Hakea sericea: Development of a model of the impacts of biological control on population dynamics and rates of spread of an invasive species

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\textbf{Abstract}

This paper reports on the development and testing of a simulation model to assess the impacts of two seed-feeding biological control agents on the dispersal of an invasive perennial tree, Hakea sericea (Proteaceae), which was introduced into South Africa from Australia during the 1850s. The agents are known to reduce seed banks at the individual plant level but the population-level effects are not well understood. The aim of the study was to estimate the extent to which the biological control has reduced the population growth and rate of spread of this species. H. sericea is a serotinous species which releases its wind-dispersed seeds en masse when the parent plants are killed, usually by fire. Field data were used to develop functions describing the fecundity of the plants and the impacts of the biological control agents as well as seedling recruitment rates and density dependent mortality. A group of experts provided estimates of the cumulative proportion of seeds that would disperse over distances from 50 to 1000 m following a fire. The estimates were used to fit various long-range dispersal functions. The Weibull distribution gave the overall best fit and was used to generate parameter sets from each expert’s estimates of dispersal. Simulations were then run using a reasonable range of fire intervals and dispersal parameters for the two experts whose estimates represented the minimum and maximum dispersal distances. Biological control agents have reduced the seed loads on H. sericea plants by more than 95%. This, in turn, reduced population growth rates, maximum seed dispersal distances and the formation of new invasion foci. Population growth rates and spread rates were positively correlated because greater dispersal distances resulted in lower densities and, thus, lower levels of density dependent mortality. Numerous previous studies have found that biological control can limit population growth rates of invasive plants, but this is one of the few to have estimated the impacts on the invasion rates and to use an individual-based modelling approach to estimate population-level effects.

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1. Introduction

The effectiveness of seed-feeding biological control agents against invasive plant species has been questioned because, supposedly, excessively high levels of seed destruction are needed to reduce the density and overall abundance of the target weed (e.g. Myers and Risley, 2000). For many plant species, natural losses during the seed-seeding transition frequently exceed 95% (Salisbury, 1942; Harper, 1977). Therefore, plant populations are generally limited by factors other than seeds and seed-feeding insects may be achieving nothing more than destroying seeds that would be lost at a later stage anyway. Biological control agents may even have a detrimental impact if they increase the survival rates of seedlings by, for example, reducing post-establishment thinning due to intra-specific competition (Myers and Risley, 2000). Evidence from biological control programmes is equivocal. For example, a 99.7% reduction in seed production of Sesbania punicea, due to the combined damage caused by two species of biological-control agents, resulted in only a marginal decline in population densities of the host plant, despite it having relatively short-lived seed banks (Hoffmann, 1990; Hoffmann and Moran, 1998). Conversely, Rees and Faynter (1997) found that even a 75% reduction in seed production could have a significant impact on the overall abundance of Cytisus scoparius.

Moran et al. (2004) have countered these arguments by suggesting that biological control agents that limit viable seed production can be effective in other ways, such as when combined with other control measures to deal with adult plants or during follow-up operations dealing with seedlings in previously cleared areas. Lower seedling densities can make control operations less costly and more efficient by allowing less expensive or less manpower-intensive control methods to be used. Seed-feeding agents can also prevent conflicts of interests by enabling those who wish to use the plant to do so whilst minimising seed production in uncultivated populations (Dennill and Donnelly, 1991). Limiting seed production may also reduce the dispersal of the weed species making it a less successful invader (Van Klinken et al., 2004), but the magnitude of this potential reduction has not yet been quantified.

One of the earliest biological control programmes to use agents that reduce seed production against a perennial alien plant invader was initiated against Hakea sericea Schrad. & J.C. Wendl. (Proteaceae) in South Africa in 1970. A key characteristic of H. sericea is its extreme serotinous habit: all of its seeds are retained in pairs in tough woody follicles which accumulate along the branches throughout the life of the plant. The wind-dispersed seeds are released en masse when the parent plant dies and the follicles dehisce, usually as a result of fires (Richardson et al., 1987). The terminal velocity of the winged seeds has been measured at 1.03 m/s in calm air and plants seldom exceed 5 m in height so most seeds will fall within tens of metres of the parent plants (Richardson et al., 1987). However, some of the seeds may be blown for considerable distances (kilometres) by the prevailing southeasterly winds. These are unusually strong for a Mediterranean climatic region (Deacon et al., 1992) but are characteristic of the coastal regions of the Western Cape during the warm, dry summer months. Continuous spells with mean velocities of 25–32 km/h (6.9–8.9 m/s), with gusts reaching twice these speeds, are frequent and can last for periods of several days. In this region, Pinus radiata, which has seeds that are morphologically similar to Hakea species, commonly disperses more than 1 km from source (Richardson and Brown, 1986). It is likely that long-distance dispersal models for pines, such as those developed by Ledgard (2001), Clark (1998), Clark et al. (1998) and Nathan et al. (2001), are applicable to Hakea species as well. Such long-range dispersal allows the plant to rapidly invade new areas by establishing founder colonies or foci far from the parent stands (Moody and Mack, 1988), making it difficult to control.

H. sericea is considered one of the most aggressive invasive species of the Cape fynbos vegetation, where it thrives particularly on nutrient-poor, sandy soils in the Cape Mountains (Fugler, 1979; Richardson, 1984; Richardson et al., 1992). It is thought to have been introduced in 1858 to a botanical garden in Cape Town and was later planted in the mountain areas, often as a hedge around livestock enclosures (Neser and Fugler, 1983; Shaughnessy, 1986; Richardson et al., 1992). It spread very rapidly from these original plantings and by 1978 it had invaded almost 4800 km² of land originally covered in ‘montane fynbos’, including remote areas where control operations would be prohibitively expensive (Neser and Fugler, 1983; Kluge and Richardson, 1983; Macdonald, 1984; Shaughnessy, 1986). Although H. sericea was promoted far less than other Hakea species, it has invaded by far the greatest area, emphasising its invasiveness (Richardson et al., 1992).

