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The role of pre-release efficacy assessment in selecting classical biological control agents for weeds—applying the Anna Karenina principle

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Abstract

The goals in selecting classical biological control agents for weeds are to identify agents that will be both safe for release and effective in controlling their target plants. The release of ineffective agents should be avoided, as these add to the costs and risks of biological control without contributing to its benefits. While the principles of host-specificity testing and risk assessment for weed biological control agents have been extensively debated and refined, there has been less attention given to assessing the probable efficacy of agents prior to release. This reluctance to undertake pre-release efficacy assessment (PREA) is probably based on concerns that it will both add to the cost of screening biological control agents and introduce a risk of wrongly rejecting effective agents. We used a project simulation model to investigate the implications of using PREA as an additional filter in the agent selection process. The results suggest that, if it can be done at a lower cost than host-specificity testing, the use of PREA as the first filter can make agent selection more cost-effective than screening based on host-specificity alone. We discuss examples of PREA and potential approaches. The impact of biocontrol agents is a function of their range, abundance, and per-capita damage. While it will always be difficult to predict the post-release abundance of biological control agents from pre-release studies, some estimates of potential range can be obtained from studies of climatic adaptation. For agents that affect the vegetative growth or survival of their target weeds, experimental measurement of per-capita damage is feasible and can contribute to a reduction in the numbers of ineffective agents released. The Anna Karenina principle states that success in complex undertakings does not depend on a single factor but requires avoiding many separate causes of failure. We suggest that, in biological control of weeds, the use of agents that are not sufficiently damaging is one such cause that can be partially avoided by the use of pre-release efficacy assessment.

Keywords: Biological control; Weeds; Agent selection; Efficacy assessment; Pre-release studies; Cost-effectiveness; Modeling

1. Introduction

Classical biological control of exotic invasive plants has a history of dramatic successes that have earned it a place as one of the primary tools in the effort to mitigate the impacts of these species on both natural and managed ecosystems (McFadyen, 1998). It is, however, a high-stakes game. Introducing exotic herbivores and pathogens as weed biocontrol agents is not an intrinsically safe operation, but one that must be made safe by the way in which it is practiced. Thus, practitioners of classical biological control are increasingly conscious of the dual expectation placed on them to achieve successful control of invasive plants, and to avoid damage to nontarget plants and adverse indirect effects. The procedures and strategies used to select biological control agents play a central role in meeting these expectations.

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The evident potential risks of introducing herbivorous insects or plant pathogens into areas where they do not naturally occur mean that extensive risk assessment is both an ethical and regulatory requirement for any such introduction. Much effort has been devoted to developing host-specificity tests in an effort to ensure that nontarget plant species will not be damaged by introduced biological control agents, and the role of host-specificity and other approaches to risk assessment have been extensively discussed in the biological control of weeds literature (e.g., Briese et al., 2002a; Evans, 2000; Louda et al., 2003; McEvoy, 1996; Sheppard et al., 2003).

Practitioners of biological control of weeds have historically been concerned that the agents they select and release will be damaging enough to contribute to the eventual control of the target weed. Numerical scoring systems developed by Harris (1973) and Goeden (1983) for prioritizing candidate weed biocontrol agents were heavily weighted towards agents with demonstrated impact. In the early decades of biocontrol of weeds, concern for nontarget effects concentrated on possible nontarget impacts on major crops and agronomic plants. But by the early 1970s this began to shift to native plants (Pemberton, 2003), requiring increased resources to accommodate more extensive host-specificity testing against a wider range of test plants. As a result, for the past few decades, selection of weed biological control agents has concentrated on host-specificity, with less effort being devoted to measuring or predicting their impact or efficacy.

We suspect that many workers believe that efficacy is affected by so many complex, interacting, and unforeseeable factors that useful predictions are essentially not feasible. This is the implication of the often-quoted remark that successful prediction of efficacy is the "holy grail" of biological control (McFadyen, 1998). There are probably two components to this reluctance to rely on pre-release efficacy assessment; one is that such studies will consume scarce resources that could better be spent on the mandatory host-specificity testing required for all agents (McFadyen, 2003), and the other is the concern that incorrect predictions may result in the rejection of agents that would, in fact, have been successful if released. The latter may be called the "false negative" problem.

While most weed agents that are released do become established (Julien and Griffiths, 1998), only a portion of those that establish contribute to successful control of the target weed. It is sometimes assumed that any agent that becomes sufficiently abundant must have some impact on the population of its target weed. This is not, however, necessarily true (Myers, 2000). McFadyen (2003), in a global review, classified 38 weed biocontrol projects as successful, but found that out of the 132 agents released, only 54 contributed to the successful control of these 38 weeds, although 98 established. Thus, a substantial portion of weed biocontrol agents, even some that have become very abundant after their release, fail to control their target. Denoth et al. (2002) showed that in 54% of successful weed biocontrol projects in which multiple agents were released, a single agent was responsible for control. This again implies that many agents have become established without contributing to control.

