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WHY THINGS BITE BACK: UNINTENDED CONSEQUENCES OF BIOLOGICAL WEED CONTROL

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INTRODUCTION

There is an upside and a downside to the current "boom market" in biological control (biocontrol), the use of living organisms to control pests. The upside is that biocontrol provides a potentially effective control technique, an alternative to chemical pesticides, and an ecological foundation for pest control strategies. As a method of weed control, biological control can claim a growing number of successes. As of the end of 1996, there have been at least 1150 planned releases of 365 species of invertebrates and fungi on 133 weed species in 75 countries (Julien and Griffiths 1998). Julien (1989) estimates that 25% of all releases made up until 1985 contributed to control; some recent estimates of success rates are higher (McFadyen 1998). As an alternative to chemical pesticides, biocontrol potentially reduces pesticide use and its undesirable effects on human health and the environment (OTA - U.S. Congress Office of Technology Assessment 1995). In contrast to chemicals, biological control organisms pose negligible human health risk, circumvent the problem of pest resistance (Holt and Hochberg 1997), and reduce the need for repeated and costly interventions to control invasive species, plants and animals that are not native to ecosystems they invade (OTA - U.S. Congress Office of Technology Assessment 1995). As an exercise in applied ecology, the scientific study of biological control systems has helped transform perspectives in pest control from an industrial to an ecological model (Levins 1986), fostering a sustainable pest control technology (Karban et al. 1997) that potentially (1) is effective, (2) requires low inputs of resources, (3) is self-perpetuating, (4) produces minimal pollution, (5) produces minimal effects on non-target organisms, and (6) is compatible with other management practices.

Increasing concern that biocontrol is often ineffective or possibly unsafe marks the downside to biocontrol. Safety concerns center on classical biocontrol in which alien organisms are introduced to control alien pests (Howarth 1983, Ehler 1991, Howarth 1991, Simberloff 1992, Lockwood 1993, McEvoy 1996, Secord and Kareiva 1996, Simberloff and Stiling 1996a, Simberloff and Stiling 1996b, Louda et al. 1997, Louda 1998, Thomas and Willis 1998). Introducing control organisms in classical biocontrol programs is generally irreversible. Unlike pesticides, control organisms cannot be withdrawn and discontinued because they have proven to be ineffective or because society has become less tolerant of their harmful side effects on nontarget organisms. There is growing public and scientific awareness that importing potentially harmful alien organisms into new environments can lead to irretrievable loss of native biodiversity and disruption of ecosystem processes (Levin 1989, Levin 1990, OTA - U.S. Congress Office of Technology Assessment 1993). Given concerns about alien species, biocontrol introductions seem like solutions from one point of view, potential problems from another. Biocontrol scientists find themselves caught up in a debate about adverse environmental effects, protocols for avoiding them, and regulations to restrict the flow of potentially harmful alien organisms across the borders of biogeographic regions.

Classical weed biocontrol is subject to some of the strictest evaluations currently made in the United States for planned release of alien organisms (Ruesink et al. 1995), and it has been held to a higher safety standard than biocontrol of insects and other arthropods. Many alien species other than biocontrol organisms (including potential plant invaders) are allowed to enter the United States as "innocent until proven guilty," but weed biocontrol organisms must meet a stricter standard of "guilty until proven innocent" (Ruesink et al. 1995). To ensure beyond a reasonable doubt that biocontrols are necessary, effective, and safe, there are protocols for (1) selecting target organisms (McClay 1989, Peschken and McClay 1995), (2) selecting effective control organisms (Harris 1973, Goeden 1983, Wapshere 1985), (3) testing control organisms for safety (Zwölfer and Harris 1971, Wapshere 1974, Klingman and Coulson 1983, Coulson and Soper 1989, Cullen 1990, Weidemann and Tebeest 1990, Coulson 1992, Harris and McEvoy 1995, McEvoy 1996, Marohasy 1998, USDA 1999), and (4) encouraging high standards of professional conduct (FAO 1994). Most scientists believe that environmental risks of weed biocontrol using host-specific control organisms are largely hypothetical and that current safeguards are adequate. However, even ardent supporters of biocontrol call for more research on environmental effects and for introduction of monitoring systems that would allow the early detection of any long-term problems.

