THE ROLE OF ECOLOGICAL MODELLING IN WEED MANAGEMENT

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Summary There now exists a range of ecological models and modelling packages which are applicable to weed management. To date, weed managers have been slow to realise the advantages of using ecological models as aids in many areas of weed management. Published applications of ecological models in weed management are discussed and the advantages of employing modelling in weed management are explored using an example.

Ecological modelling technology is evolving rapidly. Part of this process is the development of computer-based generic modelling packages. These packages offer the ability to re-cycle model components, leading to reduced model development time. A modelling project to assist the management of woody weeds is described.

INTRODUCTION

Weed science has traditionally been dominated by a pragmatic focus on the weed-killing power of various chemical and mechanical controls, and issues such as the optimal time to apply herbicides (Cousens and Mortimer 1995). Given that weed researchers, weed managers and agribusiness interests interact to define weed management problems and set research agendas, it is not surprising that these groups have confined their interests to a small group of models which address such questions. The models which have been developed specifically for weed management have tended to address the problems of controlling annual weeds, such as *Avena fatua* L., in agricultural production systems. Relatively little modelling attention has been focused on the problems of managing perennial weeds of pastoral and conservation significance. Neither has a great deal of effort been expended on examining the ecology of weeds at broader scales.

Fortunately, the ecological modelling fraternity have not been so production focused. There is now a great deal of modelling expertise and software available to investigate and solve many questions in ecology generally, and weed ecology specifically.

There is now a pressing need to bridge the gulf that exists between traditional weed management and research paradigms, and for a more holistic approach which acknowledges that weed management is a complex ecological problem and *inter alia* embraces modelling technologies as a means of:

- designing more efficient, effective and environmentally sound weed management programs,
- extending the impact of limited research budgets, and
- focusing research efforts on solving management problems.

This paper is one attempt to bridge that gulf between managers and modellers by outlining the current and potential role of some ecological models in weed management. Cousens and Mortimer (1995) offer a good overview of many of the available models and their application to weed management. After briefly introducing ecological modelling in fairly general terms, I will concentrate on presenting examples of the application to weed management of ecological models which are currently being developed within the Co-operative Research Centre for Tropical Pest Management (CTPM). I will then discuss in more general terms the role of modelling in weed management.

ECOLOGICAL MODELLING

An ecological model is any form of simplification of the relationship between a species and its environment. The breadth of this statement is reflected in the plethora of ecological models which have been described in the literature. These models range from simple rule-bases and stochastic relationships through to sophisticated process-based computerized systems describing the simultaneous interaction of multiple species and their environments. A small sample of these published models and their uses is summarized in Table 1.

The evolution of any technology is slow and deterministic in that the development of new technologies are predicated upon a chain of previous developments. The development of ecological models is no exception. Early model building efforts were characterized by the use of computationally simple difference equations and matrix algebra. With the advent of widespread, cheap computing facilities, spreadsheet programs and procedural languages such as Basic, Fortran and Pascal, modellers launched into developing processed-based models driven by one or more environmental variables. In each case, the modellers usually started building subsequent models more or less from scratch. There were few examples of similar work to use as a launching pad to start working on new species. Each attempt to model a new species meant developing a new model. Attempts to reuse computing code from older models in the development of new code was a messy and frustrating business. In response,

Table 1. Some ecological models and their applications in weed management.

Class	Applications	Taxonomic groups	Source
Climate matching	Potential distribution; Formulation of quarantine policy.	Parthenium, *Parthenium hysterophorous* L.; Silverleaf nightshade *Solanum elaeagnifolium* Cav.; Johnsongrass, *Sorghum halepense* L. Pers.	Panetta and Mitchell (1991)
Climate matching	Formulation of control policy; Potential distribution; Risk analysis.	Honey locust *Gleditsia triacanthos* L.	Csurhes and Kriticos (1994)
Climate matching	Potential distribution; Formulation of control strategy; Evaluation of biocontrol prospects.	Alligator weed, *Alternanthera philoxeroides* (Mart.) Griseb.	Julien *et al*. (1995)
Rates of spread	Identification of optimal regional or local scale control strategies; Economic analysis of control strategies.	Serrated tussock, *Nasella trichotoma* (Nees) Arech.	Auld and Coote (1980)
Exponential equation	Investigating the effects of different combinations of control methods.	*Alopecurus myosuroides* Huds.	Cussans and Moss (1982)
Leslie matrix	Understanding population behaviour.	*Poa annua* L.	Begon and Mortimer (1986)
State and transition (Markov Chains)	Economic analysis of control strategies.	Prickly acacia, *Acacia nilotica* (L.) Del.	Mooy *et al*. (1992)
Ecophysiological	Research tool to highlight aspects of growth and development that are poorly understood.	Wild oat, *Avena fatua* L.	Weaver *et al*. (1993)
Epidemic	Explaining biogeographical distribution limits.	Mainly annual ruderals	Carter and Prince (1988)

