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Demography and management of the invasive plant species *Hypericum perforatum*. II. Construction and use of an individual-based model to predict population dynamics and the effects of management strategies

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Summary

1. *Hypericum perforatum*, St John's wort, is an invasive weed of natural and agro-ecosystems in south-eastern Australia. In previous work we used a long-term data set to determine which plant traits and environmental factors influence population growth and persistence in this species. These results were then used to parameterize an individual-based model of the population dynamics of *H. perforatum*, and this model was used to make predictions about what control strategies will be most effective for populations in open and shaded sites.

2. The model was constructed using multi-level, mixed-effects statistical models of growth, survival, fecundity and damage, incorporating intrinsic plant variables, environmental variables, herbivory and spatial and temporal stochasticity.

3. We found that populations in shaded and open sites had different dynamics and responses to control strategies. Shaded populations took longer to reach infestation densities and were less affected by herbivory and reductions in survival than open populations. Open populations increased faster in response to increases in rainfall, but this was not so for shaded populations.

4. We used sensitivity testing and management simulations to predict that the most successful control strategies will involve a reduction in vegetative size in both open and shaded sites. Reductions in flowering stem size and survival in shaded and open sites, respectively, are predicted to be the next most successful strategies. Dry conditions in the austral autumn/winter adversely affect populations in both open and shaded sites.

5. *Synthesis and applications*. These models have enabled us to rank management strategies based on quantitative analysis of their potential effects on population size. This is an important tool not only for ecologists concerned with control of invasive species but for conservation biologists trying to understand the factors limiting a rare or endangered species.

Key-words: biocontrol, control, integrated weed management, simulation, stochastic.

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Introduction

Control strategies for invasive weeds can be expensive (Williamson 1998; Centre for International Economics 2001), environmentally risky (Simberloff & Stiling 1996) and have high failure rates (Crawley 1989b). This necessitates the development of methods for assessing the efficacy and cost-effectiveness of potential control strategies before implementation. Researchers have long called for a more thorough understanding of target weed population dynamics and the impacts of suitable control strategies (Crawley 1989a; Hoffman &

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Moran 1998) but this is still not commonly carried out, especially before control is implemented. Modelling provides an important, although underused, tool for exploring the consequences of different management strategies.

Modellers have taken two main strategies when using population models to evaluate control strategies. The first is to use sensitivity and/or elasticity analysis to identify the life-history stages having the greatest impact on population growth rates and which are therefore the most appropriate stages to target for control. Population models based on difference equations (Freckleton & Watkinson 1998) and matrix models (Neeser, Aguero & Swanton 1998; Shea & Kelly 1998) have been used for this purpose. This is an approach shared with those in conservation circles, where population viability analysis, mostly using matrix models, is commonly employed to predict future risk of extinction of threatened populations (Coulson *et al*. 2001). The second strategy used (sometimes in conjunction with sensitivity and elasticity analysis) is to develop models that enable the direct evaluation of management impacts on target population dynamics (Firbank & Watkinson 1986; Godfray & Waage 1991; Shea & Kelly 1998; Higgins, Richardson & Cowling 2000; Buckley *et al*. 2001). We have used a combination of these approaches. Sensitivity analysis is used to identify parameters with the most potential for influencing the invasion process, and the effects of parameters are quantified using simulations.

Cousens (1995) has stressed the need for plant population models to reflect the biology of the species in question, as well as the environmental perturbations that cause much of the variability observed in nature. By incorporating more complexity into our models, what we may lose in the ability to make generalizations we gain in being able to make predictions about the behaviour of populations, under both our original model assumptions and perturbations imposed on the system. Plant populations in the real world are composed of individuals differing from each other in size, fecundity and responses to perturbations. Model predictions are sensitive to the inclusion of individual variation, and this variation can affect population growth, equilibrium density and stability (Bjornstad & Hansen 1994; Uchmanski 2000). Model predictions are also sensitive to the inclusion of spatial and temporal stochasticity (Renshaw 1991), especially at low population sizes, such as those that occur when an invasive plant is establishing in a new area or recovering from a population crash.

Previous models of plant populations have included simple sets of difference equations (Watkinson 1980) that assume that dynamics can be captured by a simple average, matrix model (Caswell 1989) where individuals are grouped into stage or age classes, and individual-based models (IBM), where individuals are followed and population behaviour occurs as the aggregate behaviour of individuals (Dieckmann, Herben & Law 1997). In the absence of a general theory of the ecology of interacting individuals, simulation studies are the main tools for analysing the behaviour of complex IBM (Lomnicki 1999). The use of these models in ecology has expanded with the availability of useful computer software and increased speed of calculation, enabling large numbers of individual plants to be configured and to interact in computer programs (DeAngelis & Gross 1992; Judson 1994). In this study, we used IBM as a method of incorporating the full range of structuring variables (e.g. size) and stochasticity found in our previous study (Buckley, Briese & Rees 2003, pp. 481–493 in this issue) to affect the vital rates of the invasive species *Hypericum perforatum* L., a noxious weed of pastures and natural habitats in southern Australia.

A quantitative understanding of what factors affect growth, survival and fecundity is an essential first step in the understanding of population dynamics. We outlined in our previous study (Buckley *et al*. 2003) statistical methods for constructing predictive models of the vital rates of *H. perforatum*. The functions and parameter values identified were then used in an IBM to characterize population-level processes and provide virtual populations on which to test control strategies. The IBM provides a realistic model of the population dynamics on which to perform experiments by altering the parameter values and functional forms of the vital rates. In this way, the model can be used to predict how management strategies would affect population dynamics in the field. Using this approach, we can narrow down a multitude of possible management options to those predicted to lead to sustained reductions in both population size and impact on the surrounding ecosystem. The resulting best-bet management strategies can then be thoroughly field-tested.

