species showing effect sizes of <0.50. These results show that only a small fraction of augmented seeds recruit to the seedling stage and suggest that establishment processes play a major role in determining plant population density, at least at the seedling stage.

Our analysis focused on the earliest phase of recruitment, from seed to seedling. Because our analysis did not include factors that cause plant mortality during later life-history stages, we likely overestimated the relative importance of seed limitation and underestimated the role of establishment limitation to recruitment.

Why were the effects of seed addition experiments so small? We offer two non–mutually exclusive explanations. Most obviously, plant populations may be more establishment limited than seed limited, with an establishment bottleneck occurring between when seeds were deposited and when seedlings were censused during the first growing season. Alternatively, the small effect sizes may be artifacts of experimental design, generated when seeds were added to plots at biologically irrelevant densities. We first discuss several factors likely to constrain seedling establishment after seed arrival, particularly seed predation and characteristics of the plant and microsite. We conclude by discussing the experimental design of augmentation studies and providing suggestions for future studies.

The Relative Importance of Seed and Establishment Limitation

Based on the huge discrepancy between the number of seeds produced by most plant species and the number of seedlings that result, it has long been argued that the stage between seed production and seedling emergence is a critical bottleneck for plant populations (Harper 1977). Our low effect sizes for seed augmentation experiments support this observation; in practically all studies, added seeds rarely survived to the seedling stage. Thus, the seed-to-seedling bottleneck is best explained by processes that affect seed survival after seed arrival, contrary to the conclusions of many studies (Eriksson and Ehrlén 1992; Turnbull et al. 2000; Zobel et al. 2000; Dalling et al. 2002; Szentesi and Jermy 2003). Although seeds must arrive at a site before a plant can establish there, our results underscore the need to further examine factors that underlie postdispersal seed mortality.

Postdispersal factors that might constrain seedling establishment include seed viability and senescence and abiotic (e.g., light, water, nutrients, soil structure) and biotic (e.g., seed and seedling predators, pathogens, competitors) factors that affect germination, seed survival, and seedling survival. For species included in this study, germination rates under lab conditions average 90% (Royal Botanic Gardens 2002), but the effect sizes we calculated for these same species indicate that, on average, ~85% of all seeds in the field failed to emerge as seedlings. Thus, the low proportion (~15%) of seeds that emerged as seedlings cannot easily be explained by low seed viability or senescence. Rather, the consistently low proportion of seedling emergence (and early postemergence survival) observed across studies must be explained by (1) high rates of postdispersal seed predation, pathogen attack, or seedling herbivory or (2) characteristics of the plant or microsite that decrease the probability of germination.

Seed Predation and Herbivory. Seeds are generally abundant and rich in energy, thereby representing an important food source for an array of microbes, invertebrates, and vertebrates. Seed mortality by predation, particularly by vertebrates, has been thoroughly examined. However, results regarding the degree to which seed predators limit plant population sizes are mixed (Brown and Heske 1990; Louda and Potvin 1995; Brown and Human 1997; Orrock et al. 2006). In general, it is assumed that seed predation should affect the abundance of only plants that are seed limited (Crawley 2000): that is, if seed limitation is very small in magnitude, then a change in seed density due to seed predators would have little demonstrable effect on seedling density. When plants are microsite limited, most seeds will fail to establish regardless of the intensity of seed

predation; seed predators simply consume seeds doomed to mortality by other factors. If these arguments are correct, then the effect of seed predation on population density may depend on the degree to which populations are seed or establishment limited. We hypothesize that discrepancies among studies in population-level consequences of seed predation might be explained by differences among populations in the degrees of seed limitation versus establishment limitation.

Plant and Site Characteristics. In theory, some plant and site characteristics should be disproportionately important in determining the probability that a seed successfully recruits to the seedling stage, thereby influencing the relative importance of seed and establishment limitation. However, our results indicate that the effect of any given grouping variable on seed limitation is weak at best (plant height, seedling growth rate, age of first flowering, longevity, and fecundity). Of the 16 variables we explored, only disturbance, seed size, seed origin, seed presence, and seed bank longevity affected seed limitation in our meta-analysis.