there has been a call to develop more generic modelling packages which can be easily applied to different species or taxonomic groups by changing parameters rather than reconstructing models (Sutherst 1993).

Within the CTPM there has been a strong push to avoid the development of one-off models in favour of generic modelling packages or systems. So far there are three modelling tools available or nearing completion:

1. CLIMEX
2. GENSECT
3. Virtual Plants

Table 2 summarizes some of the generic modelling packages and their possible application in weed management.

BENEFITS OF MODELLING

Models are inexpensive to build and run in comparison with field experiments. Whilst the initial development costs of models may seem very high, the subsequent running costs of the model are negligible. This is not to say that models can replace field work or experimentation. On the contrary, models must be based upon rigorously designed experimentation if credible results are to be obtained. The relatively cheap running costs of models are highlighted where they are used to examine the combined effects of say different combinations of weed treatment, under a range of different environmental conditions. The marginal cost of conducting an additional field or laboratory experiment in a multifactorial investigation increases in a fairly linear manner. In contrast, the marginal cost of examining another treatment using a model is negligible. Sutherst (1993) notes that a field experiment can cost $A100 000. By comparison an analysis of implementation strategies for a new control for cattle ticks involving more than 1400 years of simulations cost less than half as much as one field experiment.

Table 2. Generic modelling packages and their application in weed management.

Name	Class of model	Typical applications	Source
BIOCLIM	Climate-matching	Assessment of quarantine threat; Risk assessment/economic threat; Development of continental or regional scale control or eradication strategies.	Busby (1991)
CLIMEX	Climate-matching	Assessing quarantine threat; Risk assessment/economic threat; Developing continental or regional scale control or eradication strategies; Biocontrol analysis.	Skarratt *et al*. (1995)
GARP	Environment-matching	Assessing potential distribution.	Stockwell (1985)
HABITAT	Environment-matching	Assessing potential distribution.	Walker and Cocks (1991)
GENSECT	Life-cycle	Understanding the nature of the problem; Identifying suitable control strategies; Teaching weed ecology.	–
INTERCOM	Ecophysiological	Understanding the nature of the weed problem; Investigating yield effects of competition; Biological control; Teaching weed ecology.	Kropff and van Laar (1993)
Virtual Plants	Physiological and architectural	Investigating the relationship between weed architecture and types of damage inflicted by herbivores and pathogens.	Hanan (1995)

Models can be used to examine combinations of external factors which are inaccessible in field conditions. Much experimentation into weed dynamics relies on the results of field experiments at one or a few locations, or laboratory experiments under a limited range of closely controlled environmental conditions. Whilst this form of experimentation produces reliable results, there is usually limited scope for managers to apply the information to decision making about weed control in all but those exact conditions. Models offer ways to extend the applicability of traditional scientific investigations by synthesizing the knowledge and applying it to combinations of conditions which have not been encountered during the experimentation.

Our understanding of a weeds biology or ecology can be tested using models. If our understanding is correct then it will be possible to build a model which provides plausible and consistent results. In short, the figures will add up. If a model produces results which are infeasible then there are three possible conclusions:

1. The model is incorrectly assembled (a programming bug).
2. Our understanding of the behaviour of the ecological system is flawed.
3. The ecological parameters or functions are incorrect.

Strenuous efforts should first be made to eliminate the first possibility. The last two possibilities are the most interesting from an ecological perspective. Depending upon the type of model, it may even be possible to automatically vary parameters in the model to make it produce feasible results. The parameters required to produce that output may indicate the areas where our knowledge is flawed, and may even indicate more realistic ranges for parameters.