Table 1 lists some examples, gleaned from the published literature, of agents that have had no significant impact on their target weeds, despite becoming relatively abundant. There are probably many additional agents that have become abundant without causing a corresponding decrease in their target, but whose lack of efficacy has not been documented. Possible causes of ineffectiveness of abundant agents include: the use of seed feeders against target weeds whose populations are not seed-limited; feeding on nonessential tissue such as parenchyma or fruit pulp; the ability of target weeds to tolerate or compensate for defoliation or other kinds of injury; damage that comes too late in the phenology of the weed to affect its reproduction or growth; and agents that trigger a strong induced defensive response in the target weed, protecting it against further damage.

Agents that become abundant without bringing about effective control of their targets are particularly likely to be associated with nontarget or indirect ecological effects (Holt and Hochberg, 2001). For example, *Urophora* spp. released against *Centaurea diffusa* Lam. and *Centaurea maculosa* Lam. have not substantially reduced the density of their hosts, but produce abundant overwintering larvae, which have become a preferred food source for deer mice, *Peromyscus maniculatus* (Wagner). This food subsidy has led to increases in deer mouse populations and raised concerns about possible increased transmission of hantavirus, a pathogen deadly to humans (Ortega et al., 2004; Pearson, 1999; Pearson and Callaway, 2003; Pearson et al., 2000).

In view of the above, we concur with Balciunas (2004) and Sheppard (2003) that greater attention should be paid to the possibility of selecting agents on the basis of their potential efficacy. For both economic and ecological reasons, the release of ineffective agents should be avoided where possible. From a benefit–cost–risk viewpoint, ineffective agents have no benefits, substantial costs for screening, rearing, release, and field assessment (probably comparable to those associated with effective agents), and nonzero risks of nontarget damage or indirect ecological effects. Such releases represent a waste of resources, contribute to the perception of biological control as a hit-or-miss strategy, and carry risks of ecological side-effects. Clearly, the only reason to release ineffective agents is as an unavoidable consequence of our inability to predict agent efficacy. In this paper, we discuss the types of evidence and studies that could be used in prediction of efficacy.

Table 1
Examples of biological control agents that have become abundant but have not had a significant impact on populations of their target weed

Agent	Target weed, location, and date first released	Notes	References
Seed-feeders, not destroying enough seed, or target weed population not seed-limited			
Algarobius prosopis (Leconte) (Col., Bruchidae)	*Prosopis* spp. in South Africa (1987)	"Despite its abundance, *A. prosopis* has contributed little to the overall control of the weed."	Impson et al. (1999)
Urophora affinis Frauenfeld and *U. quadrifasciata* Meigen (Dipt., Tephritidae)	*Centaurea* spp. in USA (1973) and Canada (1970)	Density-dependent recruitment compensates for seed reduction.	Powell (1989)
Defoliators, plant able to tolerate defoliation			
Calophasia lunula Hufnagel (Lep., Noctuidae)	*Linaria* spp. in USA (1968) and Canada (1962)	"Defoliation ... can be quite spectacular in localized areas."	Nowierski (2004)
Hyles euphorbiae (L.) (Lep., Sphingidae)	*Euphorbia esula* L. in USA (1964) and Canada (1966)	"Larval consumption of leafy spurge is apparent in dense patches. However, this feeding does not result in plant mortality."	Hansen (2004)
Feeding on nonessential tissues			
Coleophora parthenica Meyrick (Lep., Coleophoridae)	*Salsola tragus* L. in USA (1973) and Canada (1975)	"Impact on the host minimal: damage to the pith appears to have little effect on growth and seed production."	Pemberton (1986); Pitcairn (2004)
Cyrtobagous singularis Hustache (Col., Curculionidae)	*Salvinia molesta* Mitchell in Fiji (1979), Botswana (1971), Zambia (1971)	Mainly feeds externally, does not tunnel within rhizomes (unlike *C. salviniae* Calder and Sands).	Sands and Schotz (1985)
Hadroplontus litura (F.) (Col., Curculionidae)	*Cirsium arvense* (L.) Scop. in USA (1971) and Canada (1965)	Larvae mine in stem base and root crown, feed on parenchyma without damaging vascular tissue.	Peschken and Derby (1992)
Microplontus edentulus (Schultze) (Col., Curculionidae)	*Matricaria perforata* Mérat in Canada (1997)	Stem miner, develops while plants are already branching and flowering.	McClay et al. (2002)
Ophiomyia lantanae (Froggatt) (Dipt, Agromyzidae)	*Lantana camara* L. *sensu lato* in South Africa (1961)	Feeds on fleshy tissue of fruit without damaging seeds. "Widespread and abundant, but has little effect on seed viability."	Baars and Neser (1999); Broughton (1999)
Urophora cardui (L.) (Dipt., Tephritidae)	*Cirsium arvense* (L.) Scop. in USA (1977) and Canada (1974)	Stem galls develop while plants are already branching and flowering.	Peschken and Derby (1992)
Damage occurs too late in plant's phenology			
Cystiphora sonchi (Bremi) (Dipt., Cecidomyiidae)	*Sonchus arvensis* L. in Canada (1981)	Oviposits only into leaves towards the end of their expansion period.	De Clerck-Floate and Steeves (1995); McClay and Peschken (2002)
Spurgia esulae (Dipt., Cecidomyiidae)	*Euphorbia cyparissias* L. in USA (1985)	"The majority of cypress spurge flowering occurs before galls are present each spring. These flowers continue to develop seeds, and galls form on other shoots. ... does not appear to contribute to biological control of leafy or cypress spurge."	Faubert and Casagrande (2002)
Plant has compensatory regrowth			
Leucoptera spartifoliella (Hübner) (Lep., Lyonetiidae)	*Cytisus scoparius* (L.) in USA (1960)	"Large numbers of larvae may deform plants and cause stem dieback. However, flowering and regrowth often occur below the attacked shoots."	Coombs and Markin (2004)