Seed limitation has been presumed to be more common in disturbed (early successional) than in undisturbed habitats (Turnbull et al. 2000). Our results substantiate this view. Removal of adults and imposition of soil disturbance generally increased seed limitation (i.e., the number of seedlings that recruited from added seeds). However, the magnitude of the increase was small, suggesting that although disturbance creates recruitment sites, most seeds still fail to emerge. We conclude that microsite characteristics unrelated to the disturbance event itself more strongly influence the number of seedlings that emerge at a site than does seed availability.

Our results provide support for the hypothesis of a trade-off between seed size and colonization ability (Dalling et al. 1998; Turnbull et al. 1999; Levine and Rees 2002; Moles and Westoby 2002; Coomes and Grubb 2003). In particular, we found that seed limitation was more severe for species with large seeds, a result supported by a previous review that did not consider seed limitation as a continuous variable (Moles and Westoby 2002; but see Svenning and Wright 2005). Again, the magnitude of seed limitation was low, even for large-seeded species. Small-seeded species may be less seed limited than large-seeded species because of the inverse relationship between the number and mass of seeds produced (Smith and Fretwell 1974; Dalling et al. 1998). By producing smaller seeds, a species can achieve greater fecundity and presumably reach more recruitment sites, thereby decreasing seed limitation (Smith and Fretwell 1974; Jakobsson and Eriksson 2000; Henery and Westoby 2001; Moles and Westoby 2002). Small-seeded species also are more commonly associated with persistence in the soil (Thompson 1987; Eriksson

1995; Bakker et al. 1996; Bekker et al. 1998). Long-lived seed banks should further decrease the magnitude of seed limitation because viable seeds in the soil accumulate over time and can recruit into the population even in the absence of a productive seed year for that species. Our results suggest that seed limitation decreases with longevity of the seed bank.

The greater per seed recruitment of large-seeded species revealed by our meta-analysis contrasts with studies that have failed to find a strong relationship between seed mass and the number or percentage of seedlings that emerge at a given site (Eriksson 1997; Chen et al. 2002; Andresen and Levey 2004; Moles and Westoby 2004; Svenning and Wright 2005). Other studies have demonstrated that large-seeded species are relatively common as young seedlings, even though they are relatively uncommon in the seed bank (Dalling et al. 1998; Turnbull et al. 2005). Two general types of mechanism may explain this postdispersal advantage of large seeds over small seeds, that is, why establishment limitation is more severe for small-seeded species. First, large-seeded species may have a competitive advantage over small-seeded species (Tilman 1994; Rees and Westoby 1997; Turnbull et al. 1999; Levine and Rees 2002). This advantage appears to decrease as seedlings mature (Dalling and Hubbell 2002; Svenning and Wright 2005; Turnbull et al. 2005). Second, large-seeded species may experience a wider range of sites suitable for germination and establishment; their greater reserves make them better able to withstand herbivory, drought, shade, and burial, wherever they are placed (Westoby et al. 1996; Dalling and Hubbell 2002; Pearson et al. 2002; Moles and Westoby 2004; Turnbull et al. 2005)

Limitations of and Proposed Improvements to Seed Addition Experiments

The small effect of seed augmentation on recruitment may be attributed to multiple processes, including both density-independent and density-dependent mortality. However, most seed addition experiments are not designed to decipher these processes and tend to overlook key assumptions (but see Shaw and Antonovics 1986). For example, if the recruitment function (the relationship between seed input and seedling emergence) is nonlinear, the outcome of a seed addition experiment (and our estimate of seed limitation) will depend on the number of seeds added by the researcher. Imagine a system in which there is density-dependent emergence and either 25 or 1,000 seeds are added to a site. In both cases, one might find that more seedlings emerge in seed addition plots than in control plots. However, in the experiment with 25 added seeds, the per seed recruitment rate could be higher than in the study with 1,000 added seeds because the overall effect of

density would be less. Thus, the investigator might falsely conclude that the system with 25 added seeds was more seed limited than the system with 1,000 added seeds. Our standardization (eq. [1]) does not address this issue. Indeed, because most studies include only two treatments (with and without seed augmentation), fitting nonlinear recruitment functions and estimating propagule limitation (as done by Schmitt et al. 1999 for reef fish) was not possible; our only option was to fit a linear model.

