Safe sites, seed supply, and the recruitment function in plant populations

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Abstract. The extent to which plant populations are seed vs. establishment limited can be understood by quantifying the recruitment function, describing the number of seedlings that establish as a function of the number of seeds added. Here, we derive a general equation for the recruitment function based on a mechanistic model describing how the availability of safe sites (sites suitable for germination and establishment) interacts with the number and distribution of seeds added to a plot to determine the number of recruits. The parameters of this recruitment function have a direct biological interpretation that can provide insight into the processes limiting recruitment in plant populations.

Key words: Beverton-Holt function; establishment limitation; Hieracium lepidulum; microsite; plant recruitment; recruitment function; safe site availability; seed-addition experiments; seed limitation; self-thinning.

INTRODUCTION

The availability of seeds and the availability of sites suitable for seedling establishment (safe sites; Harper et al. 1961) are key determinants of recruitment in plant populations (Harper et al. 1965, Crawley 1990, Eriksson and Ehrln 1992). At one extreme, populations are establishment limited, meaning the rate of seed supply is sufficient to ensure that all available safe sites are occupied and population size is constrained by the number of safe sites. At the other extreme, populations are seed limited, meaning the rate of seed supply is low relative to the availability of safe sites so that many safe sites are unoccupied and population size is constrained by seed supply.

In reality, most plant populations are probably limited by a combination of the two processes (Eriksson and Ehrln 1992). This is because, rather than being a dichotomy, the extent of seed vs. establishment limitation falls along a gradient (Manning et al. 2004, Clark et al. 2007, Kollmann et al. 2007) that depends on the rate of seed supply relative to the availability of safe sites. A series of plots may all show seed limitation, in that seed addition results in new seedling recruitment (Turnbull et al. 2000), but the magnitude of the recruitment response could vary markedly between plots. For a given level of seed addition, plots with more available safe sites should have higher recruitment and appear more strongly seed limited. To understand the factors limiting recruitment in plant populations, this interplay between safe-site availability and seed-supply rate is of key interest.

One way to understand this interplay is through seed-addition experiments that allow us to quantify the recruitment function (Poulsen et al. 2007). This function describes the relationship between the number of seeds that are experimentally added to plots and the resulting number of recruits, and is typically a monotonically increasing curve that reaches an asymptote at high levels of seed addition. Poulsen et al. (2007) show that the form of the recruitment function can be used to infer the relative strength of seed vs. establishment limitation, and to assess the relative importance of density-dependent and density-independent processes in affecting population recruitment.

Central to this approach is quantifying the recruitment function. Poulsen et al. (2007) used the Beverton-Holt function, which has two parameters, one that estimates the proportion of seeds that would recruit in the absence of density-dependent effects, and a second that estimates the asymptotic number of recruits at high levels of seed addition under negative density dependence. While the parameters of the Beverton-Holt function have biological interpretations, the function was chosen because it often fits observed recruitment data well and the mechanistic underpinnings were not discussed.

Our aim in this paper is to bridge the gap between the underlying processes hypothesized to control recruitment in plant populations, and the functions used to quantify these relationships. To do this, we derive a general recruitment function based on a mechanistic model of how safe sites and seed supply interact to determine the number of recruits. We build on a model of recruitment in which there are a limited number of safe sites capable of supporting a single seedling, with seeds competing to occupy these safe sites. The relationship
between seed supply and the number of seedlings that recruit (the recruitment function) is then determined by the availability of safe sites and the distribution of seeds among those sites. We show that the Beverton-Holt function is a special case of a more general recruitment function, and discuss how a process-based approach applied to seed-addition experiments can reveal the mechanisms underlying recruitment patterns and links to other processes.

**Derivation of a General Mechanistic Recruitment Function**

Brännström and Sumpter (2005) describe a model for the distribution of individuals among sites that can be used to derive, from first principles, classic models of single-species population growth. Here we adapt their site-based model to the problem of estimating recruitment functions.