Methods

CONSTRUCTION OF THE IBM

The statistical analysis described in Buckley *et al*. (2003) provided functions and parameter estimates for each of the plant processes of growth, survival, probability of flowering, production of fruit and production of suckers (clonal daughter plants). We also modelled damage and herbivory by assigning a damage and herbivory score to each individual. Damage is primarily due to herbivory by the biocontrol agent *Chrysolina quadrigemina* (Suffr.) (a chrysomelid beetle); the herbivory function is derived from occasional counts of *C. quadrigemina* on plants throughout the study period. The submodels of individual plant processes were used in an IBM to create virtual plant populations where each plant was configured separately and followed growth, reproduction and survival trajectories according to the flow diagram (Fig. 1). Each plant was also assigned a quadrat as it was recruited into the population, with 60% of suckers inheriting their parent's

Table 1. Parameters used in the model; parameters for the component submodels are given in Buckley *et al*. 2003, tables 2–8

Parameter	Description	Source	Value
$Prec_{open}$	Probability of recruitment in open	(Briese 1997a) and data therein	0·3
$Prec_{shade}$	Probability of recruitment in shade	(Briese 1997a) and data therein	0·1
No. quad	number of quadrats in data set	(Buckley *et al*. 2003)	44
No. years	Number of years for which estimates of parameters available	(Buckley *et al*. 2003)	5
Lt	Local threshold, maximum number of plants observed in any quadrat	From data	100
$s_{initial}$	Initial recruit size, ln(size in cm)	Smallest plant observed in data set	2
$sds_{initial}$	Standard deviation of initial recruit size	From data	0·5
$Prec_{local}$	Proportion of suckers that grow into parental quadrat	Established from sucker data	0·6
$\bar{R}_1$	Mean summed rainfall (season 1)	Long-term meteorological data	439·08
sdR_1	Standard deviation of rainfall (season 1)	Long-term meteorological data	221·69
$\bar{R}_2$	Mean summed rainfall (season 2)	Long-term meteorological data	369·51
sdR_2	Standard deviation of rainfall (season 2)	Long-term meteorological data	148·14

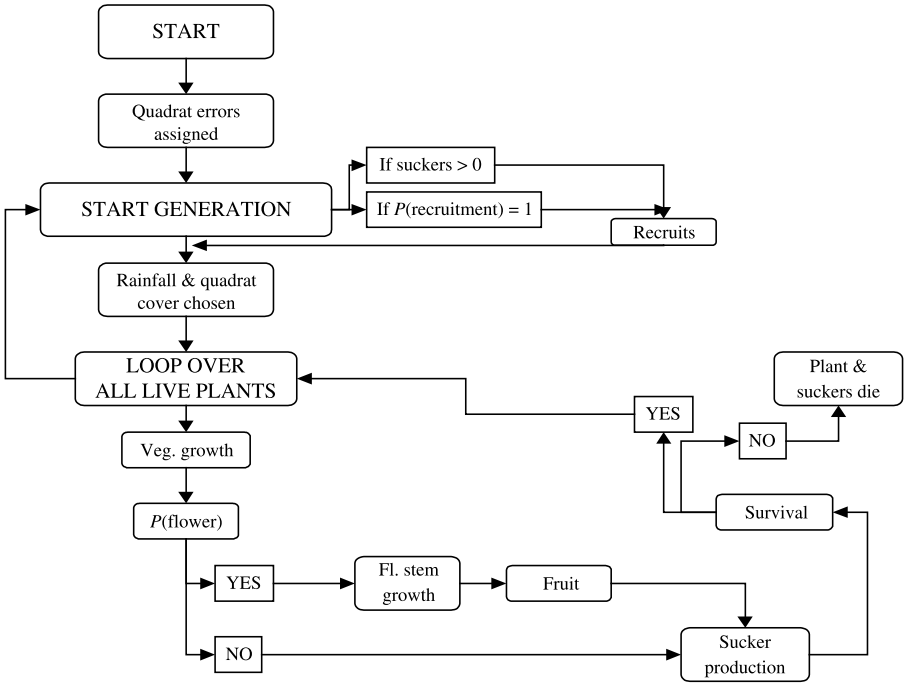

Fig. 1. Structure of the individual-based model. This diagram represents one replicate population followed until the population reached the upper population threshold (100 plants 0·5 m^{-2} quadrat). Veg., vegetative; Fl., flowering; *P*, probability.

quadrat. The model has two seasons, the first season (April–September, austral autumn/winter) is when most vegetative growth occurs and the second season (October–March, austral spring/summer) is when flowering and fruiting occur. The code for the simulation was written in object Pascal using the program Delphi 6·0 (copyright 2001, Borland Software Corporation, Twyford, Berks, UK); the source code is available on request. General parameters used in the baseline run of the model are given in Table 1, and parameter values for the growth, survival, probability of flowering, fruit production, sucker production and damage functions are given in tables 2–8 in Buckley *et al*. (2003). Demographic stochasticity is included in each of the submodels through the addition of a normally distributed error term in the vegetative and flowering stem growth, fruit production and damage functions. The result of the probability of flowering function is compared with a random number and if the random number < *Pfl* then the plant flowers. The negative binomial distribution is used to calculate the number of suckers produced from the suckering function (see below).

Spatial and temporal variation

During initialization of the model, quadrat errors were assigned (values given in Buckley *et al*. 2003, Tables 2–5). These were the estimates of the standard deviation of the random effect of quadrat in each statistical model in which it was significant. This means that plants in the same quadrat receive the same quadrat

error value and they are more similar to each other than plants in different quadrats. This similarity arises from spatial heterogeneity at the quadrat scale or the fact that plants within a quadrat are related to each other as vegetative suckers. Each quadrat was assigned an error for the probability of flowering, flowering stem growth and fruit production functions, which it retained for the duration of that replicate population. The quadrat-level effects of percentage grass and percentage bare ground cover, significant in the statistical models, were input as pairs taken at random from the full complement of data gathered over the observation period (410 quadrat years). At least 5 years of data were used to build the statistical functions of the vital rates and these year effects were included in the models, where significant. At the beginning of each 'generation' or year of the model, a random year (between 1 and 5, referred to as *i* in the following models) was chosen and all year effects in the models were for that year. Rainfall values for seasons 1 and 2 were set at the beginning of each year and were drawn from a normal distribution with mean and standard deviation calculated from 51 site years of meteorological data.

Seed bank and recruitment

As very little data were available on recruitment from the seed bank, this process was not analysed statistically. We assumed that recruitment was limited by the number of available microsites, as opposed to limited by the number of available seed. This seems reasonable due to the large persistent seed bank present under stands of *H. perforatum*, the relative rarity of recruitment events (Briese 1997b) and the presence of a long dormancy period (Campbell 1985). From the population data collected between 1980 and 1987 we identified nine 'mass germination events', defined in Briese (1997b) as > 20 seedlings m^{-2} in any single quadrat. This gave us an average number of recruits and a probability of a recruitment event in open and shaded quadrats. Recruits were assigned a size corresponding to the smallest observed among the plants included in the statistical models. Sucker recruits were assigned their parent's shade or open status, 60% remained in the parent's quadrat and the rest were given a random quadrat within the shaded or open area. The 60% estimate for local recruitment was calculated from the sucker data, using the maximum distance a sucker was found from its parent.

Component submodels

For all of the following models, *a* and *b* refer to intercepts and all other lower case letters, except for *e* and *k*, are regression coefficients (slopes). The subscript *i* refers to a year-specific effect, subscript *shade* refers to shade-specific effect, subscript *q* refers to a quadrat-specific effect, numeric subscripts 1 and 2 refer to seasons 1 and 2, respectively, and upper case subscripts refer to the submodel, e.g. $a_{i,S}$ is the year-specific intercept in the vegetative growth (S) model. The parameter E refers to a quadrat-specific error term and e refers to an individual error term.