Although there was a considerable effort to control Hakea in most of the affected areas, it soon became evident that mechanical control programmes would not succeed on their own. As a result, 1970 saw the introduction of two seed-destroying biological control agents against H. sericea in South Africa, a weevil, Eryttena consputa Pascoe, whose larvae develop in and destroy the immature fruits, and a carposinid moth, Carposina autologa Meyrick, whose larvae destroy the ripe seeds in fully-formed follicles (Kluge and Neser, 1991). Both agents have become widespread and abundant and have been credited with having at least some success in reducing the status of H. sericea as a weed (Kluge and Neser, 1991; Gordon, 1999). However, extensive thickets of the weed persist in many areas (Te Roller, 2004). Hakea species account for just 2% of the national budget for control operations but this is largely because the difficulty of working in remote areas encourages managers to prioritise more accessible areas (Marais et al., 2004). These contrasting observations suggest that the biological control agents have curbed the invasiveness (i.e. the rate of spread) of H. sericea during the last four decades, but that they have not been able to reverse the invasion in already-affected areas.

It has proved to be practically impossible to determine empirically the effect of biological control agents on the rates of spread of invasive species and doing so remains an intractable problem (Van Klinken et al., 2004). An alternate way of gaining an understanding of the dynamics of these systems is to use simulation models. This paper describes the development, parameterisation and testing of a stochastic, individual-based, spatio-temporal simulation model to compare population growth and spread rates of H. sericea over a series of generations (induced by fires) with and without the biological control agents. As the interest was mainly in
the spread of *H. sericea*, the model was optimised for long distance seed dispersal. Dynamics within stands were not modelled in detail except for density-dependent mortality of seedlings and young plants. Many studies have reported on the impacts of biological control on seed bank dynamics (e.g. Dennill and Donelly, 1991; Rees and Paynter, 1997; Hoffmann and Moran, 1998; Hoffmann et al., 1998a,b; Shea and Kelly, 2004; Paynter, 2005) but few have assessed the impacts on dispersal (e.g. Neubert and Parker, 2004; Shea, 2004) and, as far as we know, none have used an individual-based model to assess population-level impacts on dispersal, particularly the rate of spread.

2. Methods

2.1. Field methods and available knowledge

2.1.1. Field sites and sampling methods

Six survey sites (Table 1) were selected opportunistically by finding *H. sericea* stands in which there had been a ‘natural’ fire event within the previous year. The sites were first visited after the onset of rains following the fire when all of the surviving *H. sericea* seeds had germinated and become small seedlings. Straight-line transects were laid at random intervals through portions of the burnt patches and metre square plots were set out at intervals of 5 m along each transect, as used by Bond et al. (1984). During the first survey at each site the number of dead pre-fire adult (parent) plants within each metre square was recorded (the adult plants are killed by fire but remain standing for a number of years after the fire). The parent plant closest to each 5-m interval point along a transect was located. Its basal stem diameter was measured and the number of dehisced seed follicles was counted. These counts were used to determine the number of seeds/m² that had been shed by the parent plants. The number of seeds was estimated by doubling the average number of follicles per plant (to account for the two seeds per follicle) and multiplying the result by the average number of plants/m².

Seedling recruitment levels were estimated from field surveys at each of the field sites by counting the number of seedlings within each metre square. The measure of seed density relative to seedling density was used to estimate overall post dispersal seed mortality. Although some seeds would have been lost through long-range dispersal from the parent plants, this loss was assumed to have been balanced by immigration of seeds into the sample plots from other plants nearby. The sites were revisited annually, up to four times after the initial visits, to monitor the survival, growth and fecundity of the new generation of plants. The total number of plants within the metre squares was recorded and the height of the plant closest to the transect point was measured to gauge growth rates of the plants. Counts were then made of fruits that had been produced by any of the young plants within the metre square plots.

2.1.2. Impact of biological control on fruit load

A number of seed-destroying insects were introduced to control *H. sericea*, two of which have been particularly successful (Kluge and Neson, 1991; Gordon, 1999). The weevil *E. consputa* lays its eggs on the young follicles and its larvae destroy a per-
Table 2 – Maximum percentage destruction of follicles by both agents based on surveys at a range of field sites (A.J. Gordon and J.H. Hoffmann unpublished data)

<table>
<thead>
<tr>
<th>Years after fire</th>
<th>Young follicle feeder (% of new follicle production destroyed)</th>
<th>Mature follicle feeder (% of total number of follicles destroyed)</th>
</tr>
</thead>
<tbody>
<tr>
<td>4</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>5</td>
<td>10</td>
<td>1</td>
</tr>
<tr>
<td>6</td>
<td>40</td>
<td>3</td>
</tr>
<tr>
<td>7</td>
<td>60</td>
<td>10</td>
</tr>
<tr>
<td>8</td>
<td>80</td>
<td>25</td>
</tr>
<tr>
<td>9</td>
<td>99</td>
<td>40</td>
</tr>
<tr>
<td>10</td>
<td>99</td>
<td>60</td>
</tr>
<tr>
<td>11</td>
<td>99</td>
<td>80</td>
</tr>
<tr>
<td>12 and older</td>
<td>99</td>
<td>80</td>
</tr>
</tbody>
</table>

Percentage of the current year’s seed crop (its mnemonic is thus YFF). The percentage of follicles that are destroyed increases as the age of the *Hakea* population increases because the weevils are slow to colonise plants that are regenerating after fires (Gordon, 1999) (Table 2). The seed-feeding moth *C. autologa* lays its eggs on the mature follicles of all ages, selecting only for its preferred (knobbly) form and ignoring whether or not the follicle has already been damaged (Gordon, 1993, 1999) (its mnemonic is thus MFF). The larvae tunnel into the follicle and destroy the seeds. The proportion of the destroyed mature follicles from a given year also increases with time because the MFF continues laying eggs on follicles of all ages (Table 2). The figures for the MFF are, therefore, the cumulative percentage of all the old follicles on the plant that would be destroyed. This is most easily understood with an example. The MFF arrives early in year 5 by which stage a mature *H. sericea* plant may have 100 mature follicles which have escaped destruction by the YFF. During year 5 the MFF will destroy 1% of those 100 leaving 99. In year 6 the plant adds 60 more mature follicles which escape the YFF making the new total 159. The MFF now destroys 2% of the 159, leaving about 154 mature follicles, and so on.