Consider a plot divided into \( n \) sites of equal area over which \( s \) seeds are distributed and where, sometime later, we count the number of seedlings that have recruited, \( r \). We assume the \( s \) seeds are the only ones added; there is no seed input from other sources or recruitment from a seed bank. We define \( p_k \) to be the expected proportion of sites containing \( k \) seeds after the seeds have been distributed, with the expected number of seedlings that recruit from a site with \( k \) seeds defined by an interaction function \( \phi(k) \) (Brännström and Sumpter 2005). The expected number of seedlings that recruit in a plot is then given by

\[
r = n \sum_{k=0}^{\infty} p_k \phi(k). \tag{1}
\]

First, consider the case where \( s \) seeds are randomly distributed over a plot in such a way that each seed is equally likely to land in any of the \( n \) sites. For large \( n \), the expected proportion of sites containing \( k \) seeds will follow a Poisson distribution having expectation given by the average density of seeds per site, \( s/n \):

\[
p_k = \frac{(s/n)^k e^{-s/n}}{k!}. \tag{2}
\]

The expected number of seedlings that recruit in a plot is then given by

\[
r = n e^{-s/n} \sum_{k=0}^{\infty} \frac{(s/n)^k}{k!} \phi(k). \tag{3}
\]

We define a site as an area capable of supporting just one seedling regardless of how many seeds land at a site, so that seeds compete for safe-site occupancy. This equates to contest competition, in which successful individuals obtain all the resources they need for survival but unsuccessful individuals do not (Brännström and Sumpter 2005). Under this assumption the interaction function is defined as follows:

\[
\phi(k) = \begin{cases} 
1 & \text{if } k \geq 1 \\
0 & \text{otherwise.} 
\end{cases} \tag{4}
\]

Combining Eqs. 3 and 4, the expected number of seedlings that recruit in a plot as a function of the number of seeds added is

\[
r = n(1 - e^{-s/n}). \tag{5}
\]

If \( s \gg n \) (a large number of seeds are added to a plot relative to the number of sites) then \( e^{-s/n} \to 0 \) and \( r \to n \), so that the number of recruits saturates at the number of sites. This assumes, however, that all sites are suitable for germination and establishment. We can relax this assumption by introducing an additional parameter, \( b \), specifying the proportion of sites in a plot that are safe sites for seedling recruitment. All seeds that land in non-safe sites fail to recruit. The interaction function is then

\[
\phi(k) = \begin{cases} 
b & \text{if } k \geq 1 \\
0 & \text{otherwise} 
\end{cases} \tag{6}
\]

and the expected number of seedlings that recruit in a plot as a function of the number of seeds added is

\[
r = bn(1 - e^{-s/n}). \tag{7}
\]

This is the Skellam function when applied to single-species population growth (Skellam 1951) and is similar to a function derived by Geritz et al. (1984) in a related context. The parameters of this Skellam function have a direct biological interpretation: \( n \) is the number of sites, \( b \) is the proportion of those sites that are safe sites capable of supporting a single seedling, and for \( s \gg n \) (a large number of seeds are added to a plot relative to the number of sites) the number of recruits saturates at the number of safe sites, \( bn \). If \( s \ll n \) (few seeds are added relative to the number of sites, so that many safe sites are unoccupied and recruitment is strongly seed limited) then \( e^{-s/n} \to 1 - s/n \) and \( r \to bs \); the number of recruits increases approximately in proportion to the number of seeds added and a plot of \( r \) vs. \( s \) approaches a straight line with slope equal to \( b \).

The relationship between the number of recruits and the number of seeds added can be generalized to situations in which seeds are not randomly distributed but are aggregated so that some sites receive a disproportionate number of seeds. Following Brännström and Sumpter (2005) we can use a negative binomial distribution to describe aggregation:

\[
p_k = \frac{\lambda^k \Gamma(k + \lambda)}{\Gamma(\lambda) \Gamma(k + 1)} \left(\frac{s/n}{\lambda + s/n}\right)^k \tag{8}
\]

where \( \lambda \) is a (positive) dispersion parameter with smaller values of \( \lambda \) indicating stronger aggregation within sites. The Poisson distribution (Eq. 2) arises as a special case when \( \lambda \to \infty \). Assuming that seeds are aggregated within sites, so that \( p_k \) is given by Eq. 8 with dispersion
parameter $\lambda$, and that only a proportion of sites are safe sites, with the interaction function given by Eq. 6, then, substituting these into Eq. 1, the expected number of seedlings that recruit in a plot as a function of the number of seeds added is as follows (Brännström and Sumpter 2005):