It is traditionally assumed that adequate assurances of safety in biocontrol reduce the need for assurances of effectiveness. Yet each new biocontrol organism that fails to establish or achieve control wastes scarce resources and may decrease public support (Harris 1988, Howarth 1991). In the worst case scenario, biocontrol organisms may become pests themselves (Howarth 1991, Simberloff and Stiling 1996a, Louda et al. 1997), although a recent worldwide survey found only eight instances of weed-biocontrol organisms directly damaging non-target plants (McFadyen 1998). Fortunately, host specificity still provides the best assurance that biological control will suppress the target organism without harmful side effects. Experience with past introductions has shown that problem species tend to have broad host ranges. To determine whether a planned introduction of a biocontrol organism is safe, new control organisms now require extensive lab and field trials to demonstrate host specificity before approval. Yet host specificity has its limitations as a safety criterion. The most important uncertainties that remain have to do with forecasting control organism movement, evolution, and indirect effects, plus refining estimates of the severity, probability, and consequences of non-target effects (McEvoy 1996, Secord and Kareiva 1996).

In this chapter, we put safety issues into a general context of technology and its unforeseen consequences, and we suggest ways to resolve thorny scientific and policy dilemmas. The chapter has four parts.

- First, we address the belief that biological control resembles a lottery, in which more and more control organisms must be added to speed the discovery of the few that are effective.
- Second, we briefly review the scientific and sociological factors that make the lottery so seductive, leading scientists to speed up the screening of control organisms for safety while neglecting to screen species efficiently for effectiveness.
- Third, we ask whether over-prescription of biological control introductions under the lottery model leads to “revenge effects” (Tenner 1996). That is, in our rush to solve local and acute pest problems, are we creating diffuse and chronic problems that are even harder to solve?
- Fourth, we suggest ways to avoid revenge effects by applying the Precautionary Principle (O'Riordan and Cameron 1994) and following simple guidelines for decision making under uncertainty (Ludwig et al. 1993).

1. BIOCONTROL CURRENTLY RESEMBLES A LOTTERY

Discovery of biological control organisms is largely a matter of trial-and-error influenced by an individual scientist's storehouse of knowledge and experience. Designing biological control systems has been compared to a lottery (Myers 1985): the outcomes of control organism introductions are so dominated by chance that the best course is to import many control organisms (after they have passed the host specificity test), leaving the organisms to sort it out for themselves which one or combination will prove most effective. The Lottery Model continues to guide weed biocontrol decisions today, endorsed by influential investigators (Müller and Schroeder 1989). In a recent article (McEvoy and Coombs 1999), we identified two symptoms of biocontrol under the Lottery Model as "runaway importation-rates" and the "monitoring and evaluation gap."

"Runaway importation-rates" are indicated by the curves describing the cumulative number of imported control organisms pulling away from the curves describing the cumulative number of target organisms (Fig. 1A). World-wide trends show control organism species increasing faster than target organism species (Julien and Griffiths 1998) and biocontrol efforts in Oregon exemplify that trend. In the 3 decades before 1977, an average of 4 new control organisms was introduced per decade in Oregon. Since 1977, the average has been 24 per decade. The increase in biological control activity is an expected response to the relentless increase in plant invaders and the economic and environmental harm they cause. Controlling plant invaders can help protect ecosystems against the irretrievable loss of native biodiversity, a global phenomenon caused principally by habitat destruction and invasion by alien species (Wilcove et al. 1998). Yet it is perhaps surprising to find that the number of control-organism species is increasing faster than the number of target-organism species, skewed by the more profligate control programs for knapweeds *Centaurea* and leafy spurge *Euphorbia* (McEvoy and Coombs 1999). The number of control-organisms per target-organism is increasing, and some biological control systems are growing more, not less, complex in their structure. Either weed problems are becoming harder to solve, scientific effort is not responding to meet increasing demand for research on biocontrol safety and effectiveness, or our learning curve may be getting worse. If practice makes perfect, then we may be practicing the wrong things, speeding up the screening of new introductions for safety while neglecting to efficiently screen species for effectiveness.

The "monitoring and evaluation gap" describes the skewed priorities characteristic of some biocontrol programs: the activities of finding, screening, releasing, and redistributing control organisms command far more attention than the more mundane but essential activities of monitoring and evaluating effects on target and nontarget organisms (Fig. 1B). Perhaps the greatest advances in improving our understanding, prediction, and management of biocontrol could be made through more timely and informative post-release evaluation of its effects (Thomas and Willis 1998, McEvoy and Coombs 1999). Biological control programs develop by stages from finding, screening, releasing, increasing, redistributing control organisms; to damaging and suppressing target organisms; to fostering replacement of target weeds with desirable plants. It is useful to monitor progress and improve performance at each step. For example, systematic attempts to improve success in biocontrol have helped raise establishment rates in Oregon, where 81% of imported control organisms have become established (Fig. 1B). Rising establishment rates probably reflect continuity of program support, learning from experience, plus developing and exchanging new technology for releasing, establishing, and redistributing control organisms. Global average establishment rates continue to be lower, remaining around 55%, and an analysis by decade shows that there has been no overall increase in establishment rates (Sheppard 1992).