To estimate the impact of *E. consputa* on the fecundity of *H. sericea*, counts were made on follicle loads on plants at several sites. At least 20 plants were randomly selected at each of 29 sites in the Cape Province, including the six sites in Table 3. For each plant the basal stem diameter was measured and the number of mature follicles on the plant was recorded. Basal stem diameters were converted to basal stem areas which were used to plot linear regressions of fruits against basal stem area for each plant. This relationship was compared with one from South Africa that was obtained from a population before biological control had been implemented (Fugler, 1979). Reductions in follicle (seed) production were calculated by comparing relationships between plant size and the number of follicles from the post-biological control counts with the pre-biological control counts.

The biological control agents are either killed (immature stages) or disperse (adults) during fires. Adults move back into the burnt areas when the plants reach a suitable stage of development to support the insects. This process can be hastened by making deliberate manual reintroductions of the insects but the values used in this study are based on the assumption that the agents have recolonised by themselves and that there is a minimal delay between the on-set of fruit production and the arrival of the agent. The agents are assumed to spread rapidly throughout the simulated stand and to have a uniform impact on the *Hakea* plants.

2.1.3. Fire

Studies of the regeneration requirements of the tall, seed-regenerating, shrubs of the Proteaceae (Kruger and Bigalke, 1984; Van Wilgen et al., 1992; Richardson et al., 1994; Le Maitre, 1999) indicate that fires occurred naturally in fynbos at intervals of about 10–20 years. Fires are necessary to rejuvenate fynbos ecosystems which would otherwise become moribund, with the exception of limited areas where forest vegetation can establish itself (Le Maitre and Midgley, 1992; Manders and Richardson, 1992). Most fires occur in summer and autumn, whether from natural causes or human action, with prescribed management fires occurring mainly after the first winter rains to minimise the risk of losing control of the fire (Van Wilgen et al., 1992; Richardson et al., 1994).

Table 3 – Data for *Hakea sericea* stands and plants from selected populations which were sampled after fires

<table>
<thead>
<tr>
<th>Site</th>
<th>Density (plants/m²)</th>
<th>Basal area (mm²)</th>
<th>Fruits/plant</th>
<th>Seed/m²</th>
<th>Seeds/plant</th>
<th>Seedlings/m² year 1</th>
<th>Seedlings/seed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Slanghoek</td>
<td>0.30</td>
<td>7.40</td>
<td>63.00</td>
<td>35.30</td>
<td>117.67</td>
<td>9.40</td>
<td>0.27</td>
</tr>
<tr>
<td>Stettynskloof</td>
<td>0.20</td>
<td>13.20</td>
<td>54.20</td>
<td>20.10</td>
<td>100.50</td>
<td>1.00</td>
<td>0.05</td>
</tr>
<tr>
<td>Grahamstown</td>
<td>0.40</td>
<td>10.70</td>
<td>48.80</td>
<td>39.00</td>
<td>97.50</td>
<td>5.40</td>
<td>0.14</td>
</tr>
<tr>
<td>Kareedouw</td>
<td>0.20</td>
<td>6.80</td>
<td>4.50</td>
<td>1.60</td>
<td>8.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Goudini</td>
<td>0.80</td>
<td>11.80</td>
<td>86.60</td>
<td>135.10</td>
<td>168.88</td>
<td>1.96</td>
<td>0.01</td>
</tr>
<tr>
<td>Welverdiend</td>
<td>3.40</td>
<td>5.00</td>
<td>7.90</td>
<td>53.00</td>
<td>15.59</td>
<td>1.20</td>
<td>0.02</td>
</tr>
</tbody>
</table>

For more information on the study sites see Table 1.
The simulated fires were assumed to occur in autumn which is the season when recruitment of the ecologically similar seed-regenerating indigenous Proteaceae shrubs is the most successful (Bond et al., 1984, 1995).

2.2. Model structure

The description of the HakSimSpread model follows the ODD protocol suggested by (Grimm et al., 2006) where ODD is an acronym based on the major sections of the description, namely: Overview, Design Concepts and Details. The aim of the protocol is to provide a framework which makes it easier to understand the model and covers all the relevant aspects required for a comprehensive description of an individual-based model. The standard sequence in which the different aspects are presented makes it easier to locate particular information.

2.2.1. Overview

2.2.1.1. Purpose. The purpose of the model is to model the pattern of spread of *H. sericea* invasions under different scenarios. To keep the model tractable and to facilitate interpretation of the outputs, the environment in the model is assumed to be homogeneous with respect to seed dispersal and germination, seedling recruitment and seed production, and no interactions with other species occur.

2.2.1.2. State variables and scales. HakSimSpread is an individual-based, spatiotemporally explicit, stochastic, single-species, simulation model which was developed in Delphi 7. It consists of three hierarchical levels, namely the individual plants, the species (a single one in this case) and the simulated patch with a size of 1 km × 1 km. A grid (cell size 1 m × 1 m) is used to model the interactions between individuals, i.e. competition and seed dispersal. Individuals are characterised by their location on the grid (x and y coordinates). Species specific parameters characterise the life history and competitiveness (Table 4). The simulated patch is considered as being spatially homogeneous, i.e. conditions are the same across the patch and do not change in space or time. Seeds dispersing out of the simulated landscape are lost from the simulated landscape and plants occurring outside the simulated landscape have no competitive effects on plants within the simulated landscape.

2.2.1.3. Process overview and scheduling. The simulation model consists of four processes, namely germination and establishment, seed production (including the impact of the biocontrol agents), fire (releasing seeds from the plant) and seed dispersal, which are executed in that order. Processes act on either the individual plant or on the seeds. The competition grid links the species and brokers the interaction between plants. The parameters and their initial values are shown in Table 4.

One time-step represents one generation, namely from seed germination to adult plant death during a fire. Therefore, it is equivalent to the fire recurrence interval.

Plants exert a certain amount of competition into their neighbourhood. The degree of competition experienced in a cell is caused by all other plants on the grid and is stored in the competition grid. The degree of competition experienced by an individual plant is indifferent to the individual causing the competition. The germination and establishment process is influenced by the competition the seedling is exposed to and, in return, these processes update the competition grid. As all plants die during the process fire, the competition grid is reset to zero.

2.2.2. Design concepts

2.2.2.1. Emergence. The life cycles of the individual plants are modelled using empirical rules and probabilities from which the spatial pattern of the simulated patch emerges.

2.2.2.2. Sensing. It is assumed that individual plants are affected by the relative competitiveness they are exposed to. In addition it is assumed that seedlings experience the competition in the location where they have germinated.