THE ROLE OF MODELLING IN WEED MANAGEMENT

Ecological modelling clearly has an important role in weed management. It is no substitute for a good understanding of a species biology. But it is an activity which can assist weed managers and researchers in a number of ways, some described below. The coverage of model types is by no means unbiased but clearly reflects my background and experience in the field. The aim is to convey the usefulness of ecological modelling to weed management in the hope that managers in particular might seek to make better use of models and modellers in their organizations.

Potential distribution At the broadest level of weed management, questions are generally focused on the prevention of further weed invasions. Most of the analytical work of quarantine authorities in preventing weed invasions lies in assessing the weed invasion risk in particular regions. They are concerned to evaluate the risk of new weeds entering the country and becoming established, and the probability of successful eradication in the event of an accidental introduction (Sutherst and Maywald 1991). Various studies have concluded that there are few reliable morphological, ecological or taxonomic indicators of potential weediness (Noble 1989). The most reliable predictor of potential weediness is perhaps the demonstrated 'weediness' of a plant in a different country with similar climate and cultural practices. The successful application of CLIMEX to quarantine has been described by Sutherst and Maywald (1991).

Where an exotic plant is predicted to be climatically adapted to a country or region, a GIS can be used to analyse the spatial relationship between the modelled potential distribution and other spatial information such as production statistics or areas of conservation significance. This serves to ascertain the hazards associated with the invasion. This information is particularly important for quarantine and state weed control authorities wishing to formulate policies for the prevention of entry of potential weeds (Panetta and Mitchell 1991). Csurhes and Kriticos (1994) used CLIMEX to examine the potential distribution of Honey Locust in Australia, while Panetta and Mitchell (1991) used BIOCLIM to model the potential distribution of several weeds in New Zealand and CLIMEX to verify some aspects of the analysis. Figure 1 shows the results of a climatic analysis of the climatic suitability of Australia for rubber vine. Details of this analysis will be published elsewhere. The figure indicates that a large portion of the Northern Territory is climatically suitable for rubber vine. This fact has contributed to the development of a policy of the Northern Territory administration to actively seek to prevent the entry of rubber vine, and a proposal from the Queensland Government to establish an eradication zone and an active control zone within Queensland (Anon. 1994).

In attempting to decide on the proper course of management for an existing weed, it is firstly necessary to define the environment of the weed. This usually involves an interpretation of the effect of climate and disturbance regime upon the distribution of the weed. The development of a detailed population model for each new species is both relatively expensive and time-consuming, especially for perennial species. In the meantime there is a need for a more general description of the weeds habitat. In order to infer the habitat of a new weed species we can choose from a series of environment-matching programs (Table 1). Some of these programs directly infer the climatic envelope for a species based upon the spatial relationship of point distributions for known areas of suitable habitat, e.g. BIOCLIM, and in some cases areas of unsuitable habitat also (e.g. HABITAT). CLIMEX is a computer program which summarizes the overall response of an organism to temperature, moisture and day length. The underlying premises for all of the above climate-matching programs is that a species' geographical distribution is determined primarily by climate, and that climate is represented adequately by long-term average datasets. CLIMEX produces a series of indices describing the response of the species to the environment. For each location the program indicates the potential for the population to increase during favourable conditions, and the likelihood of surviving stressful conditions. These indices are combined into an overall 'ecoclimatic index' for each location (Figure 1).

The climatic indices are useful in understanding the ecology of the weed and in the formulation of a strategic management plan. For instance, the ecoclimatic index can distinguish the areas where the weed is likely to be a major pest from those areas where the environment is stressful to the weed and suitable habitat is likely to be found less frequently (*sensu* Carter and Prince 1988).

By combining different layers of information in the GIS it is possible to produce a spatial model of areas under threat of invasion by the weed. This model could then be used to produce summary statistics of area by degree of threat, or could be used to undertake an economic analysis of the benefits of various control strategies.

