Applying search theory to determine the feasibility of eradicating an invasive population in natural environments

Oscar J. Cacho, Susan Hester and Daniel Spring[†]

The detectability of invasive organisms influences the feasibility of eradicating an infestation. Search theory offers a framework for defining and measuring detectability, taking account of searcher ability, biological factors and the search environment. In this paper, search theory concepts are incorporated into a population model, and the costs of search and control are calculated as functions of the amount of search effort (the decision variable). Simulations are performed on a set of weed scenarios in a natural environment, involving different combinations of plant longevity, seed longevity and plant fecundity. Results provide preliminary estimates of the cost and duration of eradication programs to assist in prioritising weeds for control. The analysis shows that the success of an eradication program depends critically on the detectability of the target plant, the effectiveness of the control method, the labour requirements for search and control, and the germination rate of the plant.

Key words: bioeconomics, invasive species, operations research, population dynamics, weed control.

1. Introduction

Invasive plant species contribute to losses in natural ecosystem function and agricultural production; and they may also affect human and animal health (Groves 2002). In Australia, the number of naturalised alien plants continues to grow, despite many decades of quarantine laws regulating the entry of alien plant species (Groves and Hosking 1997). It is estimated that 290 plant taxa naturalised in the 25-year period between 1971 and 1995, with the rate of naturalisation increasing in the latter half of this period to around 14 plants per year (Groves and Hosking 1997). Given the large number of weeds potentially threatening Australian agriculture and the environment, and the limited resources available to address weed threats, it is important to have an understanding of the resources required to manage weed invasions. Here, we develop a method for making preliminary estimates of the cost and duration of eradication programs to assist in the allocation of limited public funds.

An important factor influencing the feasibility of eradication is weed detectability. Weeds that are not detected may influence invasion dynamics.

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For example, isolated organisms not detected until after they have set seed may cause an increase in the seedbank that requires decades to eradicate. Reasons for overlooking weeds include features related to individual plants (e.g. their size and foliage colour), their spatial arrangement (e.g. whether they are clustered or uniformly distributed), environmental conditions (e.g. the density of native vegetation) and searcher ability. Even if all above-ground organisms are detected, seeds in the seedbank would remain undetected, necessitating follow-up searches.

Search theory (Koopman 1980) offers a technique to determine the probability of detecting targets as a function of the effort expended in different search environments. The theory, which was developed originally to improve success rates in detecting military targets (Koopman 1946, 1980), has subsequently been applied to a wide range of problems, including search and rescue (Frost and Stone 2001; Cooper *et al*. 2003) and mineral exploration (Kolesar 1982).

Weed management options range from doing nothing, to containment or eradication. In this paper, we focus on eradication but the analytical principles could also be applied to a containment program. Cacho *et al*. (2006) developed a combined search and population dynamics model to study the feasibility of eradicating an invasion from a technical standpoint. In this study, we extend their model and incorporate an economic analysis. This paper builds upon Cacho *et al*. by providing a more thorough analysis of the search process, incorporating labour and herbicide input equations, undertaking cost analysis and identifying important features of weed control in natural environments.

The model described in this paper provides a quick and rigorous way of obtaining information on the resources required to achieve eradication. This type of information is routinely required by weed managers, who are often required to allocate limited budgets between alternative eradication programs. We begin with a brief explanation of search theory and the associated formulas for detection, coverage and mortality that are later incorporated into a population simulation model. Population dynamics are described based on a stage matrix that drives the spread of the weed invasion under alternative search and control strategies. Eradication effort is analysed in terms of expected years to eradication and present value of costs.
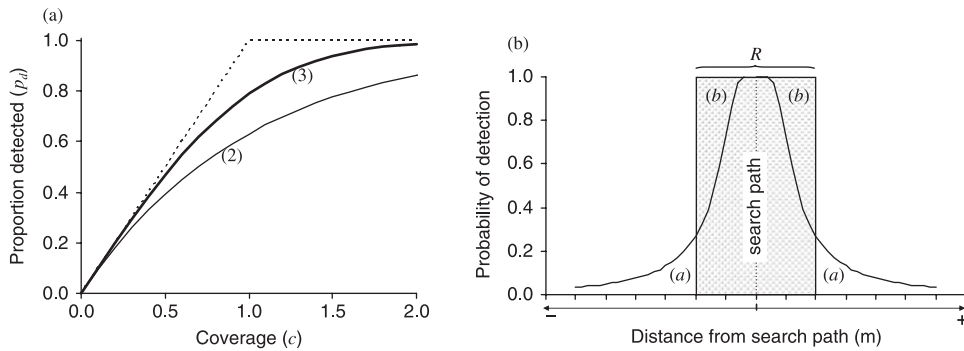
2. Method

2.1 Search and control

Search theory is based on the concept of coverage (c), defined as the ratio of the area searched over the total area of the invasion:

$$c = \frac{STR}{A} \qquad (1)$$

where A is the total area (m²) at risk of invasion, S is the speed of search (m/h), T is time spent searching (h) and R is the effective sweep width (m), which is

Figure 1 (a) Detection functions obtained with a definite range sensor (dotted line), a parallel-track search (Equation (3)) or a random search pattern (Equation (2)). (b) The inverse cube LRC (Equation (5)) illustrating the estimation of effective sweep width (R).

a measure of the *detectability* of the plant. The numerator of Equation (1) represents the area effectively searched (m²) as the product of the distance traversed (ST) and the detectability of the plant (R).