Global establishment rates in biocontrol of weeds and arthropods may be low, but if done with the right control organism, right host, and right method, establishment rates can be much higher. Following earlier recommendations (Beirne 1985), mathematical models and field experiments addressing the colonization process are being used to devise optimal release and redistribution strategies (Grevstad 1996, Memmott et al. 1996, Grevstad 1999). How to balance the inherent tradeoff between the size of each release and the number of releases (given a finite initial release stock) depends on the susceptibility of the particular

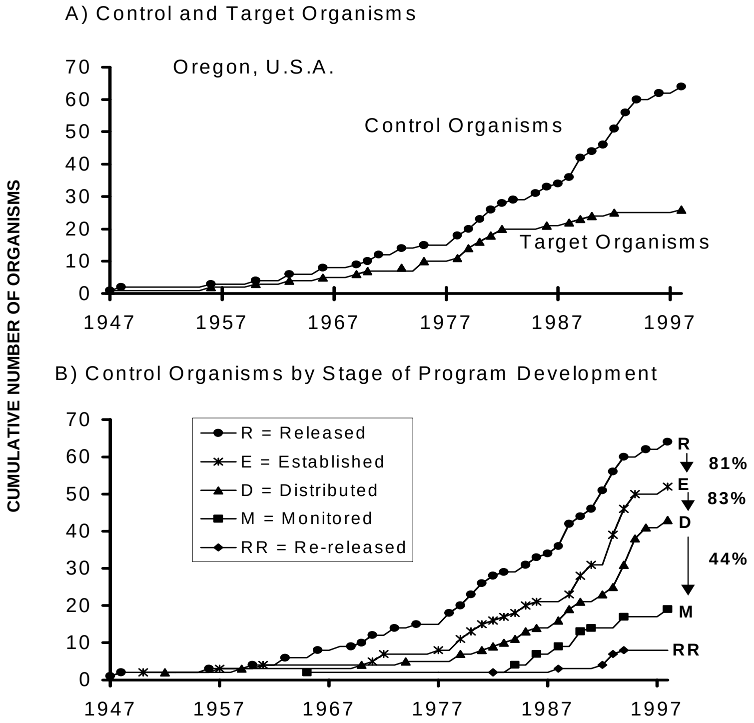

Fig. 1. Cumulative number of imported control organisms for invasive plants in Oregon, USA, 1947-1998. (A) Cumulative numbers of target and control organism species. (B) Cumulative numbers of control organisms progressing through the stages of release, establishment, redistribution, and evaluation. Number re-released refers to the number of control organism species established after repeated attempts rather than a single attempt. The percentages to the right of the figure refer to probabilities of transition from stage to stage for each step in the sequence from release through monitoring and evaluation. Note that 81% of released organisms become established, 83% of established organisms are redistributed, and only 44% of redistributed organisms are monitored and evaluated. From (McEvoy and Coombs 1999) with permission.

species to factors that put small populations at risk of extinction. These factors include demographic stochasticity, environmental variability, and Allee effects (reduced population growth at low density). In most cases, we are unlikely to have estimates of the required parameters for determining the optimum release size (fecundity, survivorship, variance in year to year survivorship, Allee effect intensity). There are logistical as well as ecological constraints operating on the number, size, timing, and spacing of releases. Nevertheless, Grevstad (1999) suggests that we can use simple rules of thumb that can tell us whether releases should be "on the large side" or "on the small side" -- a significant improvement over the current use of arbitrary release sizes

While establishment rates are climbing in some areas of the world, rates of control by established organisms are hard to gauge. Field measurements of establishment rates tend to be more reliable than those of weed suppression, which tend to be subjective and impressionistic; and attributes that promote establishment have been easier to identify than attributes that promote successful control (Crawley 1989c). It invites trouble to continue to import alien control organisms under the Lottery Model without equal efforts to thoroughly monitor and evaluate their effects on target and nontarget organisms and update assessments accordingly.

2. WHY DOES THE LOTTERY MODEL REMAIN SO SEDUCTIVE?

The rush to introduce control organisms has as much to do with human behavior and psychology as with ecology and economics. Some scientists and organizations have strong vested interests in making introductions. Their emphasis is on advertising the release and redistribution of new organisms rather than dispassionately evaluating impacts on target and nontarget organisms and exposing all their acquired knowledge to criticism by others in scientific publications. This tendency has generated a debate about whether scientists can be objective about the effects of control organisms and promote them (through personal assurances of safety and effectiveness) at the same time. There is an important distinction between science and technology: between knowledge of the world and how it is used (Wolpert 1999). It is not for scientists to make moral or ethical decisions about the use of biocontrol, as they have no special rights or skills in this regard. The strength of a scientist is not in being an advocate, but in making scientific judgements based on evidence. Scientists should not be given the right or authority to make importation decisions on their own; once they get caught up in making value judgements, they become reluctant to accept the findings of their own research when findings contradict their beliefs. Given the public concern and potential for conflicts of interest, there seems to be no alternative but to rely on regulatory bodies plus rigorous public and peer review to assess whether controls are necessary, effective, and safe.