A major limitation of the environment matching programs is that they all rely on the interrogation of long-term average datasets. This means that sporadic

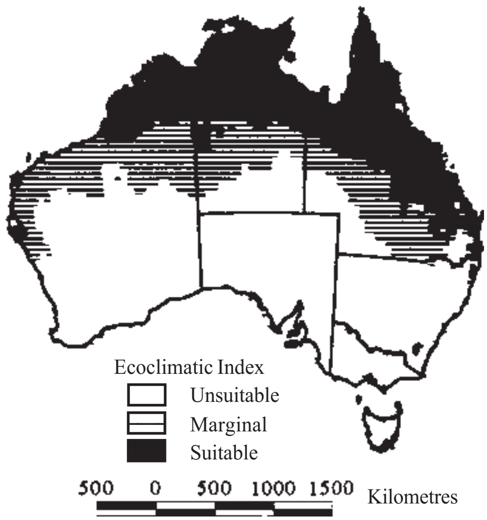

Figure 1. Potential distribution of rubber vine throughout Australia under current climatic conditions.

population recruitment and mortality events, or rapid range expansion or contraction in response to infrequent severe climatic or disturbance events cannot be modelled accurately.

Weed population models Once the overall description of the weed's relationship to its environment has been achieved, attempts can be made to construct a detailed population model. These models enable the long-term stability of the population to be simulated along with the seasonal reaction to climate and other factors. There are several sources of good descriptions of lifecycle models available (Begon and Mortimer 1981, Cousens and Mortimer 1995).

Modelling weed lifecycles hinges on describing the effect of environmental factors on the growth, reproduction and mortality processes for each defined life-stage of the weed. Lifecycle models differ greatly in their complexity, sequence and structure depending upon such factors as:

- weed longevity (ephemeral, annual, biennial, perennial),
- primary mode of reproduction (seed, vegetatively, both),
- importance of different dispersal pathways, and
- the aim of the model.

For each lifecycle, however, there tend to be a limited number of functional relationships which describe the population response to external factors or *forcing functions*. The limited number of response functions has enabled researchers at the CTPM to develop a program called GENSECT (Generic Insect). This program will enable ecological modellers to very quickly and easily create new lifecycle models by drawing upon libraries of response functions. This ability has already been demonstrated for several invertebrate species.

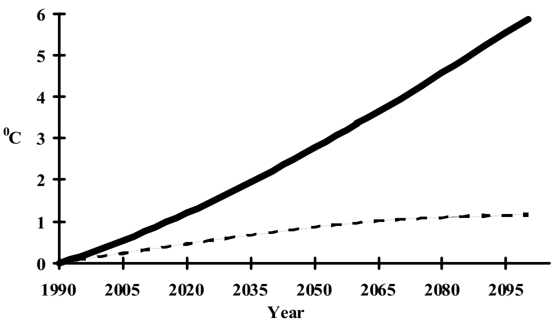

Figure 2. Global warming scenarios fall between the high increase (bold line) and low increase (dashed line). Source: Anon. (1992).

For short-lived species especially, it may be necessary to monitor the population size of the weed in the field along with as many environmental parameters as possible, at a set of representative locations. These longitudinal population studies may then reveal the nature of the relationship between population dynamics and the measured environmental parameters. Population dynamics of perennial species may be able to be adequately inferred by relating life tables built on population snapshots to historical climate and cultural datasets. Extreme caution should always be exercised in engaging in such analyses because it is possible to create a given population age structure in many ways.

Rates of spread Invasion dynamics is an area that has received scant attention from researchers, with most attention focused upon the local dispersal processes of plants. In part at least this perhaps reflects the relatively recent development of spatial analytical technology (GISs, spatial statistics, powerful computing platforms, remote sensing and image analysis, landscape ecology etc.).

Auld and Coote (1980) have prepared a model of plant spread based on population-level processes of growth and dispersal. This model was used by Menz *et al.* (1981) to assess the relative economic efficiency of four different control strategies, for three different rates of weed spread. Through the use of the model, Menz *et al.* (1981) were able to demonstrate that there was no universal cheapest weed management strategy. Rather, the cost-effectiveness of any strategy strongly depended upon the rate of spread of the population. Whilst Menz *et al.* (1981) examined only four management strategies on three rates of plant spread, the model could be used to analyse the relative cost-effectiveness of applying different management strategies in specific case studies.

As noted by Chippendale (1991), the information needed to parameterize models of plant spread such as described by Auld *et al.* (1987) are usually not available, especially not prior to, or in the early stages of a species invasion. Chippendale (1991) went on to create an empirical model based upon the known area of rubber vine at different points in time. This model was used to analyse the economics of investing in further research into control measures for rubber vine.