$$ r = bn \left[ 1 - \frac{\lambda^k}{(\lambda + s/n)^k} \right]. \quad (9) $$

When $\lambda \to \infty$ (i.e., $p_0$ follows a Poisson distribution) Eq. 9 reduces to the Skellam function (Eq. 7). When seeds are aggregated so that $\lambda = 1$, Eq. 9 reduces to the Beverton-Holt function (Beverton and Holt 1957):

$$ r = \frac{bs}{1 + s/n}. \quad (10) $$

Hence, both the Skellam and Beverton-Holt functions are special cases of the more general recruitment function given by Eq. 9 (Fig. 1). The family of recruitment curves described by Eq. 9 all have an asymptote at the number of safe sites, $bn$. They differ in the rate at which they approach that asymptote because with higher levels of aggregation more seeds must be added to achieve occupancy of a given number of safe sites.

**Interpreting the Parameters**

The general recruitment function has three biologically interpretable parameters: $n$ is the number of sites, $b$ is the proportion of those sites that are safe sites, and $\lambda$ is the degree to which seeds are aggregated across sites. These parameters allow us to estimate the relative importance of density-dependent and density-independent processes affecting recruitment (Poulsen et al. 2007). In the absence of density-dependent mortality, the relationship between $r$ (the number of seedlings recruited) and $s$ (the number of seeds distributed) will be a straight line with slope equal to $b$: seeds either land in a safe site with probability $b$ and recruit, or fail to land in a safe site and die, with the proportion of seeds lost to density-independent mortality equal to $1 - b$. Density dependence manifests itself as curvature away from a straight line: in addition to mortality resulting from failure to land in a safe site, there is mortality resulting from multiple seeds occupying the same safe site from which only one plant will recruit. For a given proportion of safe sites and level of seed addition, the total number of sites and the degree of aggregation ($n$ and $\lambda$) determine the degree of curvature away from the density-independent straight-line relationship. Fewer sites or greater aggregation mean a higher probability of more than one seed landing in the same safe site and hence stronger density-dependent mortality.

Eq. 9 was derived assuming the $n$ sites in a plot were of equal area. In these circumstances, aggregation within sites could arise if seeds were distributed in such a way that they were spatially clumped as opposed to randomly (or uniformly) dispersed across a plot. In seed-addition studies the experimenter has some control over this, and we suspect that attempts are usually made to achieve a random (or even close to uniform) spread of seeds across plots. While some degree of secondary redistribution of seeds is likely, the experimenter at least avoids a high degree of spatial clumping. Given the model we have described, random seed distribution would appear to provide a strong theoretical justification for using the Skellam function (Eq. 7) to model recruitment in seed-addition experiments.

However, even if seeds are randomly (or uniformly) distributed across a plot, variation in the size of sites capable of supporting a single seedling will lead to aggregation. Seeds distributed at random have a higher probability of landing in larger sites, resulting in larger sites having more, and smaller sites fewer, seeds than expected under an equal-area model. Hence, when seeds have been randomly distributed across plots, it may be possible to relax the assumption that all sites are of equal area and to interpret the dispersion parameter, $\lambda$, in Eq. 9 as a measure of the degree of size heterogeneity among sites.

Safe sites capable of supporting a single seedling may vary in size for several reasons. First, resource availability could vary within a plot and the area required to supply sufficient resources to support a seedling may consequently vary. Seedlings in low-resource patches may require larger sites than those in high-resource patches. Second, seedlings will differ in their initial size due to factors such as genetic differences and variation in the timing of germination, with initial differences in...
plant size often exaggerated through asymmetric competition for resources (Weiner 1990). Because resource use scales with plant size, larger plants will require larger sites to meet their resource requirements. Heterogeneity in site area may therefore arise through a combination of variation in resource availability and initial plant size, enhanced by competition for local resources.

To illustrate how the dispersion parameter in Eq. 9 can be interpreted as a measure of size heterogeneity among sites, we simulated a seed-addition experiment, fitted recruitment functions to the simulated data, and explored how variability in site area within plots affected parameter estimates. Our simulated seed-addition experiment consisted of plots each having 1000 sites, of which a proportion of sites in each plot (set to 0.1) were randomly chosen to be safe sites. The first “treatment” consisted of plots with sites that were all of equal area (set to 10 units). We simulated randomly distributing seeds across plots at five densities: 5, 25, 125, 625, 3125, and 15 625 seeds per plot, with 10 replicate plots per density. Following seed distribution, the number of recruits in each plot was calculated as the number of safe sites occupied by at least one seed. We fitted three recruitment functions to these data, the Skellam function (Eq. 7), the Beverton-Holt function (Eq. 10), and the general recruitment function (Eq. 9), using maximum likelihood assuming the number of recruits per plot was distributed as negative binomial.