Vegetative growth

$$S_{y+1} = a_{i,S} + b_{shade,S} + c_S S_y + d_S H + f_S R_1 + g_S R_1^2 + h_S B_{2,q} + j_S D_1 + l_S D_1 R_1 + m_S D_1 R_1^2 + e_S \quad \text{eqn 1}$$

S_{y+1} is ln(stem length in year $y + 1$) and is predicted by a year-specific intercept, $a_{i,S}$, a shade-specific intercept, $b_{shade,S}$, vegetative size in the previous year, S_y, herbivory, H, summed rainfall in season 1 (April–September), R_1 and R_1^2, quadrat-specific percentage bare ground cover in season 2 (October–March), $B_{2,q}$, individual plant damage (arc sine transform of percentage damage) in season 1, D_1, interactions between the linear and quadratic rainfall terms and damage, $D_1 R_1$ and $D_1 R_1^2$, and an individual plant error, e_S, generated from a normal distribution with mean = 0 and standard deviation from Buckley *et al.* (2003, Table 2).

Probability of flowering

$$Pfl_{y+1} = \frac{\exp(a_{i,Pfl} + c_{i,Pfl} S_{y+1} + E_{q,Pfl})}{1 + \exp(a_{i,Pfl} + c_{i,Pfl} S_{y+1} + E_{q,Pfl})} \quad \text{eqn 2}$$

Pfl is the probability of producing a flowering stem in year $y + 1$ and is predicted by a logistic function of a year-specific intercept, $a_{i,Pfl}$, vegetative stem size in the year of flowering, S_{y+1}, and a quadrat-specific error term, $E_{q,Pfl}$. A plant flowers if a uniformly distributed random number between 0 and 1 < *Pfl*.

Flowering stem growth

$$Fl_{y+1} = a_{i,F} + c_{i,F} Sl_{y+1} + d_F G_{2,q} + f_F B_{2,q} + E_{q,F} + e_F \quad \text{eqn 3}$$

Fl_{y+1} is the ln(length of flowering stems in year $y + 1$) and is predicted by a year-specific intercept, $a_{i,F}$, vegetative size in the year of flowering, S_{y+1}, percentage cover grass in season 2 and quadrat q, $G_{2,q}$, percentage cover bare ground in season 2, quadrat q, $B_{2,q}$, and an individual error term, e_F.

Fruit production

$$Fr_{y+1} = a_{i,Fr} + b_{shade,Fr} + d_{Fr} Fl_{y+1} + f_{Fr} R_2 + E_{q,Fr} + e_{Fr} \quad \text{eqn 4}$$

Fr_{y+1} is ln(fruit production in year $y + 1$) and is predicted by a year-specific intercept, $a_{i,Fr}$, a shade-specific intercept, $b_{shade,Fr}$, flowering stem size in the year of fruiting, Fl_{y+1}, summed rainfall in season 2, R_2, a quadrat-specific error term, $E_{q,Fr}$, and an individual error term, e_{Fr}.

Survival

$$Ps_{y+1} = \frac{\exp(a_{i,Ps} + b_{shade,Ps} + c_{age,Ps} + d_{age,Ps}S_{y+1})}{1 + \exp(a_{i,Ps} + b_{shade,Ps} + c_{age,Ps} + d_{age,Ps}S_{y+1})} \quad \text{eqn 5}$$

Ps_{y+1} is the probability of survival of a plant from year y to year $y + 1$ and is predicted by a logistic function of a year-specific intercept, $a_{i,Ps}$, a shade-specific intercept, $b_{shade,Ps}$, an age-specific intercept, c_{age}, and an age–vegetative size interaction (slope $d_{age,Ps}$). A plant survived if a uniformly distributed random number between 0 and 1 < $P_{s,y+1}$.

Sucker production

$$Su_{y+1} = \exp(a_{Su} + c_{Su}S_{y+1} + d_{Su}Fl_{y+1}) \quad \text{eqn 6}$$

Su_{y+1} is the exponential of the linear predictor of the number of suckers produced, an intercept, a_{Su}, vegetative size, S_{y+1}, and flowering stem size, Fl_{y+1}. The actual number of suckers produced per plant (x) is calculated by using the negative binomial function:

$$P_{(x)} = \left(1 + \frac{Su_{y+1}}{k}\right)^{-k} \frac{(k + x - 1)!}{x!(k - 1)!}\left(\frac{Su_{y+1}}{Su_{y+1} + k}\right)^{k} \quad \text{eqn 7}$$

k is calculated as:

$$k = \frac{Su_{y+1}}{\beta - 1} \quad \text{eqn 8}$$

where β is the dispersion parameter estimated from the quasi-Poisson statistical model (Buckley *et al*. 2003, Table 7). In the IBM, the negative binomial function is implemented by finding the zero term and obtaining subsequent terms from the recursion relationship (Crawley 1993):

$$P_{(x)} = P_{(x-1)}\left(\frac{k = x - 1}{x}\right)\left(\frac{Su_{y+1}}{Su_{y+1} + k}\right) \quad \text{eqn 9}$$

Damage

$$D_{y+1} = a_{i,D} + b_{shade,i,D} + d_D S_{y+1} + f_D G_{1,q} + g_D B_{1,q} + h_{shade,D}G_{1,q} + j_{shade,D}B_{1,q} + k_D G_{1,q}B_{1,q} + e_D \quad \text{eqn 10}$$

D_{y+1} is the arcsine transform of percentage damage and is predicted by a year-specific intercept, $a_{i,D}$, a shade–year interaction, $b_{shade,i,D}$, vegetative size, S_{y+1}, percentage cover grass in season 1, quadrat q, $G_{1,q}$, percentage cover bare ground in season 1, quadrat q, $B_{1,q}$, a shade–grass interaction, $h_{shade,D}G_{1,q}$, a shade–bare ground interaction, $j_{shade,D}B_{1,q}$, a grass–bare ground interaction, $G_{1,q}B_{1,q}$, and an individual error term, e_D.

Herbivory

During the statistical modelling process no correlates of herbivory, as measured by the number of beetles per unit vegetative size, could be found. Plants in the model were therefore assigned a herbivory score that matched the distribution of scores observed; the overwhelming majority of plants (90%) received a score of 0 and the rest received a score between 0 and 1 according to a uniform probability distribution function. The herbivory score for each plant was recalculated each year.