While importing new control organisms creates excitement and growth, revelations about effectiveness are often highly subjective. Crawley (1989c) reviewed 627 biological weed-control program and found few provided an objective measure of the depression in weed abundance because pre-release plant abundance was rarely measured and little follow-up work was carried out. Subjective evaluation reveals little of how a population is affected by abiotic factors, by age or other aspects of its structure, by population density feedbacks, or by biotic interaction with other populations. When experts were asked in an opinion survey in the Silwood International Project on Biological Control of Weeds (Moran 1985) what factors limit the effectiveness of control organisms in their weed biocontrol programs, they implicated a variety of possible causes. The percentage of all cases implicating each factor (some cases implicating more than one factor) was Climate 44%, Predators 22%, Parasitoids 11%, Disease 8%, Host incompatibility 33%, and Competition 12 % (Crawley 1986). The percentage of all cases is low, but the percentage of known cases is higher. This is because the all-too-common response to questions in this survey was "unknown" -- the % of cases for which the influence of each factor was unknown was Climate 46%, Predators 56%, Parasitoids 49%, Host incompatibility 16%, and Competition 13%. The picture of what factors limit the effectiveness of control organisms when only the known cases are considered changes to Climate 81%, Predators 50%, Host incompatibility 39%, Parasitoids 22%, Competition 14% (data on Disease was of such poor quality that it is excluded from the analysis). We conclude that biocontrol scientists often have very limited knowledge of the factors that limit effectiveness of control organisms, and much of that knowledge is subjective. Subjective evaluation of control organisms in the absence of standard, quantitative measures becomes essentially a comparative exercise limited to the scope of one person's experience. Relying on expert opinion requires scrutiny of the scientific authority of the expert. Over-reliance on expert opinion and subjective evaluation currently hinders progress in understanding, predicting, and managing weed biocontrol systems. Quantitative evaluation is needed to (1) determine whether present control organisms are adequate or whether additional control organisms are needed, (2) create a more reliable basis for comparison, interpolation, and extrapolation, (3) develop and refine principles, concepts, and predictions regarding control organism specificity and effectiveness (McEvoy and Coombs 1999).

Possible reasons for a lack of effective monitoring and evaluation include time-delays in the emergence of impacts, too little time, funding, will, and scientific know-how.

- ***Time-delays*** -- If we accept that it takes about 10-20 years for impact of biocontrol organisms to emerge (McFadyen 1998), and we observe that most control organisms in the western USA have been introduced in the last two decades (McEvoy and Coombs 1999), then some might conclude that most weed control organisms have not had enough time to reveal their impacts and evaluation can be put off until later. McFadyen (1998) pointed out that some evaluations have been undertaken too early, before control organisms have had a chance to achieve their full potential. Our view is that local evaluation can start early on after release and proceed step by step through the phases of establishment, increase, spread of control organisms, suppression of the target, and plant succession. Local evaluation can help create a more reliable basis for extrapolating these effects and processes to more global scales of space and time.
- ***Time and Funding*** -- Dollars that fuel the effort to find, screen, and release new control organisms dry up in the later stages of evaluation. Also, it is easier to fund studies of successes rather than failures, leading to bias in the overall assessment of outcomes. In our view, if funding continues to be a problem, importers and users of biocontrol organisms should cooperate to post the money up front to cover monitoring costs (McEvoy and Coombs 1999).
- ***Will power.*** A lack of will stems from scientists' dim view of monitoring -- monitoring is unattractive to researchers because it takes too long, is too boring, and frequently produces a lot of negative results (e.g. no effect, no change) with little intellectual market-value related to publication, fund-raising, or career advancement (Harris 1997). Conversely, our cooperation in the study of ragwort biocontrol shows that it is possible to investigate applied problems in a fundamental way, to balance the concerns of practical management and basic ecology (McEvoy et al. 1991, Coombs et al. 1996, McEvoy and Coombs 1999).

- ***Scientific know-how.*** In these days of specialization, few scientists combine the zoological and botanical skills to work effectively on plant-herbivore interactions and effectively bridge the divide between botanical and zoological perspectives on herbivore-plant interactions (Harper 1977, Müller 1990, McClay 1995). A zoological perspective emphasizes the resources consumed and their effects on the consumer. A botanical perspective emphasizes the plant parts left over after herbivory and their capacity to maintain a plant population. Biocontrol of weeds is a specialized business run mostly by entomologists, who must enlist the help of plant population biologists to evaluate potential and actual effects (McClay 1995). While reason, argument, and evidence play crucial roles in directing biocontrol science, we suspect these social factors play important roles as well.