The protocols for the second, third, and fourth “treatments” were identical, except the sizes of sites within plots were made unequal. All plots still comprised 1000 sites covering the same total area, but the degree of between-site heterogeneity differed among treatments (the sizes of sites were chosen arbitrarily such that the variance in site area within plots in each of the four treatments was 0, 20.0, 77.7, and 289.5, respectively). With random dispersal of seeds across plots, our prediction is that estimates of the dispersion parameter, \( k \), should be large in treatment 1, where there is no variation in site area, with the general recruitment function well approximated by the Skellam function. The dispersion parameter should decline across treatments as the between-site area variance increases.

The results from a typical experimental run are shown in Fig. 2: as predicted, \( \lambda \) is large in treatment 1 and declines across treatments. The Skellam function and general recruitment function give a nearly identical fit for treatment 1, as expected. The Beverton-Holt function provides a reasonable fit to treatment 3, where the degree of between-site heterogeneity results in a maximum-likelihood estimate for \( \lambda \) that is close to 1.

The results from single experimental runs vary stochastically, so we ran 1000 experiments in order to examine how, on average, the parameter estimates for the three functions were affected by size heterogeneity (Fig. 3). For the general recruitment function, the dispersion parameter, \( \lambda \), declined across treatments as the between-site area variance increased, although estimates varied substantially when the dispersion parameter was large (treatments 1 and 2). Estimates of \( b \) (proportion of sites that are safe) and the degree of bias in these estimates differed by function and treatment. The mean estimate of \( b \) for the general recruitment function was close to the true value (0.1), with no evident bias across treatments. In contrast, estimates of \( b \) derived from the Skellam and Beverton Holt functions were biased away from the true value when the level of between-site heterogeneity was substantially different from that assumed in the function. The trends in bias were consistent with expectations given the assumptions underlying each function. The Beverton-Holt function, for example, was biased towards higher estimates of \( b \) when sites were similar in size (treatments 1 and 2) because here the Beverton-Holt assumes greater clustering than exists. The Skellam function, in contrast, was biased towards lower estimates of \( b \) in sites with more highly varying sizes (treatments 3 and 4) because it assumes a random distribution of seeds among sites. Estimates of \( n \), the number of sites, were generally centered close to the true value across treatments for all three functions, although the general recruitment function showed some bias towards higher values of \( n \) at the highest level of between-site heterogeneity (treatment 4).

**Applying the Model**

To illustrate the application of a mechanistically derived recruitment function, we consider a situation in which plots have been measured on several occasions following seed addition, providing data on the number of seedlings that germinate and how seedling numbers subsequently change through time. We can make three a priori predictions about how the parameters of the recruitment function should change as the seedling cohort ages. First, we expect the number of sites, \( n \), to decline: as seedlings grow they will require a larger area to meet their resource requirements, meaning the area of a safe site capable of supporting a single plant will increase, and the number of sites will decline. Second, if there is ongoing density-independent mortality of seedlings, we expect the proportion of safe sites, \( h \), to decline. Third, if there is competition for safe sites as seedlings increase in size, leading to density-dependent mortality, then initial differences in plant size may be exaggerated through asymmetric competition (Weiner 1990), leading to an increase in the heterogeneity of the area of safe sites, reflected in a decline in the dispersion parameter \( \lambda \).

To explore these predictions, we analyze data from an experiment in which seeds of *Hieracium lepidulum* (Asteraceae) were added to square 0.09-m² plots at five levels (25, 125, 625, 3125, and 15 625 seeds/plot, equating to 278, 1389, 6944, 34 722, and 173 611 seeds/m²) and the number of recruits were counted at intervals from 10 to 48 months after seed addition. The data are taken from a larger seed-addition experiment in which we aimed to...
quantify how the recruitment function for *H. lepidulum* (an invasive exotic herbaceous perennial in New Zealand) differed among upland forest and alpine habitats in Canterbury, New Zealand. For illustrative purposes we present data from 90 of 1080 seed-addition plots that we established; we will present a detailed analysis of the full data set elsewhere. The 90 plots analyzed here were all located in one habitat type (creek beds within forest) in a randomized block design, comprising six randomly located blocks, with each block having three replicates of each of the five seed-addition levels. The numbers of recruits present in each plot were counted at 10, 13, 20, 26, 37, and 48 months after the seed was added in March 2003 (autumn; we conducted counts prior to 10 months, but seed continued to germinate up to 10 months after seed addition (late spring/summer), so we used this as our start date). To simplify the analysis here we ignore the blocking structure.