2.2.2.3. Interaction. Interaction among individuals is modelled through competition following the field of neighbourhood (FON) approach described by Berger and Hildenbrandt (2000). Each plant experiences a certain amount of competition, depending on its species, in its neighbourhood. This is called the zone of influence (ZOI) (Czárán, 1998; Berger and Hildenbrandt, 2000). The size of the ZOI is determined by the size of the plant itself and a constant factor specific to the species, ZOI_rel, the “relative ZOI radius”. The strength of the competition within this ZOI, the FON, is not constant, but is dependant on the distance \( r_p \) from the location of the plant following:

\[
FON(r_p) = \begin{cases} 
\text{Comp} & \text{if } r_p \leq r \\
\text{Comp} - \frac{(r_p - r)\text{Comp}}{r(ZOI_{rel} - 1)} & \text{if } r < r_p < rZOI_{rel} \\
0 & \text{if } r_p \geq rZOI_{rel}
\end{cases}
\]  

Table 4 - Parameter values for the different processes in the model

<table>
<thead>
<tr>
<th>Process</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species parameter</td>
<td></td>
</tr>
<tr>
<td>Relative ZOI radius (m)</td>
<td>2.2</td>
</tr>
<tr>
<td>Competitiveness</td>
<td>1000</td>
</tr>
<tr>
<td>Germination and establishment</td>
<td></td>
</tr>
<tr>
<td>Establishment probability (fraction of seeds)</td>
<td>0.04</td>
</tr>
<tr>
<td>Maximum establishment up to competition level</td>
<td>0</td>
</tr>
<tr>
<td>Zero establishment at a competition level higher than</td>
<td>1</td>
</tr>
<tr>
<td>Seed production</td>
<td>See Fig. 1</td>
</tr>
<tr>
<td>Fire interval</td>
<td>7, 9, 11, 20</td>
</tr>
<tr>
<td>Seed dispersal</td>
<td></td>
</tr>
<tr>
<td>Seed dispersal kernel</td>
<td>Weibull, parameter</td>
</tr>
</tbody>
</table>

ZOI stands for zone of influence.
where \( r \) is the radius of the cover of the plant and \( \text{Comp} \) is the maximum competitiveness of the species. As we are dealing with a one species system, and the absolute value of \( \text{Comp} \) is only important in multi-species system in which it describes the competitiveness of one species relative to the other, \( \text{Comp} \) is set to 1000. The FONs of all plants are superimposed to obtain the competition at each given point \((x, y)\) in space:

\[
F(x, y) = \sum_{N} FON_n(x, y) \tag{2}
\]

and finally \( F(x, y) \) is stored in a grid which is updated by the processes fire and germination and establishment.

2.2.2.4. Stochasticity. RenPatch is a stochastic simulation model—the processes seed dispersal and germination and establishment are stochastic, while seed production is deterministic to reduce the complexity of the model. Seed dispersal is modelled based on probability density functions for the distance and directions the seeds disperse in. Germination and establishment are founded on probabilities of germination and establishment, however, the establishment probabilities are modified according the competition the seedling is exposed to. The order in which the individuals are evaluated in the different modules follows the order in which they were created during the simulation (in most cases this coincides with the age of the plants).

2.2.2.5. Observation. After completion of each time step, the location of each individual is saved and is later analysed.

2.2.3. Details
2.2.3.1. Initialisation. The simulation is initialised with empty cells except for one individual established plant in the centre cell. This individual forms the initial seed source for the spread.

2.2.3.2. Input. The inputs in the model are the selected fire frequencies. As one time-step in the model represents one fire interval, the only impact the fire interval has is on the number of seeds produced per time-step. The longer the interval, the more seeds are produced. In addition, the number of seeds produced also depends on the biocontrol agents present (see Section 2.1.2)

2.2.4. Sub-models of HakSimSpread
2.2.4.1. Germination and establishment. The process germination and establishment includes two separate sub-processes: germination and establishment. Germination takes place every time-step and, as the species has no dormancy (Richardson et al., 1987), it is assumed that all seeds germinate immediately after the first substantial rainfall event that follows dispersal. Germination is characterised by a vector which relates the probability of germination to the age of the seed so that older seeds have poorer germination.

Density-dependent thinning occurs during the second phase of the process, establishment. The probability of establishment is based on a maximum probability of establishment when no competition is experienced. The impact of competition on the maximum establishment is characterised by two parameters. One parameter specifies the level of competition at which there is no effect on a seedling in a cell and a second parameter specifies the level of competition which results in the death of the seedling, reducing the probability of establishment to zero. The probability of establishment decreases linearly between these two values.

2.2.4.2. Seed production. Seed production was assumed to be deterministic and only dependent on the age of the plant. Seed production per generation, therefore, depends on two factors: the simulated fire frequency and the biocontrol regime to which \( H. \) sericea is exposed. The longer the interval between two fires, the more seeds are produced and accumulated on the plant (Fig. 1). The field data described above were used to

Fig. 1 – Simulated seed banks of \( Hakea \) sericea with and without biocontrol (YFF: young follicle feeder; MFF: mature follicle feeder). Note the log scale for the seed bank data. The cumulative seed banks decline from age 9 to 11 because the MFFs effectiveness is still increasing so that it will destroy a proportion of the previously accumulated seed bank.
define the relationship between seed production and accumulation and post-fire age, giving the number of seed produced per plant for a given fire frequency.

The biocontrol agents destroy a certain proportion of the seeds produced as described earlier. The model allows the user to assess the impacts of: no biocontrol, young follicle feeder (YFF) and mature follicle feeder (MFF) and calculate the number of seeds per plant under different biocontrol treatments (Fig. 1).

2.2.4.3. Fire. Fire kills all the existing *H. sericea* plants. The seeds are released from the seed bank on the plant as the dead plants dry out. The viability of the seeds is not reduced by the fire in accordance with the findings of Richardson et al. (1987). Combining the four fire frequencies (7, 9, 11 and 20 years) with the four possible biocontrol treatments (YFF, MFF, YFF & MFF, NONE), gives 16 different sizes of the seed bank at the time of the fire (Fig. 1).