Optimizing management tactics Lifecycle models can be useful for investigating the likely population-level impacts of various management strategies For instance, a periodic management practice which removes a proportion of adults of a weed population can be simulated, and the results compared with the situation where no control

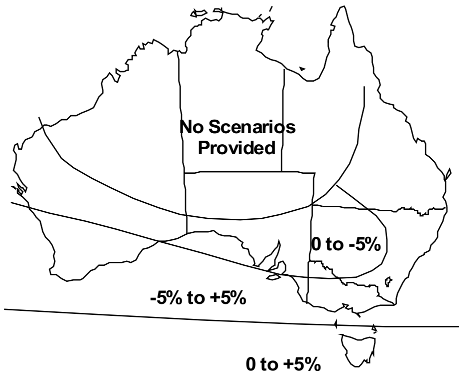

Figure 3. Predicted winter rainfall response per degree global warming (see Figure 2). Source: Anon. (1992).

is exercised, or where the mortality factor affects a different age or stage of the population.

Selecting biocontrol agents Climate matching models have been used to predict the areas within a weeds potential distribution where the weed can be successfully controlled by a particular biocontrol agent. Julien *et al.* (1995) used CLIMEX to show that alligator weed would not be controlled throughout its potential range in Australia by the alligator weed flea beetle, *Agasicles hygrophila*. This information alerted aquatic weed managers to the need to develop additional means of controlling this weed in Australia.

Climate matching programs can be used to successfully target areas for the collection of biocontrol agents (Worner *et al.* 1989, Marohasy 1995). By selecting genotypes of biocontrol agents from areas more closely matched climatically to the target country, the likely success of the introduction can be improved.

Climate change and potential distribution Anthropogenic Climate Change (global warming) is an area of weed research that has received some attention of late. Most of this effort has been directed at the direct effects of altered atmospheric chemistry and weather upon the physiology, morphology and competitiveness of weeds under altered climate conditions. There has been little detailed work on the impact of climate change on the potential distribution of weeds.

The CSIRO's Division of Atmospheric Research have produced climate change scenarios for the Australian Region using Global Circulation Models (GCMs) (Anon. 1992). The current predictions for changes in temperature and rainfall are presented in Figures 2 and 3 respectively. These predictions of climatic changes have been used to modify long-term average climate data sets to allow predictions of the potential distribution of a species under the changed climatic conditions, using the same climate-matching models described above. Figure 4 shows the potential distribution of rubber vine under the most extreme (hottest and wettest) climate change scenario for the years 2030 and 2070.

The main use for a weeds potential distribution under climate change is to assess the direction and extent of potential threats to agricultural production and conservation areas in the future. The climate sensitivity, and therefore geographic stability, of the threatened activity or area should be considered carefully in this sort of analysis. A further important use of this prediction is the assessment of the long-term prudence of current control strategies for each species.

Problem definition The first two tasks in building a model are to decide upon the aim and the form of the model. In making these decisions the weed problem must be defined accurately, to ensure that the model is built with a useful purpose in mind. Often, weed managers, researchers and other stakeholders fail to adequately define the problem(s) that they are trying to solve. This has been identified as a key reason for the failure of many integrated pest management programs (Norton 1994). By undertaking a model-building exercise, the managers and other stakeholders are forced to define the problem as accurately as possible.

Research synthesis and coordination Ecological models can provide a framework for understanding the relationship between research results. When a weed problem is first identified, or during a weed research progress review, a weed model or models can act as a useful framework for synthesizing the available knowledge on the weeds ecology or biology. The very process of scientific inquiry means that the available knowledge on any given species or production system will consist of a collection of disparate bits of information which may be only loosely connected by their relationship to the target species. A model can provide a framework for organizing the available information about a species into a useful structure from which the relationship between the different facts can be determined. This process highlights areas in which knowledge is lacking. As the potential knowledge about any particular species is essentially unlimited, it is desirable (for managers at least) to limit research to gathering that which will assist in making management decisions. That is, ensuring that research is mainly applied and accountable. Models can aid considerably in this task in several ways.

One of the tasks in building a model is to identify previously published information which contain parameters for the model. The knowledge gaps left after this stage are the areas where further research attention needs to be focused. Not all of the remaining parameters may require intensive research in order to build an adequate model. Further, not all of them will have the same urgency. In many cases the parameters can be estimated using the best knowledge available. This will enable a sensitivity analysis to be undertaken. The most sensitive parameters are the ones where the most accuracy is required most urgently and where most research attention should be aimed. The model then acts as an independent mechanism for designing and prioritizing competing research projects.