Within 20 m around each block we removed any naturally occurring *H. lepidulum* plants to minimize natural seed input. In addition, we monitored 36 control plots (six in each block) in which no seeds were added. Seedlings occurred sporadically in these control plots and to account for natural recruitment we included the control plots in our analysis (as having 0 seeds added) along with an intercept term, \( i \), in the recruitment function that

![Diagram showing recruitment functions for different treatments](image-url)
estimates the number of naturally occurring seedlings per plot based on the numbers in control plots. The general recruitment function we fitted was therefore

\[
 r = bn \left[ 1 - \frac{\lambda}{(\lambda + s/n)^2} \right] + i. \tag{11}
\]

We fitted this function to the data for each month in which plots were measured, along with equivalent versions of the Skellam and Beverton-Holt functions, in a Bayesian framework using OpenBugs version 2.10 called from the BRugs package using R version 2.6.2 (R Development Core Team 2005). We assumed the numbers of seedlings per plot followed a negative binomial distribution, and used noninformative prior distributions to allow the data to drive parameter estimation. Models were run with three chains for 100,000 iterations and thinned to retain every 10th iteration, with a burn-in of 5000 iterations. Posterior distributions of the parameter estimates for \( n \) and \( \lambda \) were highly skewed, so we used medians to characterize central tendency.

We compared the fit of the three recruitment functions to the data for each month using the deviance information criterion (DIC; Spiegelhalter et al. 2002), which is a Bayesian equivalent of Akaike’s information criterion (AIC; Akaike 1973, Burnham and Anderson 2002). The general recruitment function fitted the data best in all cases, although there was little difference in fit among functions at 10, 13, and 26 months (Table 1; DIC values differed by \( \leq 2 \)). The general recruitment function provided a better fit at 26 and 37 months (difference in DIC \( \leq 4 \)) and a substantially better fit at 48 months (difference in DIC about 60).

Panels a–f in Fig. 4A plot the number of seedlings as a function of the number of seeds added at each of the six measurements, along with the fitted general recruitment functions, while panels g–i in Fig. 4B plot changes in the parameter estimates for these functions. As predicted, the number of sites, \( n \), declines through time as the cohort ages and seedlings increase in size. The propor-
The proportion of safe sites, $b$, also declines, implying ongoing density-independent mortality. The decline is steepest between months 10 and 13, reflecting high seedling mortality in the summer following germination, with ongoing density-independent mortality to month 37, at which point the proportion of safe sites appears to stabilize at around 0.04. This estimate for the proportion of safe sites implies that the large majority of seeds and seedlings (~96%) failed to germinate or died due to density-independent processes (see also Clark et al. 2007). The importance of density-dependent mortality appears to increase through time, as evidenced by the increasing curvature of the recruitment function (Fig. 4A). Of those seeds and seedlings not lost to density-independent processes, for example, the proportion lost to density dependence at the highest level of seed addition increases steadily from 0.57 to 0.93 between

<table>
<thead>
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<th>No. months after seed addition</th>
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<tr>
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<tr>
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† Lower DIC values for measurements in each month indicate a better-fitting model, with the best-fitting models shown in boldface type.