Cases are grouped by suggested reasons for their ineffectiveness.

Finally, we consider the sequence of tests traditionally used in selecting biocontrol agents and how pre-release efficacy assessment (PREA) can be integrated with traditional testing. Host-specificity testing is, of course, mandatory. Using a project simulation model, we investigated the implications of using PREA as an additional filter for agent selection. We examined its effects on project costs and outcomes, and also the optimal sequencing of test steps: whether PREA should be the first filter, with host-specificity tests conducted only on species that show potential for impact, or the second filter, to be conducted after host-specificity testing.

2. Feasibility of efficacy assessment

In the absence of a crystal ball, factors that contribute to agent success or failure are only useful in agent selection if they can be assessed or predicted prior to release. Thus, we will focus on the kinds of evidence that can be gathered from pre-release studies.

Ecologically, a newly released biological control agent is simply a particular case of a nonnative species invading a new environment. Thus, it is useful to consider the factors affecting agent success in terms of the conceptual model proposed by Parker et al. (1999) for the ecological impact of invading species:

$$\text{Impact} = \text{Range} \times \text{Abundance} \times \text{Per-capita effect}.$$

We will attempt to assess the possible contribution of pre-release studies to predicting each of these components.

Range and abundance are closely related, and many of the same considerations apply to both of these components. If the initial colonizers are successful in producing abundant descendents in the area of introduction, the species is more likely to be successful in spreading and extending its range by natural dispersal. Deliberate redistribution is also more feasible. Both range and abundance are primarily functions of the agent's life-history characteristics and its responses to the physical and biotic environment into which it is released. Relevant life-history characteristics include fecundity, number of generations, and dispersal capability, while environmental factors include host–plant suitability, climatic conditions, and the impact of natural enemies in the release area.

Some of these factors, such as fecundity, voltinism, and host–plant suitability, are relatively easy to assess in pre-release studies. Climatic matching is a little more time-consuming, but is also approachable either through bioclimatic range modeling using tools such as CLIMEX (Julien et al., 1995; Lactin et al., 1997; Scott, 1992; Sutherst et al., 1999) or through experimental study of the effects of temperature and other physical factors (e.g., Byrne et al., 2002; McClay, 1996; McClay and Hughes, 1995). The impact of natural enemies such as predators and parasitoids in the area of introduction, however, is much more difficult to predict. Although McFadyen and Spafford Jacob (2004) reviewed some generalizations regarding levels of parasitoid attack to be expected on introduced weed biological control agents, our ability to predict levels of natural enemy attack on introduced biocontrol agents is very limited. Thus, predicting the post-release abundance of biocontrol agents from pre-release studies is very difficult.

Per-capita effect, on the other hand, is in principle quite accessible to pre-release assessment. All that is needed is to expose the target plant to known population densities or levels of attack by a candidate biological control agent, and measure its effects on some parameter or parameters relevant to the target plant's performance in the field, such as biomass, seed production, or competitive ability. Per-capita effect on an individual plant level does not necessarily translate into impact on target weed populations, and, thus, agent efficacy needs also to be considered in an ecological context. This is most clearly seen in the case of seed-feeding agents, where it is easy to show in cage experiments that increasing agent load increases seed destruction, but the effects on plant population depend on whether plant recruitment is limited by seed production (e.g., Powell, 1989). Studies and models of the population biology of the weed in the areas of infestation, such as that by Smith et al. (1997) for *Rottboellia cochinchinensis* (Lour.) W.D. Clayton, may be useful in helping to predict whether a given level of seed destruction will be effective in reducing target weed populations. For agents that affect the survival and vegetative growth of their targets—such as defoliators, gall formers, and root miners—it is certainly also true that population-level effects are not solely dependent on effects at the individual plant level. However, such agents cannot have a population-level effect if they do not cause substantial damage at the individual plant level.