The effect of c on the probability of detection depends on the search pattern (Figure 1a). The upper bound on search effectiveness is achieved by a 'definite range' sensor that detects all objects out to a specific distance on either side of the sensor, and no objects beyond that distance. In this case, the probability of detection increases linearly with coverage until both reach 1.0 (dotted line in Figure 1a). A definite range sensor can detect all targets once the entire searchable area is swept perfectly (when $c = 1$ as would result with parallel search tracks and no overlap). Thus, a single sweep of the area with a definite range sensor is all that is required to detect all targets.

At the other extreme from the definite range sensor, the exponential detection function (lower curve in Figure 1a) provides a conservative estimate of search effectiveness. This function results from a random search strategy. The proportion of objects detected (p_d) for random search is given by:

$$p_d = 1 - e^{-c}. \tag{2}$$

Random searching would be expected to produce the least detections. An intermediate detection function (dark solid curve in Figure 1a), is obtained with parallel, equidistant search tracks. The proportion of objects detected with this search mode is:

$$p_d = \theta\left(\frac{\sqrt{\pi}}{2}c\right) \tag{3}$$

where θ represents the error function:

$$\theta(z) = \frac{2}{\sqrt{\pi}} \int_0^z \exp(-u^2)du. \tag{4}$$

This function was derived by Koopman (1946, 1980) based on the geometry of sighting opportunities in the search for ships from aircraft.

The effective sweep width (R) in Equation (1) can be calculated based on the lateral range curve (LRC) showing the probability that the target will be detected as a function of its lateral distance from the searcher (Figure 1a). The efficiency of search per unit of distance covered is given by the area under the LRC.

R is computed by constructing a rectangular box of height 1 and lateral range equal to that at which the number of missed detections (b) within this range equals the number of detections (a) outside the range (Figure 1b). In this case, we could replace area (b) with area (a), and have the same number of total detections. Thus, a standard rectangle can characterise detectability for a given search method applied in a given environment. Effective sweep width is the width of the box in Figure 1(b).

The LRC illustrated in Figure 1(b) is the function derived by Koopman:

$$f(d) = 1 - \exp\left(\frac{1}{4\pi} \left(\frac{R}{d} \right)^2 \right) \tag{5}$$

where d is the distance from the search path to the target (the lateral range). This particular function represents the geometry of sighting opportunities for ships from aircraft. Koopman postulated that the probability of detection is inversely proportional to the cube of the range from the sensor to the target, and hence the function became known as the inverse cube model of visual detection (Cooper *et al.* 2003). Koopman showed that, when used to cover an area with equally spaced straight parallel tracks, the LRC in Equation (5) results in the detection function shown in Equation (3) (see Koopman 1980; pp. 75–77 for details). Equation (3) has become the standard for marine search and rescue operations, and has proven to be remarkably robust (Cooper *et al.* 2003).

We assume that an attempt is made to kill all weeds found, subject to the effectiveness of the control method used. The mortality caused by the search and control effort is:

$$m = p_d \times p_k \tag{6}$$

where p_k is the probability that a target organism will die each time control is applied and p_d is given by Equation (2) or (3) depending on the search mode.

2.2 Population dynamics

The spread of the weed invasion was modelled using a stage matrix. This is a standard technique for population dynamics modelling and is explained in detail in Caswell (2001). The stage matrix has dimensions $n \times n$; where n is the number of stages in the life cycle of the plant. The minimum size of n for

perennial plants is 4 (new seeds, seedbank, juveniles and mature plants). The value of n increases according to the number of years required to reach maturity, with juvenile stages inserted between the seedbank and the adult stages. Details of the model are presented in Cacho *et al.* (2006). Briefly, the population state transition is given by the matrix multiplication $\boldsymbol{H} \cdot \boldsymbol{x}_t$; where $\boldsymbol{H}$ is the stage matrix and $\boldsymbol{x}_t$ is a column vector of dimension n containing the number of individuals in each life stage. The stage matrix and corresponding population vector for a perennial plant that reaches maturity in one year are:

$$\boldsymbol{H} = \begin{bmatrix} 0 & 0 & 0 & F \\ P_S & P_S & 0 & 0 \\ G & G & 0 & 0 \\ 0 & 0 & P_J & P_A \end{bmatrix}; \quad \boldsymbol{x}_t = \begin{bmatrix} x_{1t} \\ x_{2t} \\ x_{3t} \\ x_{4t} \end{bmatrix} \tag{7}$$

where F represents fecundity of adults (viable seeds produced per plant), P_S is the proportion of seeds that do not germinate and survive from one year to the next, G is the proportion of seeds that germinate and survive into juveniles, P_J is the proportion of juveniles that survive into adults and P_A is the proportion of adults that survive from one year to the next. The assumption that new seeds and seeds in the seedbank have the same survival (P_S) and germination (G) rates are made for simplicity. This is an acceptable simplification, as Oli (2003) has shown that it does not affect the dynamical properties of the matrix model. For longer-lived weeds the stage matrix is adjusted by adding rows and columns representing additional juvenile stages between seedlings and adults.

The population growth rate (λ) is given by the dominant eigenvalue of $\boldsymbol{H}$, and λ is related to the intrinsic rate of increase (r) by the function $\lambda = e^r$ (Caswell 2001, p. 86). When the population reaches a steady state, $r = 0$ and therefore $\lambda = 1$. This fact was used to implement density dependence in the model by finding the value for germination (G) that results in a value $\lambda = 1$ for a given weed. This germination rate was denoted G_∞. The model was designed so that the stage matrix could be generated by answering six questions regarding the demography of the plant. These questions – that could be answered by a scientist familiar with the plant – are related to the following parameters: juvenile survival (P_J), fecundity (f), seed longevity (L_S), plant longevity (L_P), years to maturity (M_T) and growth rate (λ).