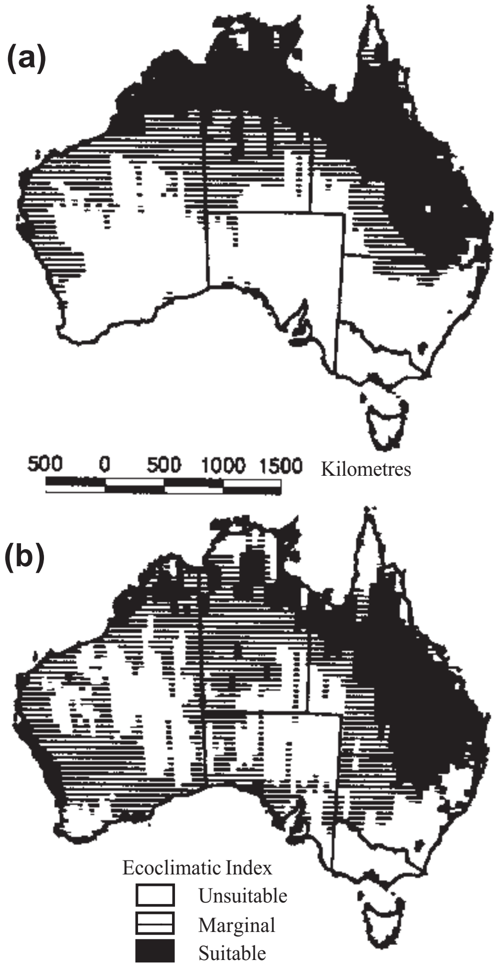

Figure 4. Potential distribution of rubber vine throughout Australia under hottest and wettest climate change scenario a) 2030, b) 2070. Source of climate change scenario: CSIRO Division of Atmospheric Research.

Local decision-making The contribution of models to decision-making at the local level of management is considerable. Generally however, land managers do not use the models directly. Researchers usually build and run the models to identify answers to questions concerning:

- the weed control decision threshold,
- the efficacy of control methods on weed populations,
- type of control method(s) to apply, and
- the optimal timing and frequency of each control method in relation to the weed's lifecycle.

This information is then conveyed to land managers in the form of an expert system, a database, or a set of 'rules of thumb'. It is easy to overlook and therefore understate the role of ecological models in management at the local level because it is indirect.

THE FUTURE

As Woodward (1992) has indicated, there is a need for population models to be linked to spatial models. This is one of the aims of my Ph.D. thesis project. I intend to build process-based population models of rubber vine and prickly acacia, at a range of representative locations using the generic population modelling package, GENSECT. Once the point models are calibrated and validated, I will incorporate them into a GIS. This will enable the population dynamics of the weeds to be gauged in response to weather and land management factors at the continental level. Using these models, we will be able to quickly and easily assess the effects of various management regimes in different locations simultaneously. We will also be able to predict the impact of climate change on the population dynamics of these species for any given location. A further aim is to examine the effects of climate change on the carbon sequestration balance within the rangelands. By linking the GENSECT models to competition models such as INTERCOM (Kropff *et al.* 1993) we hope to be able to predict the impact of alterations in CO_2 concentrations on the relative competitiveness of these C_3 weeds versus the C_4 pasture grasses in the rangelands.

By using GENSECT it will be possible to save a considerable amount of time in building the models by drawing on pre-existing algorithms and data handling routines. It will also be possible to reuse some, or all of the models in future exercises involving other species.

In building my models, I am working in close association with the staff of CSIRO's Division of Tropical Crops and Pastures in Townsville. This association is a mutually beneficial arrangement whereby the field and laboratory research investigations are being conducted with a view to providing parameters for the models. In return, the modelling activity provides a means of:

- synthesizing our current understanding of the weeds' biology,
- prioritizing research, and
- examining competing hypotheses for both spread and management.

This is one role of ecological modelling in weed management which is proving very successful.

The ultimate aim of the co-operative venture is to produce a series of models which can be used for testing and optimizing weed management scenarios. This will allow us to provide land managers and policy makers with sound advice on weed control.

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