Per-capita impact is most easily assessed in field tests in the country of origin in which densities of the candidate agent are manipulated or determined by the investigator. For example, Balciunas and Burrows (1993), through insecticidal exclusion experiments, quantified the impact of Australian insects on *Melaleuca quinquenervia* (Cav.) Blake (Myrtaceae) saplings. Similarly, Goolsby et al. (2004) used an acaricide exclusion treatment to assess the impact of the mite *Floracarus perrepae* Knihinicki and Boczek (Eriophyidae), on *Lygodium microphyllum* (Cav.) R. Br. in its native range in Australia. The impacts of several candidate European agents for control of *Onopordum* spp. in Australia were documented in field cage studies in Europe prior to their release in Australia. Briese (1996) and Briese et al. (2004) quantified the impact of various densities of the weevil *Lixus cardui* Olivier on *Onopordum* spp. in large field cages

in Spain. Similar studies were carried out with *Trichosirocalus briesei* Alonso-Zarazaga & Sanches-Ruiz (Briese et al., 2002b) and *Botanophila spinosa* Rondani (Briese et al., 2003). This type of approach is also suitable for pathogen candidates (e.g., Brun et al., 1995; Hasan and Aracil, 1991).

Assessments of per-capita impact can also be done under laboratory or greenhouse conditions. Balciunas (2004) reports comparing, under quarantine conditions, the impacts of two densities of a gall-making fly from South Africa that is being considered for release as a biological control agent for Cape ivy, *Delairea odorata* Lem. (Asteraceae). Klöppel et al. (2003) used glasshouse- and shadehouse-grown plants to predict the impact of a gall-forming cynipid wasp on *Hieracium pilosella* L. (Asteraceae). Wu et al. (1999) showed that high densities (around 200 per pot) of the planthoppers *Prokelisia marginata* (Van Duzee) and *P. dolus* (Wilson) caused up to 90% mortality of *Spartina anglica* C.E. Hubbard in a greenhouse experiment.

A promising approach to efficacy assessment is the use of experiments where the target weed is grown together with a competing plant not attacked by the candidate biocontrol agent. Measurements of the competitive interactions between the two plants in the presence and absence of the candidate agent can give a sensitive indicator of the agent's potential impacts on the target weed's performance in a setting more like the field. To date, this approach has mainly been used with aquatic weeds (e.g., Coetzee et al., 2005; Van et al., 1998) but it should also be feasible with herbaceous terrestrial weeds.

The "damage curve" (Peterson and Higley, 2001) was introduced to represent crop yield as a function of insect pest injury. It can, however, equally well be used to represent the impact of a candidate biocontrol agent at various densities on a target weed. This concept makes the useful distinction between "injury" (the amount of plant tissue removed by a pest) and "damage" (the resulting effect on the crop's yield), and emphasizes that damage is far from being a linear function of injury. A version adapted for weed biological control (Fig. 1) would relate a relevant measure of weed performance, such as seed production, growth rate, area covered, or final biomass, to biocontrol agent load. Experimental measurement of this damage curve would help to identify agents that do not have enough impact on their target to be worth releasing. Successful agents must have a damage curve that dips down to low levels at some high, but realistic, density of agents per plant. It is probably not necessary to measure the weed's performance over a wide range of agent loads. It would be adequate to compare the performance of control (uninfested) plants with those subjected to the maximum agent load that could realistically be expected to occur in the field post-release. This would occur, for instance, with galling insects when all available gall initiation sites were occupied, or with a defoliator when 100% of foliage is removed during the feeding period of the insect.

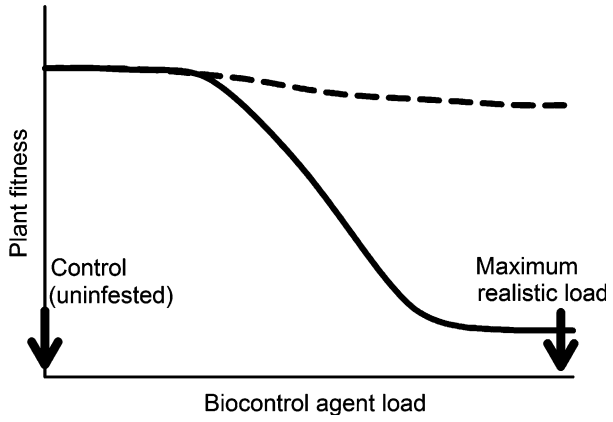

Fig. 1. Schematic representation of a damage curve for a candidate weed biological control agent, adapted from Peterson and Higley (2001). Horizontal axis is the biocontrol agent load, i.e., the number of individuals of the biocontrol agent per unit of plant biomass. Vertical axis is a relevant measure of plant performance or fitness, such as seed production, growth rate, or final biomass. Solid curve shows a damage curve for a potentially effective agent; dotted curve represents a candidate agent that has little effect on plant performance even at high loads.