2.3 Inputs and costs

Effective management of weeds involves search and control components, each with its own input requirements and costs. The search process uses labour and other resources to cover the potentially invaded area. Logistic factors such as the remoteness of the area and the difficulty of traversing the terrain will affect the search effort required, by decreasing the speed of search (S in Equation (1)) and thus increasing the time required (T in Equation (1))

for a given coverage to be achieved. If we let search effort (u) be expressed as search time per hectare ($u = 10\,000 \times T/A$), then coverage in Equation (1) becomes:

$$c = \frac{SRu}{10\,000} \tag{8}$$

where u is the decision variable, and S and R are determined by the plant–environment combination as already explained above.

Once a weed is identified, the typical focus of control is to maximise mortality, lower reproductive capacity and prevent weed dispersal (Sindel 2000). The control methods available can broadly be classified as mechanical (e.g. physical felling and removal, chain-pulling, slashing), chemical (e.g. foliar spray, cut-stump, stem injection) and biological (e.g. use of insects or fungi which attack the plant). Other methods useful in natural environments that do not fit neatly within this classification include fire, revegetation, restricting access to tourists and eliminating pest animals that disturb the soil (Odom *et al.* 2003). It is common for environmental weed control to use a combination of methods that achieve a range of objectives, such as removing existing plants, depleting the soil seedbank and reducing re-invasion (DEC 2004). These methods require different combinations of labour (L), capital (K) and herbicide (W) inputs.

The cost of an eradication program is the sum of search costs (C_S), control costs (C_C), and costs of establishment and administration of the program (C_A):

$$C = (C_S(L, K, Y) + C_C(L, K, W, Y))A + C_A(Y, A). \tag{9}$$

These costs are expressed in present-value terms and are functions of years to eradication (Y) and area invaded (A) as well as of the three inputs L, K and W. The cost functions in Equation (9) result from the number of plants detected and killed, as well as the population dynamics of the plants that survive. Since we assume that an attempt is made to kill all plants found, the inputs L, K and W in Equation (9) are ultimately determined by search effort u. In addition to affecting the inputs required u also determines the years to eradication. In a rugged environment with no access by road, labour and herbicide are the main variable inputs. Ignoring the fixed capital costs and administration costs, the costs of search and control per hectare are:

$$C_S = \sum_{t=1}^{Y(u)} u p_L \tag{10}$$

$$C_C = \sum_{t=1}^{Y(u)} \sum_{j=3}^{n} [L(D_{tj}(u), Z_j)p_L + W(D_{tj}(u), Z_j)p_w] \tag{11}$$

where p_L and p_W are the prices of labour and herbicide, D_{tj} is the density of plants in stage j at time t and Z_j is the average size of plants in stage j. Note

that the sum over j occurs only for stages 3 and above, because new seeds and the seedbank are not treated.

The functional relationships $Y(u)$ and $D_{jt}(u)$ result from the solution of a dynamic problem that involves a search-kill-reproduce cycle that ends when the plant population, including the seedbank, is eliminated. This process is explained in more detail at the end of this section.

Published studies that measure control costs for weeds of different densities and sizes are difficult to find. Three studies were found that report experimental results on the effects of plant density on the costs of removing mesquite using mechanical and chemical techniques (Campbell *et al.* 1996; Ueckert *et al.* 1999; van Klinken and Campbell 2001). Another study (Buddenhagen and Yañez 2005) measured the labour and herbicide inputs required to control quinine in the Galapagos Islands. Weed control in the latter study involved uprooting small plants and applying herbicide to cut stumps or to machete cuts in the bark of larger trees. The data from these studies were scanned using a data capture program, OCAPTURE (Cacho 2005) and are presented in Figure 2 along with fitted functions. The following functions were estimated by ordinary least squares on the log-transformed data:

$$L(D, Z) = \alpha_L Z^{\beta_L} D^{\gamma_L} \qquad (12)$$

$$W(D, Z) = \alpha_w Z^{\beta_w} D^{\gamma_w} \qquad (13)$$

where the density of the weed D is measured in stems per hectare, and plant size Z is measured relative to a mature plant ($Z = 1.0$ for a stage n). The results of these analyses for the data sets shown in Figure 2 are presented in Table 1.

Buddenhagen and Yañez (2005) found that effort (person-hours) required to control an area was positively related to both density and size (Figure 2a,b), and this is confirmed by the regression analysis in Table 1 (Source 1) where all coefficients are significant ($P < 0.05$). These results suggest that the marginal cost of labour increases with plant density and plant size (β_L and γ_L are both > 1.0). One possible reason for this is that workers had to refill their sprayer tanks with water and herbicide more often, involving travel time between the control site and the base (C. Buddenhagen, pers. comm., 2004). Other possible explanations for increasing marginal costs of labour include fatigue and high densities of plants making the terrain more difficult to traverse.