A companion study by Poulsen et al. (2007) explores the few (18) studies (consisting of predominantly short-lived species) in which multiple augmentation levels were used. Consistent with our results, they found that plants were seed limited (seed augmentation led to higher recruitment) and that mortality losses were high. In addition, they found that saturation of a system with seeds led to a much greater increase in recruitment than removal of mortality sources because ambient seed densities were so low that removing mortality affected only a few seeds. In most cases, a linear recruitment function fitted as well as nonlinear functions, suggesting only a minor role of density dependence and supporting our use of a linear model for effect size. Thus, our two studies suggest that the addition of seeds to a system can increase recruitment, but the increase in recruitment will be relatively small (because of high mortality during this critical life stage) unless very large numbers of seeds are added.

These results call into question the assumption that seed augmentation saturates recruitment sites (only 14 of 36 data sets examined by Poulsen et al. [2007] exhibited saturation recruitment functions), especially when background seed density is typically not known. Therefore, the small effect sizes observed in our study are not likely caused by researchers saturating potential recruitment sites with seeds.

The design and interpretation of seed augmentation studies would be facilitated by knowing the number of seeds deposited by natural seed rain or already present in the seed bank. If the number of seeds added to an experimental plot is not substantially greater than that in seed rain or in the seed bank, it may be difficult to detect a difference between control and experimental plots (even when populations are strongly seed limited) because of the noise induced by the naturally occurring variation in seed supply. For example, adding 25 seeds to plots with a natural seed density averaging 5 seeds plot^{-1} will be more likely to detect seed limitation than adding the same number to plots with a natural density averaging 50 seeds plot^{-1} because the background variation in recruitment should increase with seed rain.

In short, interpreting results of seed addition experiments can be misleading without knowing the recruitment function and ambient seed density, which are necessary to place a particular study plot on the recruitment function (see Poulsen et al. 2007). We urge a two-step process in designing seed addition experiments. First, measure the ambient seed rain and the preexisting seed bank. Then, add seeds at different densities in different plots, with the goal of spanning the spectrum of natural densities as well as higher densities to facilitate description of the recruitment function (Schmitt et al. 1999; Poulsen et al. 2007).

Because limitations of experimental design are an inherent part of the seed addition literature, they apply to our meta-analysis also. The questions that we can answer with our meta-analysis are constrained by the experimental design of the original studies, which may or may not have been conducted to study seed limitation.

In summary, we suggest that postdispersal mortality is very high and that establishment limitation therefore requires more focused study. We emphasize that many processes can cause postdispersal seed mortality and that each could influence long-term population abundance. Empirical tests are needed to determine which of the postdispersal processes of seed mortality manifest themselves at the population level. Ideally, such studies should include field assays to examine the extent to which recruitment into populations is seed or microsite limited, followed by studies to examine the specific mechanisms of mortality when little or no seed limitation is observed. Similarly, when seed limitation is deemed important for a population, we need to understand the mechanisms that explain the species' inability to occur in suitable sites. Uniting the strength of seed limitation with its underlying mechanisms will make it possible to predict the degree of seed limitation.

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Appendix A from C. J. Clark et al., "Are Plant Populations Seed Limited? A Critique and Meta-Analysis of Seed Addition Experiments"

(Am. Nat., vol. 170, no. 1, p. 128)

Selection of the Effect Size for Seed Limitation Experiments

There are several plausible effect sizes to measure seed limitation. The selection of an appropriate effect size depends on the type of data available as well as the functional form of the recruitment function and the question being addressed (Osenberg et al. 1999). Here we examine several effect size metrics, their underlying assumptions, and the situations in which they would be most appropriate. We also present empirical estimators of these effect size metrics and compare estimates to the theoretical values, using a subset of our data taken from the few studies that quantified recruitment over a range of seed augmentation studies (i.e., with four or more levels of seed augmentation instead of the more typical two levels of "control" and "augmentation"). From this analysis, we conclude that a linear effect size measure (which measures the number of new recruits per added seed) is the best effect size to summarize the currently available literature because (1) most studies used only two augmentation levels, precluding the use of a nonlinear effect size measure, (2) the majority of studies using more than four augmentation levels yielded an approximately linear recruitment function (Poulsen et al. 2007), and (3) the linear effect size measure matched the theoretical prediction in more than twice the number of situations matched by other possible effect sizes. Because this choice is open to argument, we also use an effect that is unadjusted by augmentation level (i.e., the total number of new recruits without division by augmentation). Below we develop our rationale in more detail.