Several considerations should be kept in mind when designing such assessments. The density of the agents used should be high enough to represent a best-case scenario, i.e., an outbreak population in which agent density is limited only by the availability of the target weed. Tests done with lower densities of agents may result in underestimating the potential impact of the candidate agent. They may also miss effects of unexpected types of injury that are significant only at high density. For instance, the weevil *Mecinus janthinus* Germar (Coleoptera: Curculionidae) was released in British Columbia, Canada, for control of Dalmatian toadflax, *Linaria dalmatica* (L.) Mill. Larvae of this weevil are stem-miners, and the main effect of the insect was predicted to be wilting of shoots as a result of larval damage (Jeanneret and Schroeder, 1992). However, after establishment of outbreak-level populations in British Columbia, heavy spring feeding by overwintered adults on the young shoot tips resulted in extensive stunting of shoots and suppression of flowering (Carney, 2003). Pre-release impact assessment using lower densities of weevils missed this unexpected "bonus" effect of an outbreak population. This means that it is necessary to develop rearing methods capable of producing sufficiently large numbers of the agent for testing. Testing should also be continued over a long enough time to allow the full effects of the agent to become apparent, and agents should be applied at the phenological stage of the plant that they would be expected to attack in the field. Studies should be replicated and valid statistical design and analysis must be

applied. Climatic and environmental conditions should be matched as well as possible to those of the area where release of the agent is proposed.

3. Simulation model

A simulation study was done to compare the implications of three different agent selection strategies on the outcomes of biological control projects. The goals of the modeling exercise were to investigate the effects on cost-effectiveness of incorporating PREA into agent selection strategies, and to determine the optimal sequencing of PREA (before or after host-specificity testing) under a range of relative costs for PREA, host-specificity testing, and field release. The model was implemented as an Excel spreadsheet.

3.1. Agent pool

A pool of 1000 hypothetical candidate agents was generated using the following parameters:

- $\mathbf{P}_{hs}$ the probability that a given candidate is sufficiently host-specific to be released.
- $\mathbf{P}_{eff}$ the probability that a given candidate is "actually effective," i.e., that, if released in the area of introduction, it would be effective in controlling the target weed. Effectiveness was considered as a binary variable, i.e., agents are either effective or not.
- $\mathbf{P}_{fp}$ the false positive rate, i.e., the probability that a pre-release assessment of an actually ineffective agent will indicate that it is effective.
- $\mathbf{P}_{fn}$ the false negative rate, i.e., the probability that a pre-release assessment of an actually effective agent will indicate that it is ineffective.

The procedure used to generate the pool was:

1. A uniformly distributed random number between 0 and 1 was assigned to each candidate. If this number was less than $\mathbf{P}_{hs}$, the candidate was considered acceptably host-specific.
2. A proportion $\mathbf{P}_{eff}$ of all candidates was assigned to be "actually effective," independently of their host-specificity.
3. As the actual effectiveness of an agent can only be known after release, it was not used directly within the model as a basis for agent selection decisions. Instead, these decisions were based on results of a pre-release efficacy assessment (PREA) assigned to each candidate based on (a) its actual efficacy and (b) the false positive and false negative rates. The proportions of candidates assigned positive or negative results (i.e., predicted to be effective or ineffective, respectively) from the pre-release efficacy assessment were obtained from:

	Pre-release efficacy assessment	
	Ineffective	Effective
Actual efficacy		
Ineffective	$(1-\mathbf{P}_{fp})\times(1-\mathbf{P}_{eff})$ (True negatives)	$(1-\mathbf{P}_{eff})\times\mathbf{P}_{fp}$ (False positives)
Effective	$\mathbf{P}_{eff}\times\mathbf{P}_{fn}$ (False negatives)	$\mathbf{P}_{eff}\times(1-\mathbf{P}_{fn})$ (True positives)

3.2. Selection strategies

Three agent selection strategies were considered:

1. *Host-specificity only*. All candidates are screened for host-specificity. If specific, they are then released in the field. No pre-release efficacy assessment is done.
2. *Specificity first*. All candidates first undergo host-specificity testing. If they are sufficiently host-specific, they then undergo a pre-release efficacy assessment. If the results of this indicate that they are effective, they are then released in the field.
3. *Efficacy first*. All candidates first undergo a pre-release efficacy assessment. If the results of this are positive, they then undergo host-specificity testing. If the results of this are also positive, they are then released in the field.

For simplicity, it was assumed that the host-specificity testing procedure gives reliable results (Pemberton, 2000). The results of the PREA, however, were subject to false positives and false negatives at set rates as described above.