In contrast to the data on quinine control, the regression results for the cost of controlling mesquite (Sources 2–4 in Table 1) suggest decreasing marginal costs per hectare as plant density increases (the β coefficients are < 1.0). This is not unexpected when spray and mechanical control techniques are used. Higher density means that more plants can be killed with a sweep of a plough or a spray gun; but the Buddenhagen and Yañez (2005) data suggest that decreasing marginal cost is unlikely to apply to labour inputs in a natural environment, where weeds must be treated individually either because of the sensitivity of non-target vegetation, or because the plants are difficult to kill.
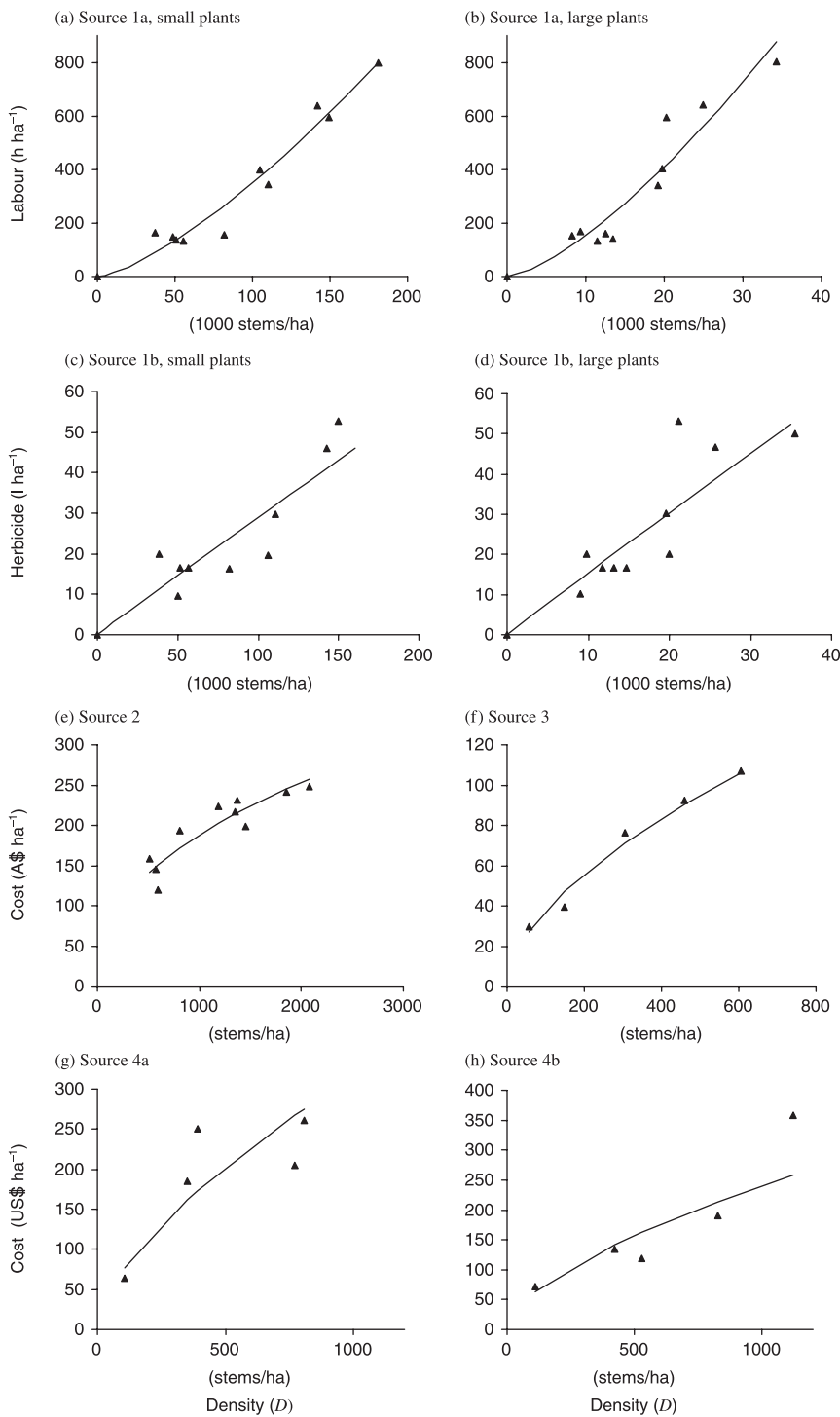
Figure 2 Effect of plant density on inputs and costs of weed control; from data sources presented in Table 1.

Table 1 Regression results for data on inputs and costs of control reported in the literature and shown in Figure 2, using the function $y = \alpha Z^\beta D^\gamma$, where Z is relative plant size and D is plant density; values in parentheses are t ratios

Dependent variable (y)	Estimated coefficients			Number of observations	R^2	Source†
	α	β	γ			
Labour (h/ha)	9.68×10^{-4} (5.22)	3.16 (9.48)	1.3 (8.27)	10	0.841	1
Herbicide (l/ha)	1.853×10^{-3} (3.85)	2.34 (5.81)	0.98 (5.37)	10	0.681	1
Cost (A\$/ha)	9.799 (5.75)	–	0.428 (5.61)	10	0.797	2
Cost (A\$/ha)	2.645 (1.67)	–	0.576 (9.43)	5	0.967	3
Cost (US\$/ha)	3.842 (1.30)	–	0.638 (3.53)	5	0.806	4a
Cost (US\$/ha)	3.409 (1.28)	–	0.616 (3.90)	5	0.835	4b

† Sources: (1) Buddenhagen and Yañez (2005), data for quinine (*Cinchona pubescens*). Treatment occurred between 1998 and 2003; (2) Campbell *et al.* (1996), data for mesquite (*Prosopis pallida*), bulldozing. Treatment occurred during October 1995; (3) van Klinken and Campbell (2001), data for mesquite (*Prosopis glandulosa*), ploughing. Treatment occurred during 1997; (4) Ueckert *et al.* (1999), data for mesquite (*Prosopis glandulosa*): a, stem spray, b, leaf spray. Treatment occurred during summer 1995.