Parameter Estimation

Ideally, one would like to determine the functional form of seedling recruitment by fitting hypothetical models of seedling recruitment to seed limitation data (number of seedlings that recruit with different densities of seeds) and interpreting the parameters of the recruitment function biologically (Osenberg et al. 1997, 1999). For example, Poulsen et al. (2007) have suggested the nonlinear Beverton-Holt recruitment function, commonly applied to fishes (e.g., Schmitt et al. 1999), as a likely model for seedling recruitment:

$$R = \frac{P_0 S}{1 + (P_0 S / R_{\max})}, \tag{A1}$$

where R is the density of recruits (seedlings) that emerge from an input density of S seeds (consisting of augmented, A, and naturally occurring, S_{amb}, seeds; i.e., $S = A + S_{\mathrm{amb}}$), P_0 is the proportion of seeds that recruit in the absence of density effects (i.e., the slope of the recruitment function at $S = 0$), and $R_{\max}$ is the maximum density of recruits (i.e., the asymptote). Seed limitation (by any definition; see below) can then be evaluated at any seed density along the curve (e.g., at S_{amb}, which indicates ambient seed density).

Fitting the functional form requires multiple augmentation levels. However, only nine of the 43 articles (representing only 18 of 163 species and 37 of the 835 effect sizes) that met our criteria for inclusion also used four or more seed densities. Therefore, parameter estimation using nonlinear recruitment functions is not a feasible approach if the goal is to examine seed limitation across the majority of the published studies. This shortcoming of the available literature requires that we take an approach that can be applied with only two augmentation levels but still reflects biological processes, at least approximately, even if the recruitment function is nonlinear. We outline two general approaches that can be used when the recruitment function is unknown. We evaluate them by reference to the Beverton-Holt recruitment function, a nonlinear function that provides a good

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general description of the available studies of seed limitation (Poulsen et al. 2007). Next, we discuss two ways of conceptualizing limitation, examine the potential effect sizes stemming from these conceptual definitions, and then determine the most appropriate effect size for our meta-analysis, given the question being asked and the design of the experiments being summarized.

Elasticity or Sensitivity

Seed limitation can be defined as the change in recruitment produced by a small perturbation to seed density (e.g., Schmitt et al. 1999; Poulsen et al. 2007; fig. A1). Thus, we can conceptualize seed limitation in terms of "sensitivity" (i.e., dR/dS, the derivative of the recruitment function with respect to seed density) or "elasticity" (i.e., $d\ln R/d\ln S = [S/R][dR/dS]$). For the Beverton-Holt recruitment function,

$$\frac{\partial R}{\partial S} = \frac{P_0}{[1 + (P_0 S/R_{max})]^2}, \tag{A2}$$

and

$$\frac{\partial \ln R}{\partial \ln S} = \frac{S}{1 + (P_0 S/R_{max})}. \tag{A3}$$