3.3. Costs

Three sets of costs were considered, for host-specificity testing, PREA, and field release, but for modeling purposes it is only necessary to vary two of these relative to the third. The cost of host-specificity testing was held at an arbitrary value of $100,000 per candidate species, while costs for PREA and field release were varied separately, in steps of $25,000, from zero to $200,000 per candidate species. "Field release" includes the costs of obtaining, rearing, releasing, distributing, and monitoring an agent once the decision has been made to release it in the field.

3.4. Simulated projects

Projects were simulated by first assigning dollar costs per agent for pre-release efficacy assessment and field

release. An ordered set of 30 candidate agents was then randomly selected from the pool of 1000 and "tested" in sequence according to each of the three strategies described above. A "success" was counted when the first "actually effective" agent was released in the field. Costs were accumulated if they are actually incurred. For example, for strategy 1 every agent incurs the cost for host-specificity testing, but only those agents found to be specific incur the cost for field release.

For each simulated project and for each strategy, the following scores were kept up to and including the first "success":

1. Cumulative costs incurred.
2. Total number of candidate agents studied.
3. Total number of ineffective agents released.
4. Total number of specific, effective agents rejected for release.

(Note that in a given run scores 3 and 4 are always the same under strategy 2 as under strategy 3; these strategies make the same recommendations for which agents to release, differing only in the order of testing and, thus, in their costs.)

One hundred replicate projects were generated for each set of costs. In each project, the winning strategy was considered to be that with the lowest cumulative costs to the first success. If two strategies were tied, both were counted as winning strategies.

Two comparisons were made, first between strategy 1 and either of strategies 2 or 3, and second between strategy 2 and strategy 3. These represent the questions, respectively, whether PREA can make agent selection more cost-effective, and if PREA is to be done, whether it should be the first or second filter used in selecting agents.

4. Results

Representative results from the simulations are shown, obtained with the following parameter values:

$$\mathbf{P}_{hs} = 0.5 \quad \mathbf{P}_{eff} = 0.25 \quad \mathbf{P}_{fn} = 0.1 \quad \mathbf{P}_{fp} = 0.5.$$

As the pool represents a pool of candidate agents from which obviously nonspecific feeders such as known pests and polyphages have been eliminated, leaving only those that are considered worth subjecting to full host-specificity testing, it is permissible to set $\mathbf{P}_{hs}$ fairly high. The false negative rate was set fairly low, at 10%, representing a not-very-stringent screening for efficacy, on the assumption that biocontrol workers will be reluctant to reject large numbers of candidate agents on the basis of an unfavorable PREA. As the price for setting the efficacy bar low, the false positive rate was set high, with a 50% probability that a candidate that is actually ineffective will be rated as effective in the pre-release efficacy assessment.

For each combination of PREA and field release costs, Figs. 2 and 3 show the probability, estimated by the proportion out of 100 runs, that a given strategy will be the winner, i.e., have the lowest (or be tied for the lowest) cost of the strategies being compared. Fig. 2 shows the outcome of a comparison between strategy 1 and strategies 2 or 3, i.e., between host-specificity testing alone and host-specificity testing plus PREA. If PREA is expensive in comparison with host-specificity testing, it will almost always be most cost-effective to use host-specificity assessment as the only criterion for agent selection. However, as the cost of PREA drops to about half that of host-specificity testing, it becomes increasingly likely that either strategy 2 or 3 will be the most cost-effective. Increasing field release costs also tend to make strategies 2 or 3 slightly more cost-effective, as they eliminate some of the costs associated with field release of ineffective agents. The outcome of a comparison between strategies 2 and 3 is shown in Fig. 3. This indicates that, in general, when PREA costs are low, strategy 3 is likely to be the most cost-effective, while when they are high, strategy 2 is preferred. Thus, whichever of the two types of testing has the lower costs should be used as the first filter in agent selection. The choice between strategies 2 and 3 is relatively independent of field release costs, as both these strategies result in the release of the same total number of agents.

Regardless of costs, strategies 2 and 3 always led to a substantial reduction in the number of ineffective agents released in comparison with strategy 1. Under strategy 1, a mean of 2.70 ineffective agents were released per project, while strategies 2 and 3 reduced this to 1.46, a reduction of 46%. The numbers are identical for strategies 2 and 3 because these strategies always make the same recommendations for agents to be released; only the order of testing, and hence the costs, differ between the two strategies. This reduction does not come at the cost of rejecting large numbers of effective agents; the mean number of "good" (i.e., effective and host-specific) agents rejected per project under strategies 2 and 3 was 0.097, or less than one per 10 projects. Mean overall rejection rates of candidate agents were 40% under strategy 1 and 55% under strategies 2 and 3. Thus, with the parameters assumed, only 15% of candidate agents were rejected because of an unfavorable PREA.