In summary, the cost of searching is determined only by search effort (u), as specified in Equation (10), but the cost of killing plants is a function of density and size of plants, as specified in Equation (11) and suggested by data reported in the literature. The exact plant sizes in the Buddenhagen and Yañez study were not known, as they report either all plants or plants > 150 cm tall. We assumed that the average size of small plants (< 150 cm) was 0.5 times the size of large plants (> 150 cm). Despite a lack of additional data points this relationship is an acceptable first approximation, as confirmed by the regression results in Table 1 (Source 1).

The number of plants treated depends on the proportion of plants found, which in turn depends on search effort. Therefore, for control purposes, the density of a life stage at a given time is given by:

$$D_{jt} = p_d(u)x_{jt} \qquad (14)$$

where x_{jt} is the jth element of vector $\boldsymbol{x}_t$ with state transition:

$$\boldsymbol{x}_{t+1} = (\boldsymbol{H} \cdot \boldsymbol{x}_t)(1 - m(u)). \qquad (15)$$

The model is solved by numerical integration of Equation (15) after the following substitutions are performed for each time period: substitute the elements of Equations (15) into (14), then Equations (14) into (12) and (13), and finally Equations (12) and (13) into (11). This process allows the model to be solved

Table 2 Parameter values used in simulations

Parameter	Value	Description
S	1000	Speed of search (m/h)
R	20	Effective sweep width (m)
p_k	0.95	Efficiency of control agent
A	10 000	Area of invasion (m^2)
x_{0n}	100	Initial number of mature plants per hectare
r	0.06	Discount rate
p_L	35	Price of labour ($/h)
p_H	5	Price of herbicide ($/l)

for any value of u. The model is solved until it converges to $x_t \cong [0]$, at which point years to eradication are given by $Y = t$. The maximum number of iterations was 100, so a simulation that stops at $t = 100$ indicates that eradication cannot be achieved at the given level of u.

3. Numerical assumptions

The numerical model was implemented in the MATLAB language (The Mathworks 2002). The assumptions of the numerical model are presented in Table 2. The starting number of organisms in each life stage was calculated based on the number of adults when the invasion is first discovered (x_{0n}) by estimating the number of seeds and juveniles that would be consistent with the observed number of adults for the given demographic parameters. Labour and herbicide input requirements were estimated as functions of weed density and size using the parameters for Source 1 in Table 1.

Three perennial weed scenarios were designed (Table 3) and simulations were undertaken for a range of search efforts assuming parallel search tracks. Scenario 1 represents the base plant; Scenario 2 represents a plant with longer-lived seeds; and Scenario 3 represents a plant that takes longer to reach maturity (three years). The demographic parameters (Table 3) were selected to ensure that all scenarios had the same expected population growth rate (λ, the dominant eigenvalue of H is 1.5), thus preventing differences in intrinsic growth rate from confounding the effects of differences in demographic characteristics.

4. Results and discussion

Initial analysis of the eradication effort was undertaken by running simulations to generate isoquants of years required for eradication depending on weed detectability and search effort (Figure 3). This plot was obtained by solving the model repeatedly for various combinations of R and u, using the base parameter values in Table 2 and base scenario in Table 3. Each isoquant represents a given number of years as indicated by labels next to the curves.
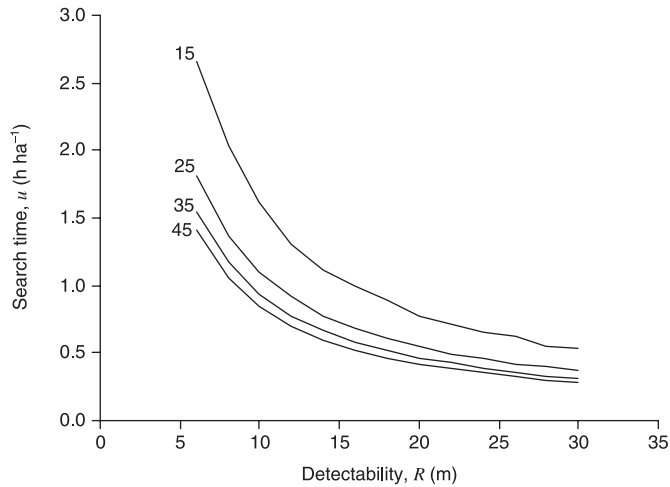
Figure 3 Isoquants of detectability against search time. Each line represents the set of detectability and search-time values that result in a fixed eradication time (years); labels (15, 25, 35, 45) indicate the number of years represented by each line.

Table 3 Parameter values used in simulations for three perennial weed scenarios: (1) base case; (2) plant with extended seed longevity; and (3) plant with late maturity

		Scenario		
		1 Base case	2 Long-lived seeds	3 Late maturity
Demographic parameters				
P_J	Juvenile survival	0.05	0.05	0.1
f	Fecundity	1500	1500	15000
L_S	Seed longevity (years)	5	10	5
L_P	Plant longevity (years)	10	10	20
M_T	Years to maturity	1	1	3
λ	Growth rate	1.5	1.5	1.5
Calculated parameters†				
G	Germination rate	0.0259	0.0207	0.017
P_S	Seed survival	0.25119	0.50119	0.25119
P_A	Adult survival	0.46416	0.46416	0.66608
G_∞	G at steady state	0.00534	0.00356	0.00119

† These parameters were calculated from the demographic parameters as explained by Cacho *et al.* (2006).