2.2.4.4. Seed dispersal. Seed dispersal is modelled stochastically using the probability distribution specified in the seed dispersal kernel for an individual plant. Six Weibull kernels can be seen in Fig. 2. The Weibull function was chosen having a mean rank of 1.3 compared with 2.0 for the inverse power. The best fit for the expert's estimates was given by the Weibull distribution \((-\ln(L) = 0.0006)\) followed by the inverse power \((-\ln(L) = 0.0038)\) and the lognormal \((-\ln(L) = 0.0145)\) distributions (Fig. 2). The Weibull distribution provided the best fit for all the different experts except JH, having a mean rank of 1.3 compared with 2.0 for the inverse power. The best fit for estimates provided by JH was the inverse power followed by the lognormal. The resulting seed dispersal kernels can be seen in Fig. 2. The Weibull function was chosen for the simulation model because it provided the best overall fit.

There is a wide range in the values for the parameters of the fitted Weibull distributions between experts (Table 7). Alpha (the scale parameter) ranges from 5.1 to 25.3 and Gamma (the shape parameter) from 0.44 to 4.00. The extreme Gamma value is for the estimate by JH which differs markedly from the others (Table 6), but there is no systematic pattern to the values of the Alpha parameter. The final fitted relationships show that most of the dispersal distributions are similar, the exception being the one for JH which has no seeds within a metre of the parent and almost all of the seeds within 100 m (Fig. 2). We used all the parameter sets from all experts, and the Weibull distribution fitted to the average estimate for simulations, but focus mainly on the results of simulations using the estimates by BW and DR as these proved to be the extreme cases.

### Table 5 – Reproductive maturation of young *Hakea sericea* plants based on repeated surveys of populations in the field (for details of the study sites see Table 1)

<table>
<thead>
<tr>
<th>Years after fire</th>
<th>Percentage of plants with fruits</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.00</td>
</tr>
<tr>
<td>2</td>
<td>0.00</td>
</tr>
<tr>
<td>3</td>
<td>4.02</td>
</tr>
<tr>
<td>4</td>
<td>39.30</td>
</tr>
<tr>
<td>5</td>
<td>81.03</td>
</tr>
<tr>
<td>6</td>
<td>89.80</td>
</tr>
</tbody>
</table>

### Table 6 – Cumulative proportions of seeds that travel different distances as estimated by five people with extensive field experience

<table>
<thead>
<tr>
<th>Dispersal distance (m)</th>
<th>BW</th>
<th>DM</th>
<th>DR</th>
<th>JH</th>
<th>TG</th>
<th>Mean</th>
<th>S. D.</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>0.50</td>
<td>0.50</td>
<td>0.75</td>
<td>0.95</td>
<td>0.50</td>
<td>0.64</td>
<td>0.20</td>
</tr>
<tr>
<td>50</td>
<td>0.65</td>
<td>0.85</td>
<td>0.95</td>
<td>0.99</td>
<td>0.98</td>
<td>0.85</td>
<td>0.13</td>
</tr>
<tr>
<td>100</td>
<td>0.95</td>
<td>0.95</td>
<td>0.99</td>
<td>0.99</td>
<td>0.99</td>
<td>0.95</td>
<td>0.04</td>
</tr>
<tr>
<td>500</td>
<td>0.99</td>
<td>0.9999</td>
<td>0.9999</td>
<td>0.999999</td>
<td>0.99</td>
<td>0.99996</td>
<td>0.01</td>
</tr>
<tr>
<td>5000</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>0.00</td>
</tr>
</tbody>
</table>

3.3. Mortality and density dependence

The available field data give an estimated mean of 0.082 one-year old seedlings per seed (range 0–0.27) over all the sites (Table 3). The net recruitment includes the mortality of seeds in the follicles during the fire, post-release predation and other losses until the seedlings reach an age of one year. For year 1–2 the mean mortality over four of the sites was 51%. Only one of the sites provided mortality data for years 2–3 and at that site it was 21%. The overall mortality at this site for years 1–3 was about 57%—only 43% of the seedlings from year 1 survived until year 3. The net survival from seeds through to young plants was, therefore, 3.49% which was rounded to a maximum probability of establishment of 0.04 for the simulation model (EstMax).

Density-dependent mortality was adjusted by varying of ZOIrel to reduce the seedling densities (per m²) to the range observed in field surveys (Fig. 3). The observed mean density at the six field sites was 0.38 plants/m² (Table 3). A value of 0.25 for the parameter ZOIrel gave a mean density of 0.25 plants/m² (for 100 simulations) and ZOIrel = 1.5 gave 0.82 plants/m², again for 100 simulations. The final simulated mean of 0.3804 plants/m² (given by ZOIrel = 2.2) is essentially identical to the observed, the main difference being that the standard deviation of the densities in the simulated data (0.04, n = 100) is much lower than in the observed data (0.24, n = 6), probably because of the larger sample size in the simulated data.

3.4. Densities in circles and net population growth rate

The net result of the dispersal and the self-thinning depends on which expert’s dispersal estimates were used to derive the parameters for the Weibull dispersal kernel (Fig. 4). The final densities after three generations decrease with increasing distance from the initial plant at different rates for the DR and
Fig. 4 – Distribution of the plants in concentric circles up to 500 m from the initial plant (which was at the centre of the circle) after three generations with a fire interval of 11 years. Note the different scales for the number of plants. The number of plants is for each successive 10 m annulus (e.g. 10–20 m, 20–30 m). Five separate runs per expert were done. Parameter values for the Weibull distribution derived from the estimates by: (a) DR and (b) by BWV (see Tables 5 and 6).

BW dispersal parameters, with the DR densities declining from 20 m and the BW only from about 50 m. The actual number of plants in each 10 m annulus from the initial plant increases up to about 100 m; it then declines rapidly from about 800 plants to less than 50 between 490 and 500 m from the initial plant. Using BW’s parameter estimates, the numbers of plants per annulus increases up to about 170 m from the initial plant and the decline from 200 to 500 m is more gradual and roughly linear instead of exponential. The more conservative dispersal estimates (e.g. DR) result in relatively few seeds dispersing more than 100–200 m from the initial plant and a reduction in population growth rates because of the high density-dependent mortality rates of the seedlings. Mean populations after three generations ranged from 41 000 plants for BW to 12 400 for DR, with the other experts estimate falling between these extremes.