5. Discussion

The model shown here is, of course, a simplification, and the strategies are caricatures of real approaches. Few biocontrol workers would adopt a pure strategy 1, releasing agents solely on the basis of host-specificity, with no regard for efficacy. Any real proposal to

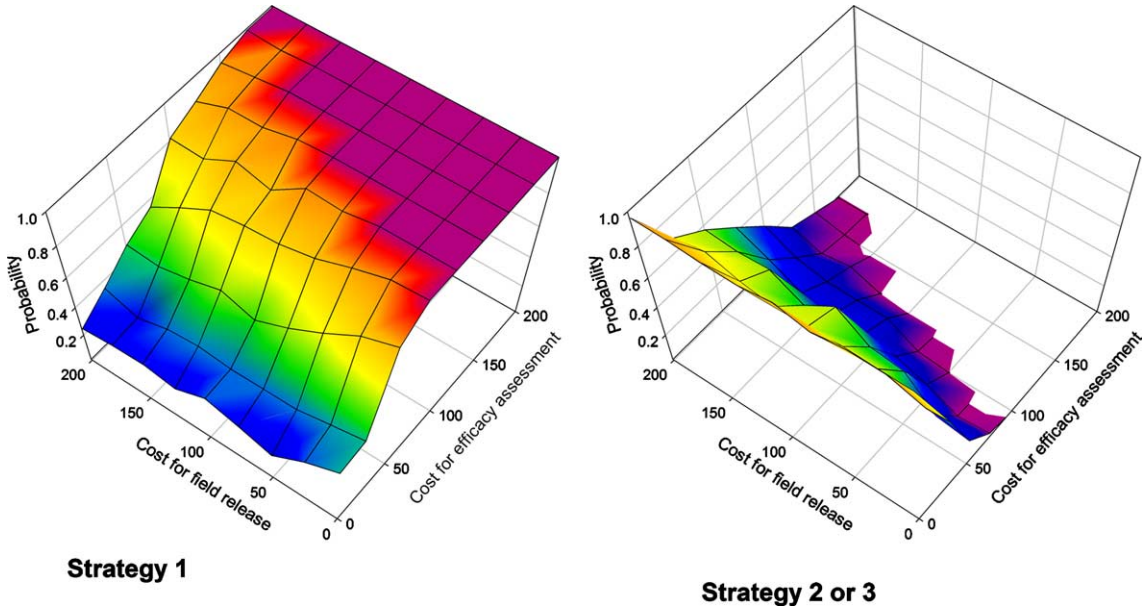

Fig. 2. Comparison of strategy 1 (host-specificity testing only) versus strategy 2 or 3 (host-specificity testing plus pre-release efficacy assessment) as influenced by relative costs of pre-release efficacy assessment, host-specificity testing, and field release. Vertical axis is the probability (estimated from 100 simulation runs) that the strategy shown will be the more cost-effective of the strategies being compared. Horizontal axes are the costs (in $1000) of pre-release efficacy assessment and field release, relative to the cost of host-specificity testing, fixed at $100,000. When efficacy assessment costs are low, particularly if field release costs are also high, either strategy 2 or 3 is likely to be more cost-effective than strategy 1.

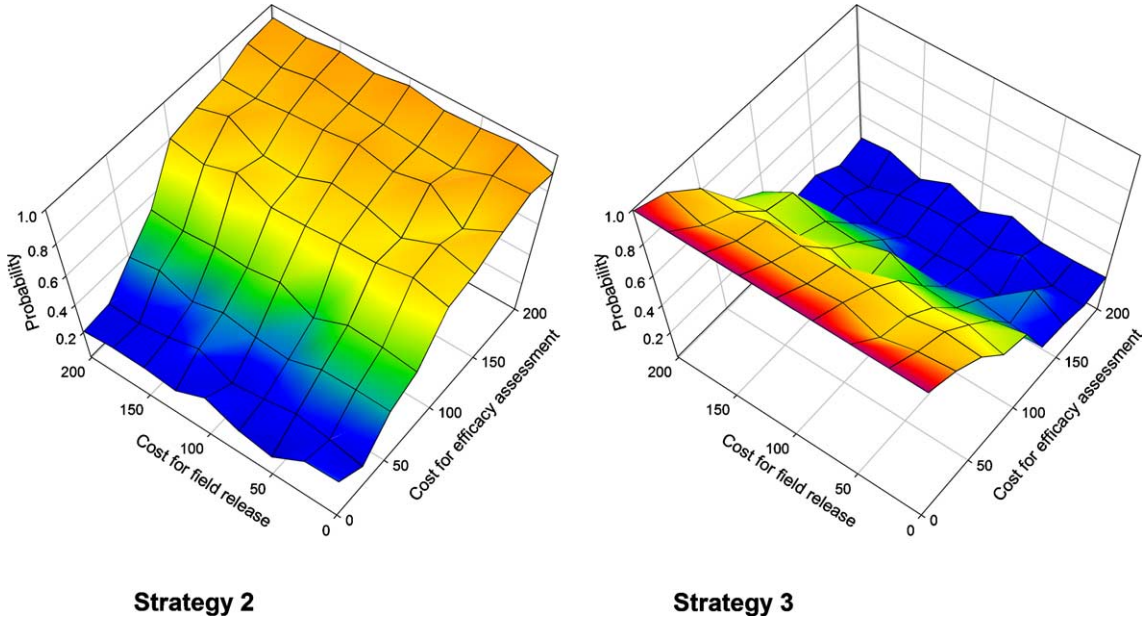

Fig. 3. Comparison of strategy 2 (host-specificity testing first) versus strategy 3 (pre-release efficacy assessment first). Axes as in Fig. 2. When efficacy assessment costs are low in relation to host-specificity, strategy 2 is more likely to be cost-effective, while if they are high strategy 3 is more likely to be cost-effective.