Two important features are illustrated here. The first is that, as the visibility of the weed decreases the search effort must be increased at increasing rates to achieve eradication in the designated number of years (moving left along a curve in Figure 3). The second important feature is that the gaps between isoquants become wider as the time to eradication decreases (moving up between curves in Figure 3); this reflects the diminishing returns to search effort.
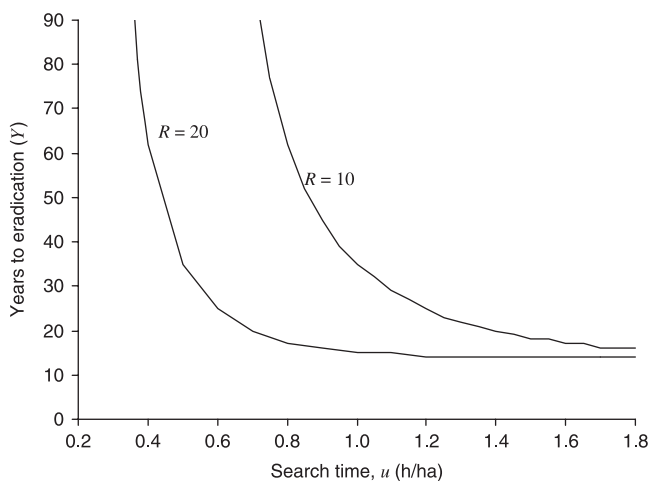
Figure 4 The relationship between time spent searching for weeds and the total number of years to eradication for two different values of plant detectability (*R*).

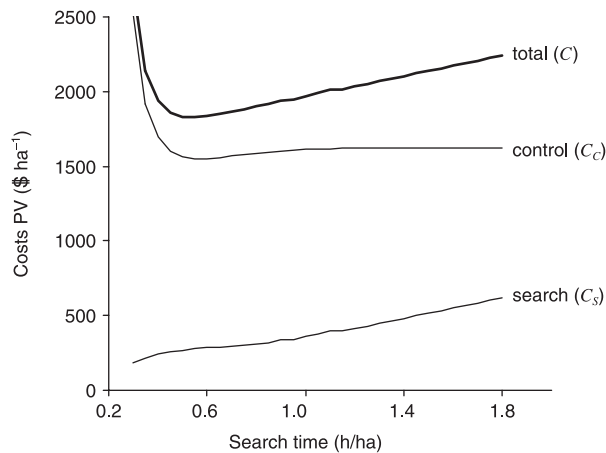### 4.1 Time to eradication

Time to eradication was found to decrease at a decreasing rate as search time increased (Figure 4). At the base case, with *R* = 20 m, the drop in years to eradication (*Y*) is rapid as search effort (*u*) increases from 0.3 to 0.5 h/ha. Further increases in search effort lead to a slower drop in years to eradication; beyond a search effort of 1 h/ha there is little improvement in time to eradication. Given the values of *R* (20 m) and *S* (1000 m/h) in Table 2, a search effort (*u*) of 1.0 h/ha represents a coverage (*c*) of 2.0, which as Figure 1(a) illustrates, achieves a detection fraction of almost 1.0, and additional search effort has little effect on the probability of detection. Decreasing *R* to 10 m results in a similar pattern (Figure 4) but shifted to the right.
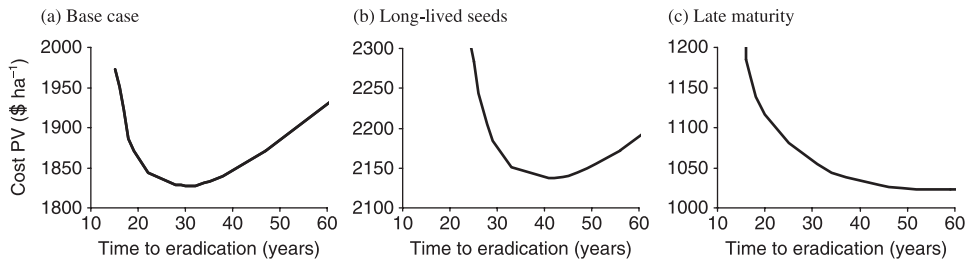
4.2 Cost of eradication

The costs associated with a range of search efforts that lead to eventual eradication of the weed are plotted in Figure 5. Total costs are high for low search efforts and rapidly fall as search effort increases. The minimum cost occurs at a search effort of approximately 0.5 h/ha, which represents coverage of 1.0 based on Equation (1) and the search parameters in Table 2. The control component of costs falls rapidly as search time increases, eventually flattening out at coverage greater than 1.0 (or *u* > 0.5 h/ha). This is because a more intense search effort reduces the number of mature plants that produce seeds, resulting in lower future weed densities which are cheaper to control.

Information from the previous two figures is combined in Figure 6 to show the relationship between total costs and time to eradication. There is an obvious

Figure 5 Costs of search and control to eradicate an invasion (present values) as affected by search effort for the base-case scenario described in Table 3.

Figure 6 The relationship between total costs of eradication (present values) and years to eradication for each of the three scenarios described in Table 3; note different ranges of values on the vertical axes to enhance readability.

lower bound to the number of years in which a plant can be eradicated (15, 24 and 15 years for Scenarios 1, 2 and 3), but this lower bound is expensive to achieve as evidenced by the costs on the left side of the curves in Figure 6. Costs decrease rapidly as the desired years to eradication are increased above the lower bound. Minimum costs occur at 31, 41 and 55 years for Scenarios 1, 2 and 3, respectively.