Fig. 4. (A) Panels (a)–(f) show the number of *Hieracium lepidulum* seedlings as a function of the number of seeds added at each of the six measurements (months 10–48). The gray circles are the number of seedlings in replicate seed-addition plots; the solid circles are the means for plots with a given level of seed addition, while the lines are the general recruitment functions fitted to the data for each measurement using Eq. 11. (B) Panels (g)–(i) show changes in the parameter estimates ($n$, $b$, and $\lambda$) from the fitted recruitment functions over time (number of months after seed addition).
As average plant mass increases and the number of sites declines, the right-hand term in Eq. 11 will tend toward 0 and the relationship between plant mass and number of recruits on a log–log scale will approach an asymptote with slope $-1/\alpha$, assuming $b$ remains constant (i.e., no ongoing density-independent mortality). This is an equation for a self-thinning asymptote, defining an upper limit to the number of plants of given mass that can occupy a plot. If the area required to meet a plant’s resource requirements scales as $M^{2/3}$ (Yoda et al. 1963) then the expected slope of the self-thinning asymptote is $-3/2$ (alternatively, if the scaling exponent is 3/4 then the expected slope is $-4/3$; Enquist et al. 1998). The right-hand term will approach 0 more rapidly for larger values of $s$ (the number of seeds added), so that plots at initially higher density will converge on the self-thinning asymptote at lower plant mass. The mechanistic model can thus be expressed as a function that describes the self-thinning trajectory of plots with different numbers of seeds added (Fig. 5). Ongoing density-independent mortality or the development of a size hierarchy (i.e., declines in $b$ or $\lambda$, or both) will tend to shift the trajectory and produce a convex self-thinning asymptote. Such variation might partly account for observed differences in the slopes of self-thinning lines (White 1981, Westoby 1984). Data from experiments in which different numbers of seeds are added to plots and the number and mass of recruits are followed through time could be used to fit both the recruitment and self-thinning functions, and to interpret the parameters in light of the theory and assumptions underpinning the model.

**DISCUSSION**

The importance of recruitment in shaping population and community dynamics, as well as ecosystem processes (Zeiter et al. 2006), highlights the need to understand the mechanisms underlying plant-recruitment patterns. In particular, the relative balance between seed limitation and establishment limitation has been a major focus of research in plant ecology (Shaw and Antonovics 1986, Turnbull et al. 2000, Zobel et al. 2000). Quantifying the recruitment function, relating seed availability to seedling production, provides a means of teasing apart these limitations (Poulsen et al. 2007).

We have derived a general equation for a recruitment function that has a mechanistic underpinning and parameters that have biological interpretation in terms of the characteristics of safe sites for seedling establishment. The model makes simplifying assumptions, some of which can be accommodated if required. We assume, for example, that all seeds added to a plot are viable. If we know the proportion of nonviable seed prior to addition then we can adjust the recruitment function accordingly. Similarly, we incorporated seed input from the background seed rain into the model by including control plots and an additional parameter in the recruitment function (see also Poulsen et al. 2007).
Formulating a mechanistically derived recruitment function should be helpful in several ways. First, as described by Poulsen et al. (2007), the recruitment function can be used to quantify the degree to which plant populations are seed vs. establishment limited. While recruitment can be understood as a balance between these two processes (Manning et al. 2004, Kollmann et al. 2007), quantitative assessments of this balance are needed.

Second, deriving a recruitment function with a mechanistic underpinning adds insight into the processes governing recruitment. In particular, using the general function, and assuming that seeds are randomly distributed across plots, we obtain estimates of the numbers of sites, the proportion of these that are safe sites, and the degree of size heterogeneity among sites. Comparing how these parameters vary among locations with different physical and biological conditions may reveal why some populations are more strongly seed or safe site limited than others.

Finally, the mechanistic underpinning may more naturally suggest hypotheses that can be experimentally tested. In our Hieracium lepidulum example, we could hypothesize how the size and availability of safe sites should change through time, leading to a priori predictions about how the form of the recruitment function should vary. The ability to make clear predictions may facilitate the design of experiments better equipped to test these, and lead to the development of more refined models on the basis of experimental data that fail to match those predictions. Likewise, a mechanistic model may naturally suggest extensions to other situations, such as the relationship between plant mass and seedling numbers that we derived. Ultimately, the interplay between data and models should lead to a more in-depth understanding of the processes governing recruitment.

Of course the applicability of any model depends on how well it captures the biology of the situation to which it is applied. Other recruitment functions, derived from models with different mechanistic underpinnings, may be appropriate in other circumstances (Poulsen et al. 2007). For example, where a primary cause of seed loss is predation but predators are satiated at high seed densities, a model that incorporates positive density dependence may be appropriate (Blundell and Peart 2004). The characteristics and availability of safe sites, however, are considered key drivers of plant recruitment (Harper et al. 1965, Grubb 1977), suggesting the recruitment function derived here should have wide applicability.

Acknowledgments
Thanks to Wendy Ruscoe for discussion and Phil Hulme and two referees for helpful comments on the manuscript. This work was funded by the Bio-Protection Research Centre and the Miss E. L. Hellaby Indigenous Grasslands Research Trust.

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