Sensitivity expresses the effect of seed augmentation on an absolute scale (change in recruitment per seed), whereas elasticity gives the effect on a relative scale (the proportionate change in recruitment for a proportionate change in seeds). Graphically, these definitions correspond to the slope of the recruitment function (on an absolute or log-log scale) at a given seed density. The most appropriate density to evaluate the slope is the ambient seed density (S_{amb}). If $S_{amb} = 0$, then elasticity is undefined (because both R and $S = 0$ and a proportional change cannot be defined).
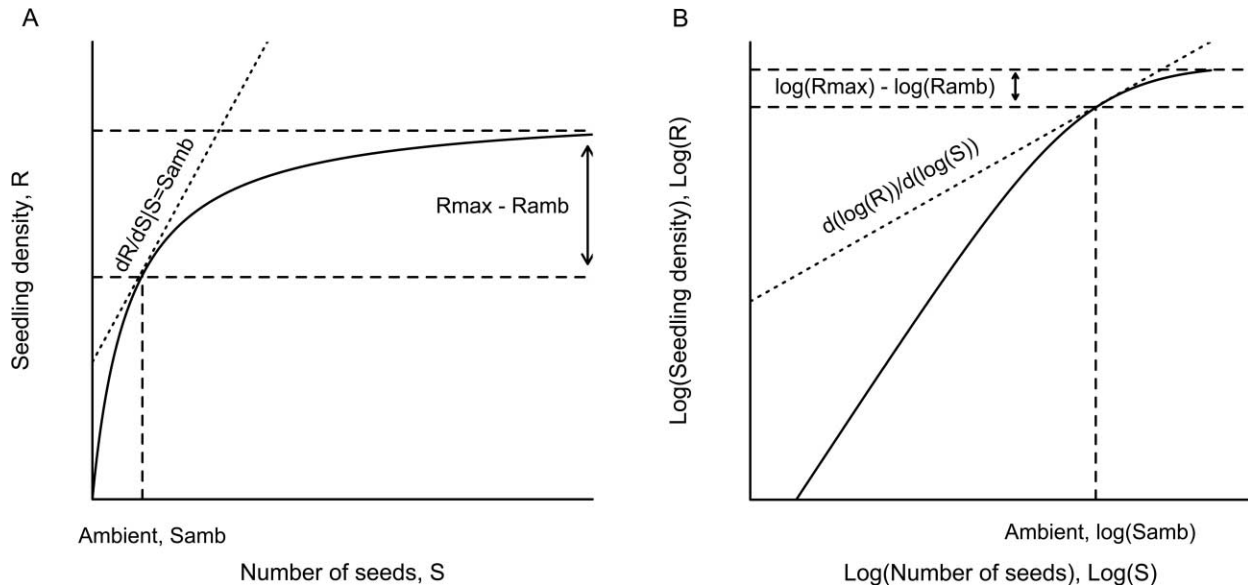

Figure A1: *A*, Density of emerged seedlings or recruits, *R*, versus the number of seeds, *S*, assuming a Beverton-Holt recruitment function. The dotted line represents the slope at $S = S_{amb}$, where S_{amb} is the number of seeds occurring naturally without seed augmentation. The arrow demonstrates the difference between the maximum seedling emergence, R_{max}, and seedling emergence at ambient conditions, R_{amb}. *B*, Same as *A*, but on a logarithmic scale: log *R* versus log *S*.

Limitation

The effect of a putatively limiting factor can also be assessed by a comparison of the ambient state of the system with that achieved after the limitation factor has been eliminated (Osenberg and Mittelbach 1996; Schmitt et al. 1999). In the context of seed limitation, we can compare the recruitment when seeds are not limited (i.e., supplied in excess: $R_{\max}$) with recruitment at the ambient seed density (R_{amb}). This difference can be measured on an absolute scale (i.e., "absolute limitation": $R_{\max} - R_{\mathrm{amb}}$; fig. A1*A*) or on a relative scale (i.e., "relative limitation": $R_{\max} - R_{\mathrm{amb}}$ or $\ln(R_{\max} - R_{\mathrm{amb}}) = \ln(R_{\max}) - ln(R_{\mathrm{amb}})$; fig. A1*B*).

Empirical Estimates of Seed Limitation Using Two Treatments

Because most empirical studies use only two seed densities (e.g., control and augmented), we must select an effect size that requires only two densities and is therefore linear on some scale. We present four general candidates and discuss their relationship to the above conceptual definitions of seed limitation (all variables defined in the main text).

Absolute response. The quantity $R_{\mathrm{exp},i} - R_{\mathrm{cont},i}$ measures the absolute change in recruitment (seedling density) between the augmented (experimental) and control treatments: $R_{\mathrm{exp},i}$ and $R_{\mathrm{cont},i}$ are the average densities of seedlings in the experimental and control plots, respectively, in the *i*th study. This measure approximates the conceptual definition of absolute limitation if the augmentation level is sufficiently high to saturate the system and eliminate seed limitation (i.e., if $R_{\mathrm{exp},i} = R_{\max}$).

Relative response. The quantity $R_{\mathrm{exp},i}/R_{\mathrm{cont},i}$ (which can be log transformed without a qualitative change in meaning) measures the relative change in recruitment. It approximates relative limitation if the augmentation level is sufficiently high to saturate the system and eliminate seed limitation. This effect size measure will be problematic if $R_{\mathrm{cont},i} = 0$.

Per seed response. The quantity $(R_{\mathrm{exp},i} - R_{\mathrm{cont},i})/A_i$ measures the absolute change in recruitment per seed. It approximates the conceptual measure of sensitivity if the recruitment function is linear or if A_i is small relative to the nonlinearity.