4.3 Sensitivity analysis

The area that can be covered per unit of time is given by the product of effective sweep width (R) and search speed (S). There is likely to be some interaction between R and S. Other things being equal, a searcher walking fast or searching from a moving vehicle would be expected to have a lower R than a searcher walking slowly, because he/she would be more likely to miss more distant plants.

The isoquants in Figure 3 show the negative relationship between R and the search time required to achieve eradication in a given number of years.

Table 4 Sensitivity analysis results expressed as elasticities of key variables with respect to a selection of model parameters

With respect to:	Elasticity of		
	u^*	Y^*	C^*
Search and control parameters			
Effective sweep width (R)	−1.33	0.50	−0.16
Speed of search (S)	−1.33	0.50	−0.16
Efficiency of control agent (p_k)	−1.75	−2.55	−0.48
Economic parameters			
Price of labour (p_L)	−0.18	0.33	0.97
Price of herbicide (p_H)	0.18	−0.33	0.03
Labour input coefficient (γ_L)	−2.45	5.00	7.87
Herbicide input coefficient (γ_H)	−0.09	0.17	0.18
Biological parameters			
Germination rate (G)	0.98	−1.33	1.49
Juvenile survival (P_J)	0.66	−0.83	0.22
Fecundity (f)	0.66	−0.83	0.21
Plant longevity (L_P)	−0.08	0.33	1.53
Time to maturity (M_T)	−0.02	0.07	0.31
Initial number of mature plants (x_{0n})	−0.01	−0.17	−0.01

These curves can be used to estimate the elasticity of search time with respect to R, but a more interesting measure is the effect of R on the cost-minimising search time (u^*); the corresponding years to eradication (Y^*) and the total cost of the operation (C^*). The sensitivity of these three variables to other model parameters is also of interest.

Results of sensitivity analysis for a selection of search, biological and economic parameters are presented in Table 4. These results are expressed as elasticities of the three key variables (u^*, Y^* and C^*) with respect to each parameter, measured at base-case values of all other parameters. While recognising that a cost-minimising solution is not strictly optimal, because benefits are not considered as discussed below, we will refer to u^* as the optimal solution for convenience.

The elasticities of the three key variables (u^*, Y^* and C^*) with respect to R are the same as with respect to S (Table 4), because R and S appear as a product in the numerator of the coverage Equation (1). Both parameters have a strong negative effect on u^* (the elasticity is −1.33), but relatively small effects on Y^* (0.5) and C^* (−0.16). Thus, as the detectability of the plant (or search speed) increases, it is optimal to reduce search time per hectare and lengthen the time to eradication, and this results in lower costs.

The efficiency of the control agent (p_k) is a key factor, as evidenced by the fact that it is associated with the highest elasticities for u^* and Y^* (Table 4). Both variables are elastic (−1.75 and −2.55 for u^* and Y^*, respectively), so their values indicate that an increase in the proportion of weeds killed by the control agent results in a more than proportional decrease in search time and

time to eradication. A higher p_k also results in lower cost (the elasticity of C^* is –0.48).

Of the economic parameters, the coefficient of the labour input equation (γ_L) is the most important (with elasticities of –2.45, 5.00 and 7.87 for u^*, Y^* and C^*, respectively). The base value of this coefficient (1.3 in Table 1) implies diminishing marginal returns to labour, because increasing amounts of labour are required for weed control as the density of plants increases. Elasticities indicate that changes in γ_L result in more than proportional changes in all three key variables. Increasing labour requirements through γ_L results in a reduction in the optimal level of search labour, and a corresponding increase in time to eradication as well as a significant increase in total cost.

Given that labour is the key input in a search and control operation, it is worth noting that the elasticity of C^* with respect to the wage rate (p_L) is slightly less than unity (0.97), implying that an increase in wage rate results in a less than proportional increase in cost. This is because the higher wage rate elicits a slight decrease in search time (u^* elasticity is –0.18) resulting in a small increase in time to eradication (Y^* elasticity is 0.33).

Regarding biological parameters, the optimal management of the invasion is adjusted to some extent in response to changes in demographic characteristics of the plant. This adjustment occurs through the cost-minimising search time (u^*). The management response to biological parameters, however, is less than proportional to changes in parameter values (Table 4). Germination rate is the biological parameter to which the model is most sensitive (elasticities are 0.98, –1.33 and 1.49 for u^*, Y^* and C^*). The fact that both Y^* and C^* are elastic with respect to G is explained partly because increasing the germination rate results in higher plant densities, which are more expensive to control. This result also reflects lower seedbank longevity, given that seeds that germinate are subtracted from the seedbank, resulting in a reduced time to eradication.

4.4 Implications for weed control in natural environments

Two features of weeds that make them generally more difficult to eradicate than other pests is that seeds are not detectable until they germinate and can survive in the soil for a long time. Our model accounts for these facts by including life stages representing new seeds and a seedbank. Our model also accounts for the effects of plant density and plant size on the labour and herbicide inputs required to kill plants that are found. An interesting finding of this study is that the demographic parameters of a weed can have a substantial effect not only on the eradication costs, but also on the shape of the cost function.