The net recruitment per generation also was markedly affected by the choice of dispersal parameters and intervals between fires (Fig. 5). For BW’s estimates the number of plants increases rapidly with increasing fire intervals in the 1st generation (Table 8) but increasingly more slowly in the 2nd and 3rd generations respectively. The same pattern is evident when using DR’s estimates but the highest population growth rate

![Fig. 5](image)

**Fig. 5** – Relationship between the interval between fires (years) and the number of established young plants per parent for successive generations of Hakea plants. Ten runs with random fire intervals were done for each expert’s seed dispersal estimates. For more information see the text. BW: Weibull seed dispersal kernel parameters based on estimates of cumulative seed dispersal by BW; DR: the same for DR.

| Table 8 – Relationship between the number of seedlings per parent and the interval between fires for successive generations of Hakea |
|---|---|---|---|
| Expert | Generation number | Linear regression of fire interval (years) and plants per parent (Y) in each generation | Mean number of plants in each generation |
| BW | 1 | Y = 4.30 × years + 3 | 61.3 |
| | 2 | Y = 2.15 × years + 3 | 1810.3 |
| | 3 | Y = 1.34 × years + 3 | 33049.4 |
| DR | 1 | Y = 1.34 × years + 3 | 32.5 |
| | 2 | Y = 1.28 × years + 3 | 627.9 |
| | 3 | Y = 0.63 × years + 3 | 7295.3 |

Two experts (BW and DR, see Table 5) estimates of the cumulative seed dispersal were used to derive the parameters for the Weibull seed dispersal kernel. An x-intercept of 3 was used throughout because that is the age of first seed production.
3.5. Impacts of biological control on seed dispersal

Although only the Weibull distribution was used in the later simulations, we did some initial sensitivity tests using all the kernels. The measure we looked at in the sensitivity analysis was the maximum distance at which we can expect to find a seed with a given probability of 0.95, from now on referred to as ‘maximum dispersal distance of a seed’. If the negative exponential relationship (the “standard” seed dispersal curve in most studies) is used, then reductions in seed numbers per plant from 1000 to 500 seeds have little effect on the maximum dispersal distance of a seed, changing it from 47 to 39 m (Table 9). But a reduction from 100 to 50 seeds changes the distance from 14 to 9 m, a much greater proportional impact. The most sensitive dispersal kernel is the Weibull distribution, which gave a greater probability of long-range dispersal than the others. A reduction from 1000 to 500 seeds reduced the maximum distance from 86 to 56 m, and from 100 to 50 seeds from 16 to 9 m. The inverse power seems to be the next most sensitive dispersal kernel parameters derived from the different experts seed dispersal estimates (Table 6) found that those based on DR’s estimates had the most limited dispersal and those of BW resulted in the most extensive dispersal (see Fig. 4). The reduction of seed banks due to biological control has a marked impact on the distances seeds travel. Using DR’s parameter values, the reductions in plant densities are greatest between 40 and 70 m for the MFF, with the YFF having a greater impact than the MFF (Fig. 6), as would be expected from their impacts on seed banks. The greatest differences for the YFF and for both agents are in the 0–30 m range. Both agents together have a major impact, with no seeds reaching beyond 140 m and very low densities throughout. Using BW’s estimates, the reductions are less marked for the YFF and MFF on their own (Fig. 7), but for both together the density reduction is similar to DR’s parameter estimates. The greatest differences between no agents and MFF are from 40 to 90 m and 0 to 20 m for the YFF and for both agents. The reduction in the maximum distance travelled by seeds is much less for both agents, with a few seeds still reaching 330–350 m and one plant to 380 m, well beyond the distances reached using DR’s parameter estimates. This extra distance would be important for establishing new foci and would be very important for increasing spread rates in subsequent generations.

3.6. Impacts of biological control on population growth and dispersal

The analyses of the outcomes of using the Weibull dispersal kernel parameters derived from the different experts seed dispersal estimates (Table 6) found that those based on DR’s estimates had the most limited dispersal and those of BW resulted in the most extensive dispersal (see Fig. 4). The reduction of seed banks due to biological control has a marked impact on the distances seeds travel. Using DR’s parameter values, the reductions in plant densities are greatest between 40 and 70 m for the MFF, with the YFF having a greater impact than the MFF (Fig. 6), as would be expected from their impacts on seed banks. The greatest differences for the YFF and for both agents are in the 0–30 m range. Both agents together have a major impact, with no seeds reaching beyond 140 m and very low densities throughout. Using BW’s estimates, the reductions are less marked for the YFF and MFF on their own (Fig. 7), but for both together the density reduction is similar to DR’s parameter estimates. The greatest differences between no agents and MFF are from 40 to 90 m and 0 to 20 m for the YFF and for both agents. The reduction in the maximum distance travelled by seeds is much less for both agents, with a few seeds still reaching 330–350 m and one plant to 380 m, well beyond the distances reached using DR’s parameter estimates. This extra distance would be important for establishing new foci and would be very important for increasing spread rates in subsequent generations.

3.7. Spatial pattern

The formation of new foci, and the clustering effect this has on seedlings, can be clearly seen in the distribution of seedling around the parent plants. Using DR’s parameter estimates,
only one plant becomes established more than 150 m away (Fig. 8). This then forms the nucleus for the 2nd generation plants which clump around it. Using BW’s parameter estimates, six plants occur beyond 150 m, one of them more than 400 m away (Fig. 9). These long-range dispersers then become the nuclei for the 2nd generation which is far more evenly spread over the model domain than is the case using DR’s parameter estimates. The model was not set-up to track seeds which dispersed outside the modelling domain, but it is reasonable to deduce that few 2nd generation seeds will have dispersed beyond the borders for DR’s parameter estimates compared with those of BW.

An indirect estimate can be obtained from seeds which dispersed diagonally into the corners and thus could disperse more than 500 m without being lost. It is not possible to compare different distance classes with each other directly, but nevertheless it is possible to compare the same distance class between different dispersal kernels and treatments. The number of seeds (plants) which were between 500 and 510 m ranges from about 1350 for BW to 30 for DR (Fig. 10), with the others falling between these two. The numbers decline steeply, partly because the area of the 1000 m x 1000 m square model domain that remains decreases rapidly after a radial distance of 500 m from the parent (only the corners are left). Only one

Fig. 6 – Mean density of seedlings in each 10 m annulus from the initial parent plant by the third generation. Four iterations were used with the cumulative seed dispersal estimates from DR, the Weibull dispersal kernel and an interval of 11 years between fires.