BASELINE MODEL RUNS

The IBM was initialized and run until the population of plants in one of the quadrats reached the maximum observed value (*LT*), whereupon the run was terminated. This comprised one repetition but if *LT* was not reached within 300 years the run was also terminated. When the model was run longer, populations in the quadrats rose to unrealistic densities because negative density dependence could not be detected in the observed data and was not therefore included in the model. For this reason, we only looked at populations in the early stages of establishment and growth and the summary statistic used was time taken to reach the infestation density of 100 plants per quadrat (*T*). Data from 500 replicate populations in total were gained in this way and used to characterize the baseline behaviour of the model. A snapshot sample of the individual plants alive in a population was taken at year 5 of each repetition, giving up to 500 sample generations for validation purposes. At the end of each year summary statistics for the population were calculated and output to file, giving sets of population level values within each repetition that could be compared with the validation data.

Validation of the IBM

The original data set used to construct the statistical functions was used to validate the results of the IBM (for details of the nature and extent of the data see Buckley *et al*. 2003). Validation was therefore not an independent test of the model predictions; the aim was to show how well the parameterized model reproduced the patterns of variation in the data. Size distributions, the number of fruit produced, longevity, proportion of the population originating from seed vs. suckers and proportion of the population flowering were compared between the model outputs and the validation data.

Sensitivity testing

In order to determine which input parameters had most effect on determining time to infestation (*T*) we ran a sensitivity analysis. The input parameters (Buckley *et al*. 2003, Tables 2–8; Table 1) were sampled between ±10% either side of the estimated value using Latin hypercube sampling (McKay, Conover & Beckman 1979). Latin hypercube sampling ensures that all of the specified parameter space is sampled by dividing

each parameter range (in this case the estimated parameter ±10%) into intervals (1000 intervals were used) that are chosen with equal probability and not replaced and a particular value from within each interval is chosen at random; see Rushton *et al*. (2000) for more detail on a similar analysis. In this way 1000 sets of test parameters were generated. We then ran the IBM with each of the parameter sets for open and shaded sites separately, recording the average time to infestation (T) from each run. We used linear regression to determine which parameters had a significant effect on T, and as approximately 100 F-tests were performed on each data set we used the Bonferroni correction to avoid making a type I error (Crawley 2002). In total we tested 101 parameters in the shade model and 94 parameters in the open model.

CONTROL STRATEGIES

Details of the known ecology of the invasive species *H. perforatum* are given in Buckley *et al*. (2003). Management of *H. perforatum* has not been successful on wooded sites in south-eastern Australia. The management strategies currently employed include introduction of biocontrol insects (Briese 1997a), controlled grazing (Campbell 1997), over-sowing of competitive pasture plants (Moore & Cashmore 1942), controlled burning (Briese 1996) and the use of herbicides (Campbell & Nicol 1997), all of which have drawbacks in shaded sites or natural woodland, where up to 85% of *H. perforatum* infestations occur (Shepherd 1983). It was therefore of some importance that we modelled populations in open and shaded sites separately. The biocontrol insect *C. quadrigemina* defoliates plants and does control infestations in some areas. However, due to its slow rate of increase, inability to colonize shaded sites and the ability of *H. perforatum* to regenerate during its summer aestivation, *C. quadrigemina* alone cannot control infestations (Briese 1984, 1997a). The main impact of the recently introduced mite *Aculus hyperici* (Liro) is to stunt the growth of plants (Wapshere 1984; Willis, Ash & Groves 1995; Jupp & Cullen 1996). *Aculus hyperici* is proving to be a promising control agent, as introduced populations of the biocontrol agent have reduced *H. perforatum* biomass at both open and shaded sites in south-eastern Australia (Mahr *et al*. 1997). We focused mostly on testing management strategies suitable for use in natural ecosystems, as this is where control is least successful at the moment.

In addition to sensitivity testing of the IBM we sought expert opinion as to which viable and potentially effective management strategies should be tested using the IBM. A blank matrix listing potential management strategies (e.g. fire, biocontrol, herbicides) along the top and effects on individual- and quadrat-level processes along the side was circulated to a number of land managers and weed scientists familiar with the *H. perforatum* system. In this way we identified those management strategies currently in use, or which showed potential, and whose effects on *H. perforatum* were known to some extent. This allowed us to marry the theoretical process of manipulating functions and parameter values with what the results mean in terms of practical manipulations that can be undertaken in the field, making our study more relevant to potential end-users. Huffaker (1966) suggested that increased summer rainfall led to population growth in *H. perforatum*. We therefore also examined how rainfall affects the time to infestation (T) by simulating dry and wet conditions.

The baseline population model was used as a starting point for implementation of manipulations; those examined (based on those identified through the consultation process) were: (i) 10%, 20% and 50% reductions in vegetative size; (ii) 10%, 20% and 50% reductions in flowering stem size; (iii) 10%, 20%, 50% and 90% reductions in survival; (iv) setting the damage score to 0 and ±50% of its value; (v) damage was also set to its maximum value for all plants occurring in one year out of every three in order to simulate cycles of *C. quadrigemina* damage described in Briese (1997b); (vi) setting the herbivory score to 0; (vii) changing the proportion of plants getting a 0 herbivory score in the baseline model from 90% to 45%, thereby making herbivory more widespread among plants in the population; (viii) dry conditions (called drought hereafter) in each season, defined as the level of rainfall under which fall 10% of observations in the data set, this was implemented by changing the parameters R and sdR (Table 1) to 128 mm and 27 mm, respectively, in season 1, and 181 mm and 24 mm in season 2; (ix) wet conditions in each season, defined as the level of rainfall above which fall 10% of observations in the data set, this was implemented by changing the parameters R and sdR (Table 1) to 880 mm and 105 mm in season 1, and 690 mm and 102 mm in season 2.

Results

BASELINE MODEL BEHAVIOUR

In all analyses results from shaded and open quadrats are presented separately unless the results were identical for both.

Time to infestation

Figure 2 shows the time to infestation (T, in years) for approximately 500 simulated populations. The smooth lines are generated from kernel density estimates, using a Gaussian kernel (implemented as 'density' in R version 1·3·1). The algorithm used in density disperses the mass of the empirical distribution function over a regular grid of at least 512 points, and then uses the fast Fourier transform to convolve this approximation with a discretized version of the kernel (The R Development Core Team 2002). The algorithm then uses linear

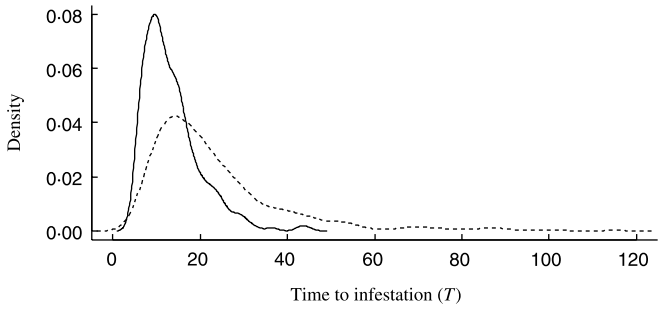

Fig. 2. Time to infestation (T, in years) for open (solid line) and shaded (dashed line) quadrats; open and shaded distributions differ significantly according to the non-parametric Kolmogorov–Smirnov test, $D_{max} = 0{\cdot}37, n_1 = 500, n_2 = 500, P < 0{\cdot}00001$, with shaded quadrats ($\bar{T} = 24{\cdot}2$, SD = 15·0) taking longer to reach infestation densities on average than open quadrats ($\bar{T} = 13{\cdot}9$, SD = 7·5).