Relative per seed response. The quantity $[(R_{\mathrm{exp},i} - R_{\mathrm{cont},i})/A_i](S_{\mathrm{cont},i}/R_{\mathrm{cont},i})$ (where $S_{\mathrm{cont},i}$ is the seed density in the control treatment and presumably equal to S_{amb}) measures the relative effect of a proportionate change in seed density recruitment. It approximates the conceptual measure of elasticity if the recruitment function is linear on a log scale or if A_i is small relative to the nonlinearity.

These effect sizes, although linked to conceptual definitions of seed limitation (see above definitions), also have potential shortcomings. The absolute and relative responses can lead to problems comparing studies that used very different augmentation densities; for example, all else being equal, a larger effect size will result from the addition of 1,000 than from adding 100 seeds. Such was the case in our meta-analysis, where the densities of sowed seeds varied by more than an order of magnitude among studies. By standardizing the absolute response by the density of seeds sowed, the per seed response gives a measure of "return on investment" (recruits seed^{-1}). However, if the recruitment function is nonlinear, this metric will give smaller effect sizes under higher augmentation levels, even if all else is equal. The relative response and relative per seed response can lead to problems when there is no recruitment in the control (which was the case in many of our studies).

No matter which measure of effect size is used, it should match the question being asked and the design of experiments being summarized and should be interpreted in light of how limitation is defined. If the augmentation was small (relative to any nonlinearity), then the per seed response or relative per seed response can be interpreted as the marginal return per seed (i.e., sensitivity or elasticity). In this case, the relative response and absolute response cannot be clearly interpreted because their magnitudes are greatly influenced by the degree of augmentation and not by the biology of the system (see Osenberg et al. 1999). In contrast, if the augmentation was large and eliminated seed limitation, then either of the per seed responses would be a poor choice for an effect size because their magnitudes decline with augmentation density (and fail to match any of our definitions of seed limitation). When augmentation saturates the systems, then either relative response or absolute response is a better choice and can be interpreted as limitation (sensu Osenberg and Mittelbach 1996). Of course, the challenge is that with only two augmentation levels, one cannot know where a system lies along the recruitment function (i.e., whether the augmentation range occurred over a relatively linear portion of the function or the maximum augmentation level saturated the system); see figure A2.
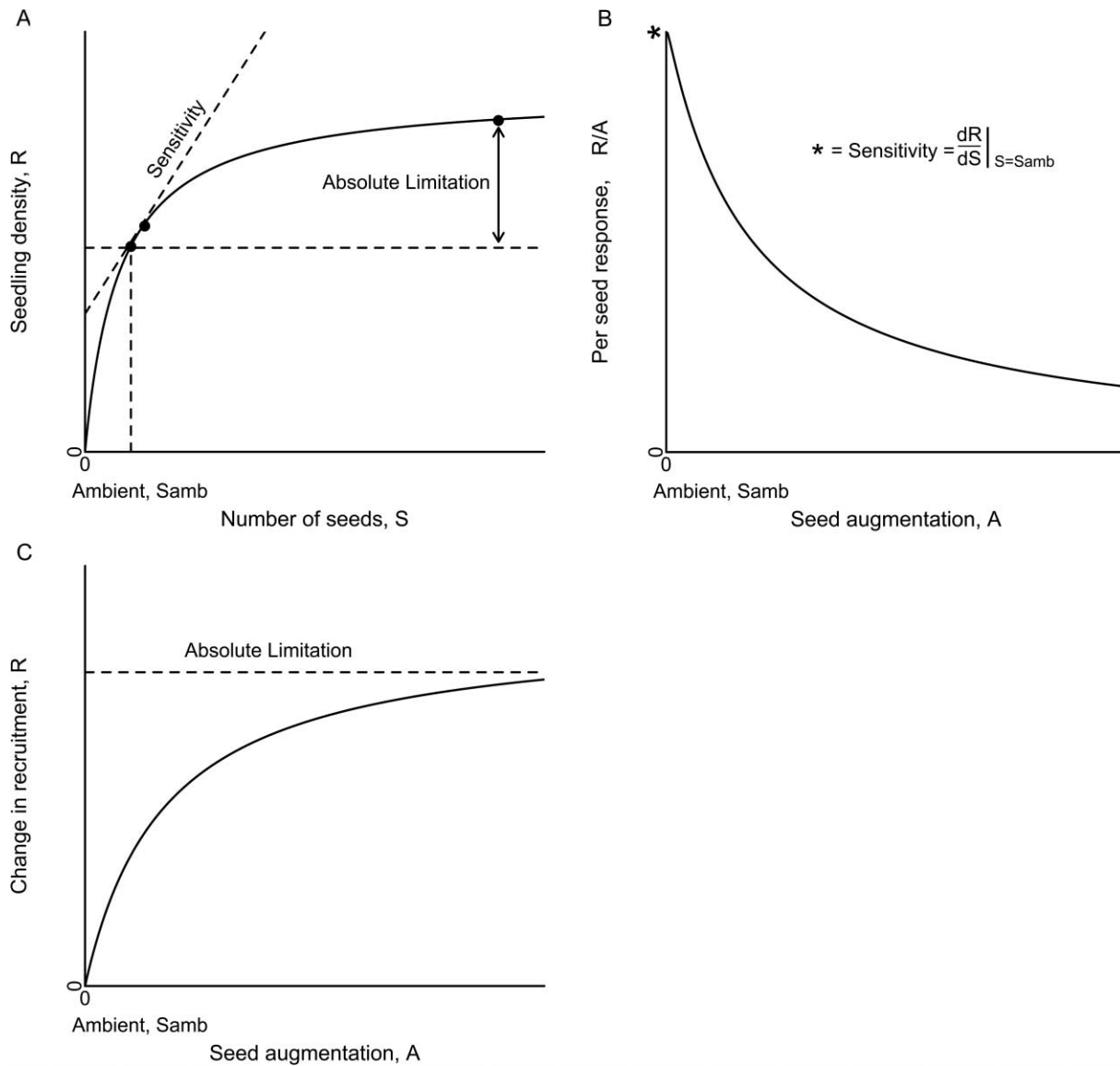