The steepness in the control organism curve in the last two decades (Fig. 1A) looks very much like the work of momentum investors: additional control organisms are being introduced before prior introductions have had a chance to work. An economic argument supporting the Lottery Model is that some economies of scale (lower production costs per control-organism species) can be achieved by screening many control-organism species simultaneously rather than sequentially, even though lower rates of introduction generally mean lower aggregate economic and ecological costs. An ecological argument supporting the Lottery Model is that unpredictable outcomes favor imaginative trial-and-error as the best approach. Predicting biocontrol has been the "holy grail" of ecological analysis, but researchers have had difficulty finding attributes of organisms or environments that reliably predict a species' behavior outside its native home. Some obvious factors to consider are the intrinsic rate of increase (r), abundance in the native habitat, taxonomic isolation of the target organism from potential nontarget organisms, climate and habitat matching, and vacant niches (Williamson 1996). However, with some notable exceptions among forecasts of plant invasions (Rejmánek and Richardson 1996, Reichard and Hamilton 1997), statistical generalizations about invasions have so far tended to be weak and unreliable (Williamson 1996). Also, a coherent mathematical framework for analyzing invasions and their ecological effects has only recently emerged (Williamson 1996, Shigesada and Kawasaki 1997). As a result, practitioners of biocontrol who actually make the decisions and place the bets in the biocontrol lottery find themselves whipsawed by conflicting and often unsubstantiated claims made by analysts: argument by example leads to rebuttal by counter-example, and the confused practitioner returns to simple trial-and-error as the best approach (McFadyen 1998).

Over-reliance on trial-and-error involving many control organisms delays the development of rational alternatives. Alternatives include experimental screening of each candidate control organism prior to release or making educated guesses based on expert intuition, data bases, and mathematical and experimental models. Two basic approaches have been used alone or in combination when assessing a weed control organism's potential for suppressing the target organism (Wapshere et al. 1989): extrapolating measurements from the area of origin to the area of introduction using carefully matched field situations (Wapshere 1985) or identifying important and researchable attributes of control organism and target organism biology (Harris 1973, Goeden 1983). Alternative ways to develop biological control programs using a minimum number of control organism species include critical attributes, targeted disruption of pest life cycles, and combinatorial ecology.

- ***Critical Attributes.*** Species with desirable biological properties can be selected based on expert intuition, data bases, and mathematical and experimental models. The more these approaches relate to each other, the better each becomes. Research and development of weed biocontrol organisms has remained rather empirical, or worse, anecdotal. The few attempts to develop model experimental systems to investigate attributes shared by an entire class of biocontrol systems include studies of Scot's broom (Fowler et al. 1996, Memmott et al. 1996, Rees and Paynter 1997), ragwort (McEvoy and Rudd 1993, McEvoy et al. 1993, McEvoy and Coombs 1999), and purple loosestrife (Blossey 1995, Blossey 1996, Grevstad 1996, Grevstad 1999). Data bases like the Julien Catalog (Julien and Griffiths 1998) and Silwood Project (Moran 1985, Crawley 1986, Bergelson and Crawley 1989, Crawley 1989c, Crawley 1989b, Crawley 1989a, Crawley 1990) are being used to catalog and analyze large amounts of data on biological weed control organisms. One of the best predictors of control effectiveness is whether or not a species was known to be effective elsewhere in the world (Crawley 1989c). This finding is enough to justify efforts to create and maintain global data bases of weed biocontrol organisms. Further investment in data bases may increase understanding of underlying causes and the practical development of new, unprecedented biocontrol systems in the future.
- ***Targeted disruption of pest life cycles.*** A second alternative is targeted disruption of weed life cycles, which means using field studies and mathematical models to identify which life-cycle transitions and pathways contribute most to population growth, which are most easily disrupted, and using this information to improve targeting of pest vulnerabilities (Müller 1990, Lonsdale et al. 1995, Rees and Paynter 1997, Shea and Kelly 1998, McEvoy and Coombs 1999). Analyzing the sensitivity of model outputs to changes in parameter values (Caswell 1997, Tuljapurkar and Caswell 1997), scientists ask "what if questions" such as this: if a control organism or other mechanism were to block this life cycle transition, what would be the effect on the growth rate of the pest population? This approach, is founded on the classical notions in biology of stimulus, to describe a change in the environment, and response, to describe the resulting change in the organism. It avoids the confusion about stimulus and response that creeps into writing about biological weed control (Harris 1981) and ecology (Harper 1982) with the use of anthropomorphic and emotive concepts like "stress." Targeted disruption of life cycles also refines the concept of a target site, from plant parts to plant life-cycle-transitions. Attacking a plant part is very different from attacking life cycle transitions, just as killing an individual plant is very different from suppressing and regulating a weed population. Only structured population models make an explicit link between individual behavior or demography and population dynamics, and such models can be combined with factorial experiments to achieve more reliable inferences about cause and effect, as in studies of ragwort biocontrol (McEvoy and Coombs 1999).