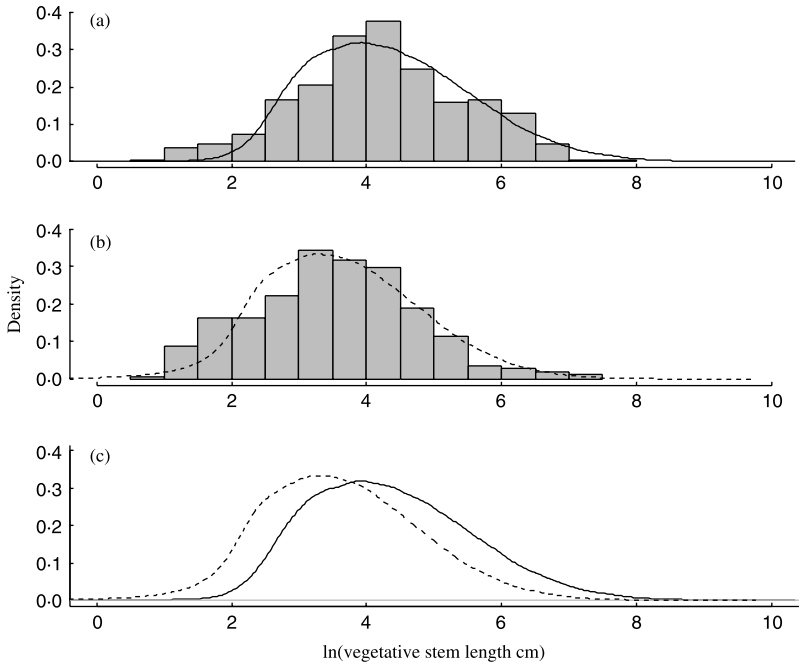

Fig. 3. Vegetative size validation data are compared with model output for (a) open quadrats, (b) shaded quadrats; (c) model output from open (solid line) and shaded (dashed line) quadrats are compared.

approximation to evaluate the density at the specified points. The time to infestation (T) was compared between open and shaded sites using the non-parametric Kolmogorov–Smirnov test. Open and shaded distributions differed significantly, $D_{max} = 0{\cdot}37, n_1 = 500, n_2 = 500$, $P < 0{\cdot}00001$, with shaded quadrats ($\bar{T} = 24{\cdot}2$, SD = 15·0) taking longer to reach infestation densities on average than open quadrats ($\bar{T} = 13{\cdot}9$, SD = 7·5).

Validation

Output from the 'snapshot' sample generations was compared with the individual plant data used to build the model; these comparisons are presented in Figs 3–5. Population level variables were also compared (Figs 6–8); these were calculated for the validation data using one population per site per year ($n \leq 20$) and are therefore not as well characterized as for the individual plant data, for which all plants in all sites were used ($n \leq 350$). A description of the data used for validation is given in Buckley *et al.* (2003).

The model output and validation data agreed well for size distributions (Figs 3 and 4), fruit production (Fig. 5) and proportion of the population flowering (Fig. 6). However, the distributions of the proportion of the population derived from suckers differed quite substantially between the model output and validation data (Fig. 7). It was clear that either the data used to estimate suckering rates for individual plants were not of good-enough quality to predict rates in the field, or the model used did not reflect the underlying process. The validation data presented in Fig. 7 were not the data used to build the suckering submodel, coming rather from destructive harvests of the quadrats where all plants harvested were assessed for either seed or sucker origin. The data used to build the suckering submodel were collected during one season only from excavation of plant root systems in the field. For the

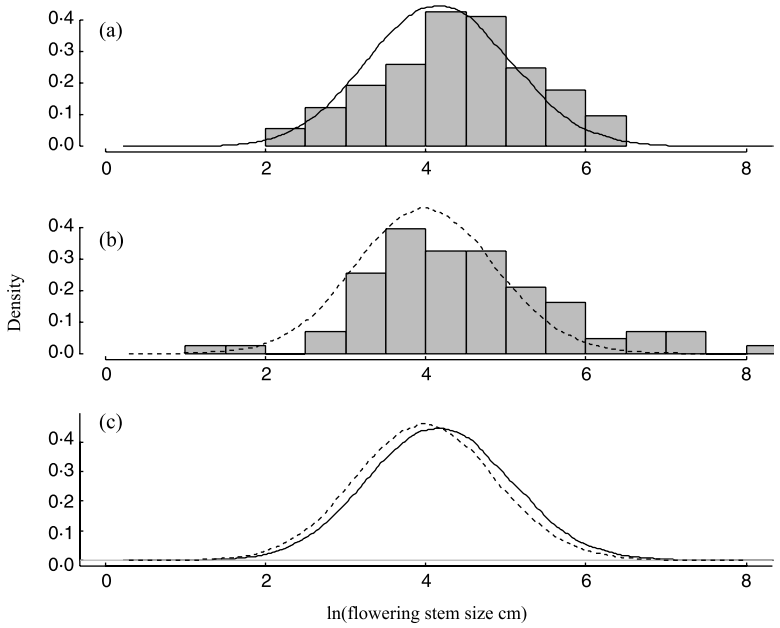

Fig. 4. Flowering stem size validation data are compared with the model output for (a) open quadrats, (b) shaded quadrats; (c) model output from shaded (dashed line) and open quadrats (solid line) are plotted for comparison.