Figure A2: *A*, Beverton-Holt recruitment function with two levels of seed augmentation. The first augmentation is small, and the per seed response or relative per seed response can be interpreted as the marginal return per seed (i.e., sensitivity or elasticity). The second augmentation is large and saturates the system. Therefore, either the relative response or the absolute response would be better choices for quantifying seed limitation. In the meta-analysis data set, most experimental studies augmented seeds at a small level relative to the saturation point of the recruitment function. *B*, As augmentation level increases from 0 to high values, the per seed response starts at the theoretical value corresponding to sensitivity (see fig. A1*A*) and declines to 0. In other words, the slope of the *Sensitivity* line in *A* becomes flatter as seed augmentation increases (i.e., moves farther out along the recruitment function). As a result, per seed response best estimates sensitivity when augmentation is small relative to the nonlinearity in the recruitment function. *C*, As augmentation increases from 0, the absolute response (difference in recruitment between the augmented and control treatments) increases from 0 to a maximum. This maximum corresponds to absolute limitation. Thus, the absolute response is best when augmentation saturates the system and should be interpreted in the context of absolute limitation.

Comparison of Effect Sizes

Relative per seed response cannot be calculated from the available literature because ambient seed density is rarely reported in seed augmentation studies. Thus, to help determine which of the other effect sizes (relative response, absolute response, or per seed response) best approximates seed limitation in our collection of studies, we compared each of them to theoretical expectations based on the few studies that had four or more augmentation levels and thus allowed us to fit the nonlinear Beverton-Holt recruitment function (see Poulsen et al. 2007). We calculated effect sizes for the 37 studies (consisting of 18 species, many of which were sown under different conditions) reported by Poulsen et al. (2007). We first calculated the three different effect sizes for each study, using data (density of seeds sown and density of recruits) from the control treatment and the treatment with the greatest number of sown seeds. We then compared each effect size to its corresponding theoretical effect size by assuming that the true recruitment relationship was described by the Beverton-Holt function with the parameters estimated by Poulsen et al. (2007):

$$\text{absolute limitation}: \ R_{\max, i} - R_{\mathrm{amb}, i},$$

$$\text{relative limitation}: \ \frac{R_{\max, i}}{R_{\mathrm{amb}, i}},$$

$$\text{sensitivity}: \ \frac{\partial R_i}{\partial S_i} \big|_{S_{\mathrm{amb}}},$$

where i serves as an index for the ith study, other terms are defined as above, and sensitivity is the slope of the recruitment function evaluated at the ambient seed density.