Our focus on the cost of the eradication and not the benefits of eradicating the invasion earlier rather than later reflects the urgency of decisions on weed eradication relative to the time, cost and methodological difficulties associated with estimating the non-market benefits of eradication. Two additional pieces of information that would be required if eradication benefits were to be considered are a function linking weed density to flows of environmental
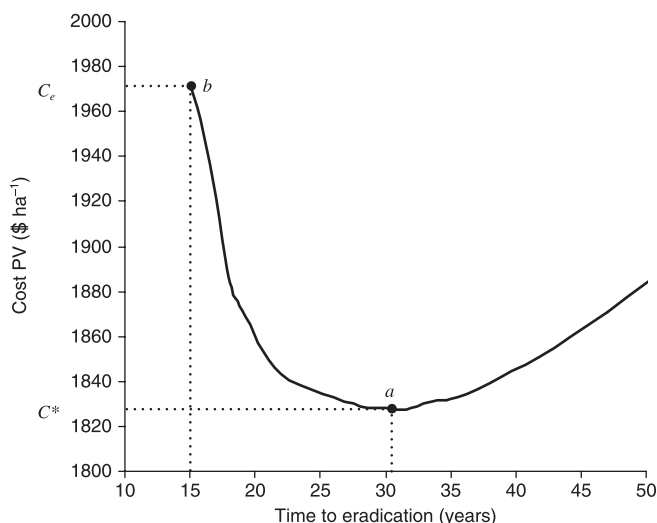
Figure 7   Estimating the cost difference between the earliest possible eradication (C_e) at point (b) and the cost-minimising strategy (C^*) at point (a).

services, and a function describing the demand for these environmental services. Having such information would allow an agency to evaluate whether eradication is the right course of action, or whether containment or doing nothing should be pursued instead. For example, if the benefits of early eradication are high, such as when biodiversity losses are non-reversible, the optimal time to eradication will occur earlier than under cost minimisation.

Figure 7 shows how the model could be used to assist allocation decisions in a national park threatened by a weed invasion. Model results indicate that the cost of eradicating the invasion is minimised by applying a search effort of 0.53 h/ha, leading to eradication in year 31. The cost of this strategy is $1,827/ha in present value terms (point (a) in Figure 7). The land manager may consider the possibility of attempting to eradicate the invasion as early as possible (15 years in this case). To do this the search effort must be increased to 1 h/ha at a cost of $1972/ha (point (b) in Figure 7). In deciding whether to spend the additional $145/ha the land manager will need to consider the opportunity cost of these funds not being allocated to other projects. For example, if the prolonged presence of the weeds would require costs in excess of $145/ha in present-value terms to restore environmental benefits, it may be cost-effective to eradicate the invasion as early as possible.

5. Applying the model

Given our primary objective of providing preliminary estimates of eradica-tion costs quickly and at low cost, it is important that our approach can be implemented using readily available data. In many cases, the demographic data required to implement a stage matrix model are available from scientific

studies of the species in its natural habitat. Alternatively, it may be possible to obtain approximate values from experts. Detectability can be estimated at low cost using a method recently developed by Robe and Frost (2002). The method generates data on both detections and missed detections ('non-detections') in experiments designed to replicate the conditions faced on actual search missions. For example, actual or artificial weeds would be placed in known locations at different distances from a marked search path to be followed by the searchers. Each time a weed is detected, the position of the searcher on the search path would be recorded on a hand-held GPS, giving the distance between searcher and detected weed. Information on all detected weeds and their distance to the searcher would then be used to generate a cumulative detection curve. One would also record the distance between searcher and undetected weeds, giving the cumulative non-detection curve. Where the two curves cross is half the effective sweep width (R). With an estimate of R, combined with information on the area over which searching will take place and the search resources planned for that area, it is possible to compute search effectiveness using Equations (1) and (2) for a random search or Equations (1) and (3) for a parallel search pattern.

The costs of calibrating and applying the model can be reduced by developing tables for effective sweep width (R) and growth rate (λ) of different plant-type/environment combinations. Arguably the development of such tables would be an attractive research investment, as it would contribute to rapid and efficient evaluation of proposed eradication efforts.

Our results indicate that both the probability of killing a plant that is treated and the amount of labour required for control have a strong influence on the cost of eradication. Therefore another important research investment would be in the development of more effective (and less labour intensive) control techniques.

Our analysis was based on labour and herbicide production functions derived from a small dataset of a woody weed in the Galapagos Islands. Unfortunately there are no other data of this type available in the literature. Although the functional forms used for the production functions are standard and well accepted, the values of the parameters will vary with the situation and, as shown above, estimated costs are especially sensitive to the labour input parameter. Clearly, there is a need for more studies of the type undertaken by Buddenhagen and Yañez (2005), which allow the number and size of plants killed to be related to the amount of labour and herbicide required.

Application of the model to an actual weed-control program will require the cost function to be described in more detail. In particular, the cost of transporting the crew to the site, per-diem costs during field work, and the annual costs of administering the program would need to be considered. Thus, land managers would need to gather detailed cost data in order to improve the efficiency of their control programs. An interesting question is whether the efficiency gains in the control program will cover the additional costs of gathering and analysing cost information.

The potential to use search theory to improve the efficiency of invasive species management is promising. The model in its current form can be used for general planning and evaluation of an eradication program, and preliminary allocation of resources at a general level. Once a decision is made to eradicate a weed population search theory offers other useful techniques, such as Bayesian updating of probability maps, to assess and improve the efficiency of the eradication program over time. This is an interesting topic for future research, preferably in collaboration with managers of actual eradication programs.

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