Fig. 7 – Mean density of seedlings in each 10 m annulus from the initial parent plant by the third generation. Four iterations were used with the cumulative seed dispersal estimates from BVW, the Weibull dispersal kernel and an interval of 11 years between fires.
Fig. 8 – Diagram showing the location of the parent plant and the established young plants of the 2nd generation with the four different combinations of biocontrol: None, YFF, MFF and Both derived using the Weibull dispersal kernel and the parameter estimates from DR.

Seed was dispersed as far as 680–690 m in five model iterations using DR’s parameters, with 600 m being the furthest that seeds consistently reached. Using BW’s parameters, 1–3 seeds consistently reached 700 m (Fig. 10). The percentage of the total population that was dispersed more than 500 m from the parent plant was highest for BW and lowest for DR with the other experts in between (Fig. 11). This same pattern holds for the actual number of plants dispersed for more than 500 m.

Fig. 9 – Diagram showing the location of the parent plant and the established young plants of the 2nd generation with the four different combinations of biocontrol: None, YFF, MFF and both, derived using the Weibull dispersal kernel and the parameter estimates from BVW.

4. Discussion

The outputs from the simulation model provide compelling evidence that biological control can play a role in limiting

Fig. 10 – Number of seedlings per 10 m annulus that were dispersed more than 500 m from the parent plant. Weibull dispersal kernel parameters based on each expert’s estimate of the cumulative seed dispersal curve and a fire interval of 11 years.
the rate of invasion of a given area, and in decreasing the population growth rates and, thus, the densities of the resulting stands relative to those without biological control. Hakea sericea is capable of producing and accumulating large numbers of seeds (Richardson et al., 1987) and maintaining a positive trend in the numbers of follicles (and thus seeds) per plant up to a very high density of 5.5 plants/m² in a mature stand (Bond et al., 1995; WJ. Bond pers. comm. 2005). Its high fecundity, combined with heat-resistant, woody follicles (fruit) and well-dispersed seeds, made it the most successful of the four Hakea species which invade fynbos (Richardson et al., 1987). The interaction between dispersal distance and net population growth rates, due to high density-dependent mortality in the dense stands that formed when dispersal distances were relatively short, was to be expected (Auld and Coote, 1980; Moody and Mack, 1988), but the magnitude of the reduction in population growth was greater than expected. Using DR’s dispersal parameter estimates, the population after three generations was only 30% of the one using BW’s estimates. The simulation model was kept simple by deliberately excluding spatial and temporal variations in the simulated environment, plant growth and fecundity, seed predation and seedling and adult mortality, although these are important factors (Bergelson et al., 1993; Hastings et al., 2004; With, 2004). This was done deliberately to reduce the amount of data required, and the complexity of the model outputs, and to focus on the main factors of interest to this analysis: seed dispersal patterns, overall fecundity versus the interval between fires, population growth rates and density dependent-mortality. Therefore, the results of this study are believed to have captured the major patterns in the outcomes and provide a reasonable reflection of the actual impacts on invasions by Hakea sericea. One aspect that was not assessed was spatial and temporal variability in the effectiveness of the biological control agents which can be an important determinant of the overall level of control achieved (Fagan et al., 2002), but field observations in H. sericea stands show that the agents are almost uniformly present by the time the plants are flowering and producing fruits (A.J. Gordon, unpublished data), so this should not be a significant issue for the simulated area of 1 km².

As noted in the introduction, this study is the first that we know of to use an individual-based model to quantify the impacts on seed dispersal patterns and, thus, on invasion rates. The reductions in H. sericea seedbanks due to biological control have a significant impact on both its ability to disperse for long distances and on its net population growth rates, especially when the parameters used in the dispersal kernel favour relatively short distance dispersal. The same effects were observed when the interval between fires was varied and similar impacts could be expected from any other factors which reduced the number of seeds per plant. High fecundity (i.e. propagule pressure) and high seedling recruitment rates have been recognised as key attributes of successful invaders for a long time (Salisbury, 1961; Baker, 1965 in Baker, 1968); for a recent review see Rejmánek et al. (2005). One of the earliest attempts to model the dispersal of an invading species made this link explicit by relating the population diffusion rate and the population per capita growth rate (Skellam, 1951) and this approach has recently been revitalised by linking it to matrix and diffusion models (Neubert and Caswell, 2000; Neubert and Parker, 2004; Shea, 2004). Thus, if fecundity plays a key role in the success of a particular invader, as seems to be the case in H. sericea (Richardson et al., 1987), then reductions in seed production which lead to reduced spread rates, like those found in this study, are to be expected. A detailed simulation model of pine invasion rates also found that rates of spread were particularly sensitive to dispersal parameters and that seedling establishment and juvenile survival also interacted significantly with mortality of recruits (Buckley et al., 2005). Neubert and Parker (2004) found similar interactions in a detailed model for Cytisus scoparius which incorporated biological control. These results all suggest that variation in mortality, whether density-dependent or density-independent, is a critical factor as well.

Modelling of seed dispersal, particularly long-range or long-tailed seed dispersal, is a rapidly growing field as shown by the numerous papers published in this field in recent years (e.g. Clark, 1998; Clark et al., 1998; Higgins and Richardson, 1999; Ledgard, 2001; Nathan et al., 2001, 2002, 2003; Higgins et al., 2003; Levin et al., 2003; Tackenberg et al., 2003a; Katul et al., 2005; Trakhtenbrot et al., 2005). These papers have found that the rates and patterns of spread of species with long distance dispersal are very sensitive to a range of factors, including the form of the function used in the model (Clark et al., 1998; Greene et al., 2004), life-history of the organism, and inherent uncertainties in data used to set up the models (Clark et al., 2003). Some authors have suggested mixed dispersal models should be used rather than single functions, either because different processes dominate for short than for long-distance dispersal (e.g. laminar flow versus turbulence or updraughts) or because long distance dispersal is seen an unusual rather than simply a rare event (Greene and Johnson, 1995; Higgins and Richardson, 1999; Horn et al., 2001; Nathan et al., 2002;
Higgins et al., 2003; Soons et al., 2004). Others have argued that thermal updrafts are more important than shear induced turbulence (Nathan et al., 2002; Tackenberg, 2003; Tackenberg et al., 2003b). Detailed mechanistic modelling suggests that the small fraction of the seeds lifted above a pine forest canopy may be dispersed for kilometres (Williams et al., 2006). Greene (2005) found that high intensity but short-period wind velocities are needed to abscise Taraxacum seeds, so that seeds which require lifting out of their receptacle in the fruit, like Hakea, are mainly dispersed during turbulent wind conditions which facilitate their spread.