If augmentation levels are small relative to the nonlinearity of the recruitment function, then the per seed response should match sensitivity closely, but the other effect sizes should not perform well: that is, absolute response $\neq$ absolute limitation and relative response $\neq$ relative limitation. If augmentation leads to saturation of the system, then the per seed response should not equal its theoretical value (i.e., sensitivity), but the relative and absolute responses should equal their theoretical values (i.e., relative limitation and absolute limitation, respectively), indicating that they would be better choices of effect sizes. Thus, by comparing the observed and theoretical expectations, we can determine which metric applies most often and how it should be interpreted in light of the recruitment function.

The per seed response matched (within 30%) its theoretical counterpart more often (15/37 comparisons) than did the absolute response (12/37) or the relative response (4/37); in six cases, none of the effects matched. In some cases, the poor fit resulted from the presence of zeroes or the inability to estimate $R_{\max}$ (e.g., in some cases, the best estimate of $R_{\max}$ was ∞, precluding the estimation of limitation; i.e., there was no asymptote). Given its poor performance, we do not consider the relative response further (adding a constant to deal with zeroes did not help its performance).

Most interestingly, the per seed response and the absolute response performed in opposite ways, and their performance depended on the qualitative shape of the recruitment function. When the recruitment function was demonstrably nonlinear (i.e., a Beverton-Holt function was a better fit to the data than a linear model; see Poulsen et al. 2007), the absolute response did well (11/14 matches) and the per seed response did poorly (1/14). However, when the function was not demonstrably nonlinear, the absolute response did poorly (1/22 matches) and the per seed response performed best (22/22 matches). In this data set, recruitment functions that were approximately linear ($n = 22$) were more common than demonstrably nonlinear ones ($n = 14$); in one case, we could not evaluate the shape of the function.

We predicted this result on the basis of the expected match/mismatch between the empirical estimates and their theoretical counterparts and the conditions under which they should apply. Our results further highlight the importance of selecting effect size metrics by matching effect size metrics to characteristics of the system and a model of the system's response (Downing et al. 1999; Osenberg et al. 1999). No effect size metric will match all questions or study systems. Indeed, this is the key problem in our application: which metric works best, how should it be interpreted, and how might we discern the studies to which the effect size metric should be applied (and, more importantly, not be applied)? Because we cannot examine the recruitment function for most of our studies (because they have only two augmentation levels), we do not know whether the function is relatively

linear over the augmentation range or whether the highest augmentation level is near the asymptotic recruitment value. Knowing this would help us differentiate between studies in which per seed response (or absolute response) is most suitable and reveal how the effect size should be best interpreted (i.e., as sensitivity or as absolute limitation). Instead, we seek a general approach that we can apply to all studies (because we lack specific knowledge about most studies).

Our analyses (using Poulsen et al.'s [2007] data set) suggest that the per seed response matches theoretical expectations more often than other effect size options. Furthermore, it is expected to work best when the nonlinearity is relatively small. Because the majority of studies (22/36) failed to detect a nonlinearity in the recruitment function, we have chosen to use the per seed response as our primary response variable in our meta-analysis. We note, however, that this metric will not behave well in some cases (e.g., where the augmentation leads to saturation). In these cases, which cannot be identified, given the available data, the per seed response will underestimate seed limitation as defined by sensitivity, and a more appropriate variable would be the absolute response, which corresponds to the concept of absolute limitation when augmentation saturates the system.

This ambiguity is an unfortunate consequence of the types of studies that are available in the seed limitation literature. We remain hopeful that our analysis will lead to more useful empirical studies that can facilitate future analyses derived from estimation of the recruitment function.

Appendix B from C. J. Clark et al., "Are Plant Populations Seed Limited? A Critique and Meta-Analysis of Seed Addition Experiments"

Data Files

Data, including the citation of the original study, life-history information, and effect size calculations, for the evaluation of seed limitation in undisturbed and disturbed plots and the effect of disturbance are available as both an Excel file and a tab-delineated ASCII file.

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