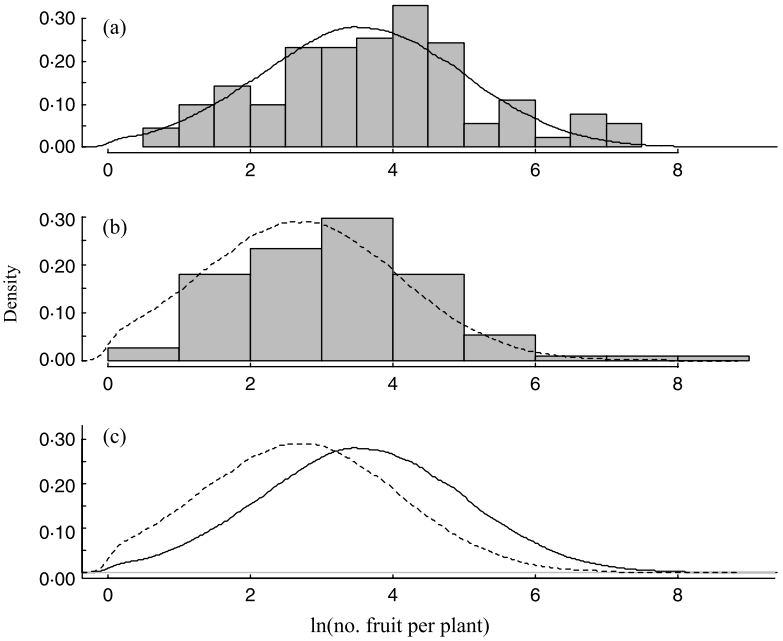

Fig. 5. Number of fruit from the model output compared with the validation data for (a) open quadrats, (b) shaded quadrats; (c) both open and shaded model outputs are compared.

longevity model (Fig. 8), output from the shaded quadrats matched the validation data quite well, whereas in the open quadrats the model appeared to be predicting shorter life times (by around 1 year) than those observed in the field.

Sensitivity testing

The significant parameters alone accounted for 63·7% of the deviance in time to infestation (T) in the shade model and 89·7% of the deviance in the open model; significance levels and the deviance explained by each parameter are given in Table 2. The parameters each accounting for > 1% of the deviance can be grouped as parameters affecting vegetative recruitment (d_{Su}, a_{Su}), seed recruitment ($Prec$), stem size (f_s, g_s, $c_{i,F}$) and rainfall in season 1 ($\bar{R}sdR_1$). For shaded sites seed recruitment accounts for more of the deviance than vegetative recruitment but the opposite is the case for open sites.

CONTROL STRATEGIES

Time taken to reach to infestation density (T) was the variable used to compare the control models with

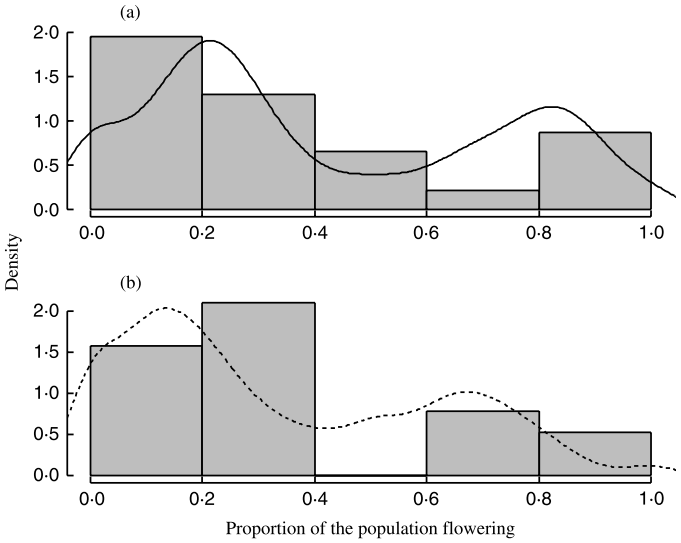

Fig. 6. Proportion of the population flowering each year for (a) open and (b) shaded quadrats; validation data are shown by the bars and model output by the lines (solid for open quadrats and dashed for shaded quadrats).

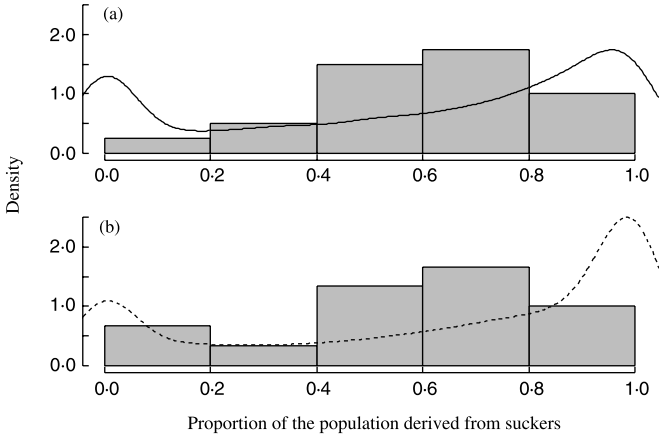

Fig. 7. Proportion of the population derived from suckers in (a) open and (b) shaded quadrats; validation data are shown by the bars and the model output by the solid (open) and dashed (shade) lines.

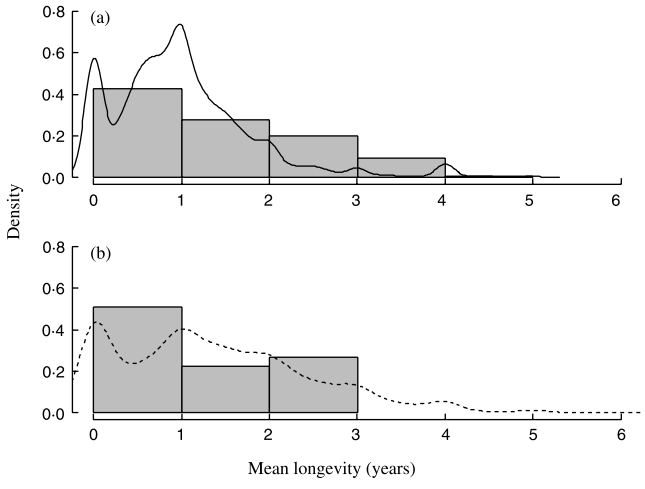

Fig. 8. Mean longevity of plants in the population expressed as the mean age at death of plants for the validation data (bars) and model output (lines) for (a) open (solid line) and (b) shaded (dashed line) quadrats.