- ***Combinatorial ecology.*** A third alternative exploits the combinatorial ecology of biocontrol through coordinated manipulation of disturbance, plant competition, and natural enemy regimes (McEvoy and Coombs 1999). Outbreaks of weeds result from an imbalance in activators and inhibitors of population growth. Top-down control using low numbers and low diversity of control organisms can be effective in suppressing target-organism populations provided care is taken (1) to avoid introducing propagules and disturbances that trigger weed recruitment, and (2) to conserve bottom-up control mechanisms that reduce the supply of resources fueling weed population growth either by lowering resource-renewal rates (by avoiding disturbances) or by increasing demand for resources (by enhancing competition with other plant species) (McEvoy et al. 1993, Rees and Paynter 1997, McEvoy and Coombs 1999). This approach promises to address the need for a community ecology perspective (identified in the discussion of critical attributes above) in researching and developing biocontrol organisms for weeds.

In summary, biocontrol of weeds continues to resemble a lottery, emphasizing rapid screening of candidate control organisms for safety while neglecting to screen them efficiently for effectiveness. Even those skeptical about predicting effectiveness of biocontrol organisms concede that advances in understanding, prediction, and management of biocontrol could be made through more timely and informative post-release evaluation of impacts on target and nontarget organisms. It is useful to recognize stages in the development of biocontrol (release, establishment, increase and spread of control organisms, suppression of the target organism, and plant succession replacing the weed with other plants), and then analyze progress step by step. Factors working against effective monitoring and evaluation of the impacts on target organisms and nontarget organisms in biological weed control programs include time delays in the control process plus too little time, funding, will, and scientific know-how. These factors explain but do not excuse the low level of quantitative monitoring and evaluation in biological weed control.

While some practitioners have been playing the lottery in weed biocontrol, alternative frameworks for predicting effects of introductions have been neglected. Between the extremes of introducing all control organism species at once, or introducing them one at a time, lies a worthy alternative: introducing a carefully chosen subset of candidates based on pre-release studies of their potential effectiveness. Such studies could be based on appropriate application of all the tools of the trade, including experimental studies of each species and educated guesses informed by expert intuition, databases, and mathematical and experimental models.

3. REVENGE EFFECTS AND THE LOTTERY MODEL

Over-prescription of biological control introductions encouraged under the Lottery Model can lead to “revenge effects” (Tenner 1996). In our rush to solve local and acute pest problems we may be creating diffuse and chronic problems that are even harder to solve. By adding more and more control organisms to make pest control more reliable, we may end up making it less effective and more risky

(McEvoy and Coombs 1999). Revenge effects could arise in four possible ways: (3.1) Scarce resources are diverted from more profitable alternatives for managing pests, (3.2) One control organism undermines another, more effective control organism, leading to increase in pest density, (3.3) One pest is replaced by another pest that can be even harder to control, (3.4) Control organisms introduced to promote environmental and economic health end up undermining it by harming non-target organisms. Each of these revenge effects is reviewed below.

3.1 Scarce resources are diverted from more profitable alternatives for managing pests.

The Precautionary Principle (O'Riordan and Cameron 1994) requires examination of the full range of alternatives, including no action. Revenge effects of the first kind arise if (3.1.1) by focussing on introducing new control organisms we neglect to conserve and augment established ones, (3.1.2) by relying on foreign control organisms we overlook the use of natives, (3.1.3) by emphasizing biological control we disregard integrated control combining biological, mechanical, cultural, chemical control in appropriate ways, or (3.1.4) by concentrating on mitigating harm caused by established invaders we neglect to predict and prevent new invaders.

3.1.1 *Conserving and augmenting established control organisms.*

One way to reduce demand for new control organisms is to augment and conserve existing ones. However, biological control has become so complex and technologically fragmented that introducing, augmenting, and conserving control organisms are regarded not merely as separate approaches, but separate subcultures. Biological control workers frequently spend their professional careers in just one of the subcultures. For example, biological weed control emphasizes introducing new control organisms and the approaches of augmenting or conserving control organisms already resident in an area are rarely used (Wapshere et al. 1989, McFadyen 1998). Conservation techniques, which involve the identification and manipulation of factors that influence the abundance and effectiveness of control agents, have only recently received serious attention as a way to enhance weed control (Newman et al. 1998).