The possibility of using an analytical mechanistic model rather than a phenomenological model was considered but not attempted in this study largely because of the difficulties in collecting the data needed to test and properly parameterise these models (see Nathan et al., 2003 for a discussion of this issue). Two phase models as discussed above were also considered but also would be difficult to set up given the very limited available information, leaving relatively simple functions as the most parsimonious option. Given that the parameterisation of the dispersal was based on solely on expert opinion, some corroboratory evidence was needed to test whether the simulated dispersal patterns were representative of the actual patterns in the field. Katul et al. (2005) provided a simplified and apparently robust model for independently estimating dispersal but this still requires estimates of the vertical wind velocities which were not available. However, Tackenberg et al. (2003a) have developed an approach which is based on their standard weather conditions and only requires data on the release heights and the terminal velocity of the seeds. If those weather conditions are accepted as suitably representative or conservative – their wind speeds were lower than those reported by Deacon et al. (1992) – and a terminal velocity of 1.0 m/s (Richardson et al., 1987) is used – the Wind Dispersal Potential (WDP) for a reference distance of 100 m ranges from 4 for a 1.0 m seed release height to 6 for a seed release height of 5 m (Fig. 4 in Tackenberg et al., 2003a). A WDP100 of 4 is equivalent to a between 1.6 and 3.2% of the seeds reaching more than 100 m from the source and a WDP100 of 6 to 6.4–12.8% (Table 3 in Tackenberg et al., 2003a). In this study the expert estimates of the proportion of the seeds reaching 100 m from the parent ranged from 0.10 to 0.01 (Table 6) which is rather more conservative. In addition, the simulations used by Tackenberg et al. (2003a) were for grassland environments which generally have smoother canopies and less turbulent near-ground conditions than shrublands or forests (Jarvis, 1985), leading to lower WDPs. The close correspondence with the independent estimate provided by Tackenberg et al. (2003a) suggests that the dispersal parameters used were conservative and, thus, that the dispersal patterns simulated in the model may even underestimate actual values in invaded areas. Genetic analysis has indicated that seed dispersal distances in Banksia hookeriana - which has a similar growth form and wind-dispersed seeds with a higher terminal velocity and thus lower WDP than H. sericea—may exceed 1.6 km (He et al., 2004). Some of the Banksia seeds may have been transported similar distances by parakeets but, given this proviso, the Banksia data support the argument that our simulations of seed dispersal distances may be conservative.

This analysis used a Weibull function for the dispersal kernel, primarily because this function gave the best overall fit to the estimates of the cumulative proportion of the seed dispersed versus distance from source. Greene et al. (2004) have argued that the lognormal function is the best one to use for plants because it can be interpreted mechanistically, provides a better fit to actual field data (it does not require highest seed densities at source), and may allow for greater long-range dispersal than other functions. We did not have field data to compare but, given the low release height for Hakea (<5 m) compared with taller plant species, it is likely that the greatest seed densities might be around the plant source so the lognormal would not necessarily give the best fit. Our analysis also found that the maximum distance reached by a seed was most sensitive to changes in the number of seeds at the source (for more than 50 seeds) when a Weibull function was used. The lognormal function was less sensitive in these situations.

Our findings also do not support the note by Richardson et al. (1987) that a 20% increase in seeds would increase dispersal distances by 80%. This finding was based on the use of a negative exponential function and can only be the case when the seed numbers at the source are <50. Neubert and Parker (2004) found that more than 95% of seeds of the ant-dispersed seeds of Cytisus scoparius needed to be destroyed to stop invasions but their study only examined short-distance dispersal mechanisms (metres) and not the long-distance dispersal used in this study.

A key feature of the simulated dispersal patterns is the formation of new invasion foci around individual plants which dispersed far from their parent (Figs. 8 and 9). The number of foci formed in the 2nd generation is far greater when the dispersal parameters allow for greater long-range dispersal (Fig. 9) than for less long-range dispersal (Fig. 8). These patterns interact with the impacts of biological control on the number of seeds to determine both the number of foci and the distance at which they establish. The clustered patterns output in this simulation confirm the importance of nascent foci in accelerating the spread of an invading species (Auld and Coote, 1980; Auld et al., 1983; Mack, 1985; Moody and Mack, 1988; Clark et al., 1998), especially given that density-dependent thinning is low in new foci but increases rapidly as the density in the vicinity of the foci increases with each succeeding generation of plants. The ability to establish distant foci was severely limited by reductions in the seed banks as well. If the agents are also able to rapidly colonise these founder populations then they can have a significant impact on the rate of spread and, ultimately, on the overall costs of control operations.

Although there are questions about how the degree of seed destruction needed for effective biological control using a seed feeding agent (e.g. Myers and Risley, 2000), it is likely that the reduction in seedling densities following biological control, and the reductions in rates of spread may still make this a cost effective option (Moran et al., 2004; Van Klinken et al., 2004). This study has shown that both population growth and spread rates of H. sericea are reduced by the biological control agents. Initial clearing of dense Hakea stands (75–100% canopy cover) costs about R500/ha compared with about R50/ha for sparse stands (1–5%), and the relationship between cover and cost is roughly linear (Marais et al., 2004). Using BW’s dispersal
parameters and fire intervals of 11 years to get a high population growth rate, the 4th generation has a population of about 210,000 plants in 100 ha (1000 m × 1000 m) or 2100 plants/ha, a dense stand. Using the same conditions and DR’s dispersal parameters would result in about 72,500 plants. With both biological control agents, the populations would be 5 and 7 plants, respectively. Assuming the plants are evenly distributed, even if the number of plants after biological control was 10-fold greater than the model predicts, the densities would still be so low that the cost saving would be of the order of 50–90% of the pre-biological-control cost. The saving would decline to about 25–50% if there were 1000-fold more plants after biological control. The results of this modelling exercise show that biological control using seed feeders can be a cost-effective method, as argued by Moran et al. (2004), even when the reductions in seed banks are lower than seems to be the case for H. sericea.

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