Table 2. Sensitivity testing identified the following parameters as having a significant impact on time to infestation (T); significance was determined by comparing the P-value with the critical P as calculated using the sequential Bonferroni correction (Rice 1989). Parameters are ranked in order of the amount of deviance they explain

Parameter	Open (O) or shade (S)	Deviance explained (%)	P-value	Critical P (sequential Bonferroni)
d_{Su} equation 6	O	27·2	< 2·2e-16	0·0006
	S	10·6	< 2·2e-16	0·0005
Prec	O	9·6	< 2·2e-16	0·0005
	S	24·9	< 2·2e-16	0·0005
a_{Su} equation 6	O	14·3	< 2·2e-16	0·0006
	S	7·8	< 2·2e-16	0·0005
f_S equation 1	O	12·8	< 2·2e-16	0·0006
	S	5·8	< 2·2e-16	0·0005
	O	4·7	< 2·2e-16	0·0006
	S	2·6	< 2·2e-16	0·0005
g_S equation 1	O	2·1	< 2·2e-16	0·0006
	S	1·5	2·1e-11	0·0005
$c_{i,F}$ equation 3	O	1·8	< 2·2e-16	0·0005
	S	0·6	3·2e-5	0·0005
sdR_1	O	1·0	< 2·2e-16	0·0006
	S	1·4	8·2e-11	0·0005
l_S equation 1	S	0·6	4·4e-5	0·0006
c_{Su} equation 6	O	0·6	< 2·2e-16	0·0006
$a_{3,F}$ equation 3	O	0·6	< 2·2e-16	0·0008
$a_{4,F}$ equation 3	O	0·1	0·0001	0·0008
	S	0·6	2·5e-5	0·0006
$s_{initial}$	O	0·4	7·8e-12	0·0005
Number of seed recruits	O	0·3	1·5e-10	0·0005
$Prec_{local}$	O	0·3	3·3e-10	0·0005
$c_{1,Ps}$ equation 5	O	0·2	7·8e-7	0·0007
e_S equation 1	O	0·2	1·0e-5	0·0006
$c_{i,Pfl}$ equation 2	O	0·2	2·8e-5	0·0007
$a_{2,Pfl}$ equation 2	O	0·2	1·3e-5	0·0007
e_F equation 3	O	0·1	5·1e-5	0·0006
$a_{2,Ps}$ equation 5	O	0·1	9·6e-5	0·0007
$d_{0,Ps}$ equation 5	O	0·1	0·0002	0·0008

the baseline model behaviour. Table 3 shows T for the baseline model (shade and open) and the control models. As T was normally distributed, a two-sample t-test was used to determine whether the differences between the baseline and control models were significant. To correct for the use of multiple t-tests we used the Bonferroni correction to determine significance.

Manipulation of intrinsic plant variables

Reducing vegetative stem size was the most effective control strategy, with reductions of just 10% resulting in a highly significant ($P < 0{\cdot}00001$) increase of over 50% in T for populations in both the open and shade; reductions in size cause populations to take longer to get to infestation densities. When vegetative size was halved, T increased up to the maximum allowed in the model (300 years) in both open and shaded populations. For shaded populations, a reduction in flowering stem size was the next most effective strategy, whereas for open populations reductions in survival had a greater effect on T than reductions in flowering stem size. Only a reduction of 50% or more in survival led to a significant (but small) increase in T for shade populations. Substantial increases in T were achieved in both open and shaded populations when survival was reduced by 90%.

Manipulation of extrinsic, environmental variables

Setting the damage score to zero only led to a significant decrease in T for shaded populations; no damage leading to faster population growth. Open populations were unaffected by any manipulation of the damage score. Increasing or decreasing the damage score by 50% had no effect on either the open or shade populations. In order to simulate cycles of *C. quadrigemina* damage, we set damage to 100% once in every 3 years (with normal levels of damage in the intervening years), this being only relevant for open populations as *C. quadrigemina* is not active in shaded populations. Such periodic damage led to a significant increase in T, more than doubling the time to infestation. Setting herbivory to zero led to a significant, but small, decrease in T (from 13·9 to 12·6) in the open populations only, with a lack of herbivory leading to faster population growth. Increasing herbivory by 50% led to a significant increase in T (slower population growth), also in the open populations, whereas in the shade populations a similar increase in herbivory led to a marginally

Table 3. Time taken (T, in years) to reach infestation densities ($LT = 100$) was used to compare control strategy models with the baseline model. T-tests were used to assess significance between the baseline and control models for both open and shade quadrats; actual P-values are reported, variables significant at the *** or ** level are significant even under Bonferroni correction (Bonferroni $P = 0{\cdot}0025$) for multiple tests

	Time to infestation					
Model	(T)	Mean	SD	t	d.f.	P
Baseline	Shade	24·2	15·0			
	Open	13·9	7·5			
−10% vegetation size	Shade	37·6	26·9	9·7	782	< 0·00001***
	Open	22·2	12·8	12·5	800	< 0·00001***
−20% vegetation size	Shade	82·7	52·5	24·0	579	< 0·00001***
	Open	49·6	24·6	31·0	588	< 0·00001***
−50% vegetation size	Shade	> 290	Not established			
	Open	> 290	Not established			
−10% flowering size	Shade	28·0	18·3	3·61	959	0·0003**
	Open	15·9	8·0	3·98	991	< 0·00001***
−20% flowering size	Shade	31·7	20·1	6·64	921	< 0·00001***
	Open	18·7	10·1	8·41	915	< 0·00001***
−50% flowering size	Shade	101·9	47·8	34·64	596	< 0·00001***
	Open	49·0	18·9	38·59	649	< 0·00001***
−10% survival	Shade	25·4	16·7	1·20	985	0·23
	Open	16·4	8·7	4·76	973	< 0·00001***
−20% survival	Shade	25·3	16·6	1·11	986	0·27
	Open	20·3	11·6	10·25	849	< 0·00001***
−50% survival	Shade	27·3	18·1	2·98	962	0·003*
	Open	63·7	28·9	37·23	564	< 0·00001***
−90% survival	Shade	213·0	74·0	55·9	566	< 0·00001***
	Open	254·3	28·5	182·2	539	< 0·00001***
0% damage	Shade	19·5	11·4	−5·58	930	< 0·00001***
	Open	13·5	6·6	−0·97	980	0·34
−50% damage	Shade	22·6	14·6	−1·71	995	0·09
	Open	13·8	6·9	−0·32	989	0·75
+50% damage	Shade	24·8	15·9	0·66	993	0·51
	Open	13·6	6·5	−0·71	977	0·47
100% damage 1 in 3 years	Shade	96·4	62·9	25·0	555	< 0·00001***
	Open	31·1	18·1	19·6	662	< 0·00001***
0% herbivory	Shade	22·8	14·2	−1·49	993	0·14
	Open	12·6	6·4	−2·96	973	0·003*
+50% herbivory	Shade	22·2	14·4	−2·08	994	0·04*
	Open	20·9	11·2	11·59	867	< 0·00001***
Drought (season 1)	Shade	250·7	62·7	78·52	555	< 0·00001***
	Open	136·8	35·3	75·98	542	< 0·00001***
Drought (season 2)	Shade	24·7	16·3	0·54	989	0·59
	Open	13·6	6·5	−0·69	979	0·49
Flood (season 1)	Shade	32·6	23·2	6·77	854	< 0·00001***
	Open	11·1	4·7	−7·24	834	< 0·00001***
Flood (season 2)	Shade	24·3	15·9	0·11	993	0·92
	Open	13·8	6·8	−0·36	987	0·72

***$P < 0{\cdot}00001$, **$P < 0{\cdot}001$, *$P < 0{\cdot}05$.

significant ($P = 0{\cdot}04$) and small (2 years) decrease in T (faster population growth).