3.1.2 *Using native control organisms.*

A related way to be more frugal with introductions is to make better use of native species. Native insects commonly cause considerable damage to weed species, but their use in biological control is often overlooked. Those who favor classical biocontrol are inclined to believe that natives are already doing the best they can, and it is not good enough. However, there is increasing experimental as well as observational evidence that native insect herbivores can control plant abundance and distribution in some cases (Nowierski et al. 1999), and use of native organisms for biological control is growing more common (Julien and Griffiths 1998). There are examples where native insects are artificially increased or otherwise manipulated for the control of exotic weeds (Sheldon 1997, McFadyen

1998). The native weevil *Euhrychiopsis lecontei* (Dietz) appears to be a promising agent for control of exotic Eurasian watermilfoil (*Myriophyllum spicatum* L.), but factors that limit success need to be identified and manipulated for control to become predictably effective (Newman et al. 1998). We can expect to see more examples of weed control using native control organisms in the future.

3.1.3 *Integrated control strategies.*

A third way to enhance biocontrol using fewer natural enemies is to use biocontrol in combination with chemical, cultural, mechanical control as part of an Integrated Weed Management program (Wapshere et al. 1989). Few studies have attempted and reported the research needed to determine how these tactics work together in practice (Briese 1996), perhaps because users of biocontrol continue to hope for "complete control" by control organisms unaided by other tactics. Complete control is biological control's notion of a silver bullet, defined by Webster's as "a magical weapon…that instantly solves a long-standing problem."

3.1.4 *Predicting and preventing invasions.*

A fourth way to reduce demand for new control organisms is to prevent plant invasions from occurring in the first place. There are a variety of ways to manage biological invasions, ranging from prediction, prevention, early detection, and treatment. Inadequate or misdirected research or regulatory oversight may leave potentially serious risks unaddressed (Pemberton 1995). With scientific attention focused on using introduced control organisms to mitigate harm by current plant invaders, we may invite trouble by neglecting adequate screening and quarantine procedures to predict and prevent the arrival of future plant invaders. Plant introductions, such as woody plants (Hughes 1994) and pastoral plant species (Lonsdale 1994), are largely unregulated and seldom screened for weed potential, yet they entail well-known risks that have not yet been effectively addressed in North America (OTA - U.S. Congress Office of Technology Assessment 1993). Awakened to the risks of a previous open-door policy toward alien species, scientists and policy makers have spawned a growing number of theoretical and practical frameworks for diagnosing invasions and prescribing remedial measures (Williamson 1996, Shigesada and Kawasaki 1997).

3.2 One control organism undermines another, more effective control organism, leading to increase in pest density.

Adding more and more control organism species increases the chance that some interactions will be antagonistic, as in cases where (3.2.1) one control organism preys on another, (3.2.2) one interferes with another's access to the shared resource, or (3.2.3) one reduces the resources available to another. An assessment of the implications for weed control posed by antagonistic interactions must determine whether direct, negative effects on the plant by the antagonist outweigh the indirect, positive effect on the plant created by the antagonist acting via intermediate species (Fig. 2).

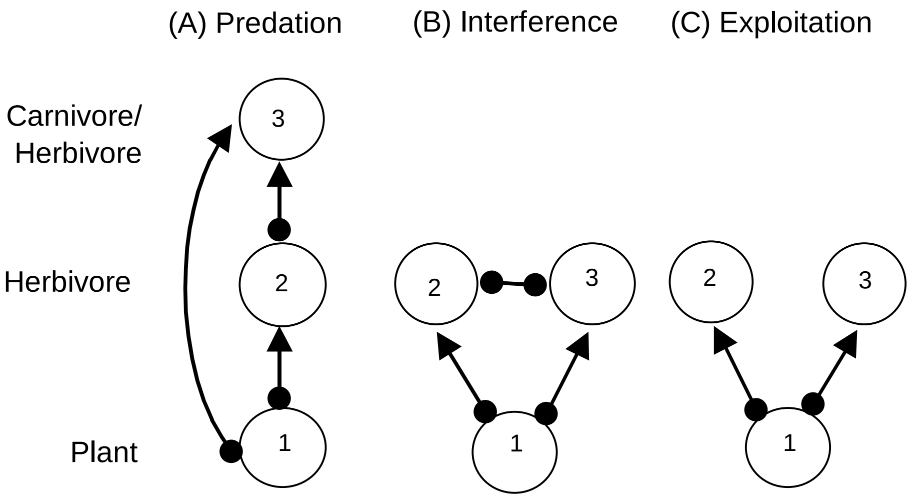

Fig. 2. Interactions among populations in a weed biocontrol system including (A) predation, (B) interference competition, and (C) exploitation competition. Populations are represented as circles, a positive effect of one population on another is represented by an arrow while a negative effect is represented by a filled circle. No arrow means no direct interaction between two variables.