release a new biological control agent always makes a case for its expected impacts, even if this is based only on generalities rather than specific data. Strategy 1 in this model represents, in simplified form, the approach of those practitioners who believe that it is not useful to invest significant time and effort in PREA, and that the only real test of an agent is whether it works after release. Strategies 2 and 3 represent those who are willing to invest time and resources in PREA, and are prepared in principle to drop an agent before release if there is not enough evidence that it is likely to be effective.

For these reasons, the results presented here are only illustrative. The exact outcome of the simulations depends on the percentages of host-specific and effective agents in the candidate pool, and the false positive and false negative rates of the PREA. However, these results suggest that, if PREA can be done at a lower cost than host-specificity testing:

1. It can make the selection of agents more cost-effective than the alternative of releasing every host-specific agent regardless of its likely efficacy. This advantage increases as costs related to field release increase.
2. It will be more cost-effective to use it as the first filter in agent selection, and only conduct host-specificity tests with candidate agents that show promising results from the PREA.
3. Regardless of costs, using PREA as a filter for agent selection can lead to significant reductions in the number of ineffective agents released.

These conclusions do not depend on assuming a high level of reliability of the PREA procedure in identifying effective agents. In the example shown, 50% of candidate agents that received a favorable PREA were in fact ineffective.

In practice, the costs for conducting PREA will vary considerably, depending on the target weed and the agent being tested. For easy-to-culture, multivoltine agents on target weeds that are easy to grow, costs of PREA may be lower than host-specificity trials, since only a single host—the target weed—needs to be evaluated. If the agent quickly kills the target, or entirely prevents seed production (e.g., Sobhian et al., 2004), the PREA may not take much time. However, it may take many generations of attack before quantifiable impacts are observed on the target weed. For univoltine agents, this may make PREA cost prohibitive. Likewise, host-specificity tests are frequently performed on portions (e.g., cuttings, bouquets, and individual leaves) of the test plant, while assessment of impact will almost always need to be done with entire plants. Impact of seed predators may be difficult, since some weeds, under laboratory conditions, will not produce viable seeds, or even flower. Many of these shortcomings can be overcome by conducting PREA under field conditions in the area of origin (see Balciunas, 2004, for a brief review of various overseas impact assessments).

Per-capita impact assessments measured at the plant level are less likely to be useful for seed-feeding candidate biocontrol agents than for agents affecting the survival or vegetative growth of their target weeds. For seed-feeders, population-level impact is a function of their abundance—directly related to amount of seed destroyed—and of the importance of seed in the population dynamics of the weed in the area of introduction. As post-release abundance is genuinely hard to predict, so too is population-level impact of seed feeders.

Tolstoy began his classic novel *Anna Karenina* with the famous sentence "Happy families are all alike; every unhappy family is unhappy in its own way." Diamond (1997) coined the "Anna Karenina principle" as a metaphor for the requirements for success in complex undertakings, explaining that "We tend to seek easy, single-factor explanations of success. For most important things, though, success actually requires avoiding many separate causes of failure." Achieving successful biological control is certainly a task where failure may be due to an array of causes, and, thus, one that cannot be reduced to easy, single-factor rules. Some of the many possible causes, such as mortality of biological control agents due to natural enemies, are very difficult to foresee and, thus, to avoid. However, other causes, such as lack of climatic adaptation, or biotype incompatibility, are foreseeable. We suggest that the use of agents that are insufficiently damaging to their targets, even at high densities, is one foreseeable cause of failure that can be at least partially avoided by pre-release efficacy assessment.

Among practitioners of classical biological control of weeds, the need for selecting effective agents is receiving new emphasis, and pre-release assessment of a candidate's potential impact is often urged (Cullen, 1995; Harris, 1991; Hopper, 2001; McEvoy and Coombs, 2000; Sheppard, 2003; Strong and Pemberton, 2001). Likewise, the "International Code of Best Practices for Classical Biological Control of Weeds" urges practitioners to select effective agents (Balciunas, 2000; Balciunas and Coombs, 2004). We hope that the simulation models and discussions we present here, by demonstrating that pre-release tests of efficacy can be cost-effective, will help contribute to wider use of such assessments.

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