Drought in season 1 had a profound impact on T, resulting in highly significant ($P < 0{\cdot}00001$) and substantial increases in T (225 years and 123 years for open and shaded populations, respectively) which means slower population growth. Neither drought nor high rainfall had any effect in season 2. High rainfall in season 1 led to different results in shade vs. open populations. It led to a significant ($P < 0{\cdot}00001$) increase in T (slower population growth) in shade populations and a significant ($P < 0{\cdot}0001$) decrease (faster population growth) in open populations.

Discussion

We have confirmed that the IBM presented here is a good representation of the data used in its construction, producing populations similar in size distributions and flowering probability to the populations observed in initial studies (Briese 1997b; Buckley *et al.* 2003). The model does to some extent reflect the idiosyncrasies of the data set used to build it. The most serious of these is the dearth of data available on the behaviour of seedlings and small plants (< 6 cm stem length). The model and data diverge when comparison of the proportion of the population derived from

suckers is made. We have reservations about the model of sucker production for which we used parameter estimates from a quasi-Poisson model; the quasi-likelihood approach makes an assumption that may not accurately reflect the underlying biological processes. More data are clearly needed in order to formulate better models of daughter clone production, especially as sensitivity analysis highlighted the importance of vegetative reproduction parameters. The simulation model can, however, be easily modified to incorporate better models of individual plant processes as they become available. By working closely with weed managers, we have developed a model that, although complex, has components that are easily interpreted in terms of the biology of the species. Moreover, the model can be used to test practical management strategies prior to expensive and time-consuming field tests.

Our results indicate that populations in open and shaded sites have different dynamics and respond differently to some management and disturbance regimes. This has implications for the management of populations in natural (mostly wooded) ecosystems in south-eastern Australia. Shaded populations take longer to reach high densities (24·2 years for shade populations vs. 13·9 years for open populations), high levels of rainfall cause shaded populations to have slower growth, herbivory does not affect shaded populations as much as open populations, and reductions in individual survival in shaded populations have very little effect unless survival is consistently reduced by as much as 90%. Currently herbivory of *H. perforatum* is mostly by the biocontrol agent *C. quadrigemina* and it has been noted previously that *C. quadrigemina* is ineffective in shaded areas (Briese 1984). This matches our predictions from the model constructed here using long-term individual plant data. The poor response of shaded populations to increases in rainfall is possibly due to sunlight being the limiting factor in these sites, leaving plants unable to exploit all of the water resources available. Open populations are not limited by sunlight and show a faster population growth rate in response to wetter conditions. Due to the high rate of sucker production, the death of individual plants has little impact on the invasion dynamics, especially in shaded populations, where recruitment from seed is lower than in open populations.

This IBM reflects the complexity inherent in field populations of *H. perforatum*, such as plants of varying age and size with differing fates, environmental heterogeneity at a small spatial scale and also heterogeneity at a temporal scale. Some of the environmental influences can be assigned to the influence of rainfall or surrounding vegetation, but the rest is expressed as 'noise' at either the individual level or at the quadrat level. With both deterministic and stochastic models we can predict how an average population will respond, but if stochasticity is incorporated into a model we can quantify the uncertainty of model predictions. Our predictions of how control strategies retard population growth are therefore presented with standard deviations of the distribution of values obtained from 500 simulated populations (Table 3). The standard errors of the means are very small (due in part to the large number of simulations used) and we are therefore confident in our estimate of the mean values of T, although any particular simulation can fall anywhere within the wide distribution of values defined by the mean and standard deviation. Being quite open about the levels of uncertainty in our predictions, due to levels of stochasticity we know occur in the field, gives weed managers important information enabling them to assess how likely management is to succeed on any particular population, and to design better experiments for testing management strategies.

Density dependence has not been explicitly included in this model due to the lack of data available to model these effects satisfactorily. This is a feature shared with Shea & Kelly's (1998) model of biocontrol agent impact on the invasive plant *Carduus nutans*. A small positive effect of density dependence was detected during statistical analysis of the data on which our IBM is based. However, when the density-dependent effect was incorporated in the IBM no qualitative differences in the results were obtained (Y.M. Buckley, unpublished data). We excluded the positive density dependence from the model due to its lack of explanatory value, poor characterization and lack of impact on the results. As we also confine our analysis of the dynamics to populations in an initial increase phase, and hence at low density, we can assume that density-dependent effects will be minimal.

CONCLUSIONS AND RECOMMENDATIONS FOR MANAGEMENT OF *H. PERFORATUM*

We predict that the most effective management strategies for both open and shaded sites will concentrate on reducing the size of vegetative parts of *H. perforatum*. *Chrysolina quadrigemina* defoliates plants but is not effective alone, especially in shaded sites (Briese 1984). This is backed up by the lack of impact of increasing herbivory or damage functions (primarily based on data collected to assess *C. quadrigemina* impact) in the shaded populations in the IBM. Intense periodic damage, characteristic of *C. quadrigemina* infestation, does slow down population growth in open sites, however, as shown by the increase in T predicted from the model incorporating maximal damage every 3 years. The mite *A. hyperici* is establishing well in south-eastern Australia and stunts plant growth (Willis, Ash & Groves 1995) and our results predict that, through its effects on individual plants, it will be able to retard growth rates of *H. perforatum* populations. Fire as a control strategy (Briese 1996) was not tested using this model as the impacts of fire on individual plants is not well known.

Herbicide treatment can cause reductions in survival as high as 90%, the only level at which substantial increases in T were achieved through manipulating

survival in shaded sites. Kill rates of up to 100% have been achieved using split applications of fluoroxypyr and triclopyr + picloram (Campbell & Nicol 1997, 2000), fluoroxypyr having the additional advantage that it is selective and does not harm grasses or clover in pasture situations. From our model, we predict that herbicide control, causing a sustained reduction in survival of at least 90%, will be an effective control strategy in both open and shaded sites. Other considerations, such as cost and potential damage to native plants, will have to be taken into account, especially in natural areas.

Drought adversely affects population growth in both open and shaded sites in season 1 (austral autumn/winter), possibly through negative effects on rosette growth at this time. It is important, however, to note that populations reduced by drought have the potential to re-establish quickly if further control measures are not undertaken. All of the control strategies tested here are assumed to be effective over time. It is important that control measures are sustained as populations of *H. perforatum* can build up to infestation densities from just a few seeds in a very short period of time (approximately 10–20 years).

In order to increase the predictive power of this model more research is needed to determine which factors affect the early stages of plant growth and recruitment, both from seed and suckers, under different conditions, including fire treatment. The results of these studies can easily be incorporated into the IBM constructed here in order to make more accurate predictions about invasion dynamics and control strategies.

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