3.2.1 *One control organism preys on another.*

Most scientists agree that weed-biocontrol organisms work best if free of predators, parasites, or pathogens (Goeden and Louda 1976). Ridding the control organism of natural enemies is a good way to cut down on the number of control organism introductions required for biological control. In the case of spotted knapweed *Centaurea maculosa* Lamarck, Harris (1990) estimates that one seed-destroying insect species freed from natural enemies abroad in Canada can do the damage of seven back home in Europe.

Despite the advantages of releasing herbivores free from predators, parasites, and pathogens, these carnivorous organisms commonly reduce the impact of herbivores introduced for weed biocontrol. Three categories of interaction commonly occur in classical biocontrol programs in which one control organism species consumes another.

First, some species used to control arthropod pests have adverse effects on a species used to control plant pests. Mites in the family Phytoseiidae, including specialist (i.e. *Phytoseiulus persimilis* A.H.) and generalist (i.e. *Typhlodromus pyri* Scheuten) predators used for biocontrol of pest spider mites, suppress Oregon populations of a beneficial spider mite *Tetranychus lintearius* Dufour imported for control of gorse (*Ulex europaeus* L.) (Paul Pratt, personal communication). *Bacillus thuringiensis* var. *kurstaki* applied for control of forest-pest insects harms the cinnabar moth *Tyria jacobaeae* (Lepidoptera: Arctiidae) used to control ragwort *Senecio jacobaea* (Asteraceae) (James et al. 1993).

Second, some species used to control plant pests function at two trophic levels as carnivores and herbivores. Most scientists believe that facultative carnivores should not be used for biological weed control. Some practitioners are not so sure, holding out hope that the control organism's direct, negative effect will outweigh its indirect, positive effect on the target plant (Fig. 2A). Take the case of spotted knapweed *C. maculosa* and several of its control organisms, a moth *Metzneria paucipunctella* Zeller (Lepidoptera: Gelechiidae) (the superior interference competitor that functions as a predator and a seed-feeder) and two gall-flies *Urophora affinis* (Frauenfeld) and *U. quadrifasciata* (Meigen) (Diptera: Tephritidae) (the superior colonizers believed to be the more desirable biological control organisms). An observational study of the pattern of association among the three species within 10 field sites suggests that these species are distributed randomly and independently among heads (Story et al. 1991). Put the insect species singly or in combination on plants in cages and the seed destruction by moth and fly larvae appears to be greater than with the moth or flies alone, despite the fact that *M. paucipunctella* larvae kill 19-67% of *U. affinis* larvae (Story et al. 1991). The evidence is equivocal because the artificial conditions of closed cages restrict movement, and the design confuses an increase the number of consumer species with an increase in the number of consumer individuals. The introduction of facultative carnivores illustrates how inadequate science and overly-optimistic management have contributed to growth in number, size, and complexity of biological weed control systems.

Third, some species used to control plant pests appear to be especially vulnerable to acquiring predators and parasites. High rates of parasitism rates are reported for gall midges (Diptera: Cecidomyiidae) including rates of 20-50% in Montana for the case of *Spurgia esula* Gagne introduced to control leafy spurge *Euphorbia esula* L. and rates of 20-90% in Idaho, Washington, and California for the case of *Cystiphora schmidti* Ruebsaamen introduced to control of rush skeletonweed *Chondrilla juncea* L. (Asteraceae) (Rees et al. 1996; Coombs, unpublished observations). The same is true for some Lepidoptera, including parsitism rate of 30-60% in Oregon populations of *Leucoptera spartifoliella* Huebner (Lyonetiidae) for control Scot's broom *Cytisus scoparius* (L.) (Fabaceae) and rates of 2-10% in Washington, Montana, and Oregon populations of *Metzneria paucipunctella* (Gelichiidae) for control several species of knapweeds *Centaurea* spp. (Asteraceae) (Rees et al. 1996; Coombs, unpublished observations).

3.2.2 One control organism species interferes with another's access to the shared resource (interference competition)

If biocontrol scientists can't agree about what it means for biocontrol when control organisms eat each other, it is small wonder they pay scant attention to more subtle forms of interference competition. According to the opinion survey cited earlier in this chapter (section 2), competition limits the effectiveness of weed-biocontrol organisms in only 13% of known cases (Crawley 1986). Interspecific competition for food is notoriously difficult to document in the field, even when it occurs; this is one reason why there is a persistent debate in ecology concerning the importance of this force (Denno et al. 1995, Stewart 1996). Several categories of interaction along a continuum are best lumped here: competition that involves a negative-negative interaction, asymmetric competition that implies unequal negative-negative interactions, and amensalism that involves negative-zero interaction.

One control organism species may interfere with another's access to shared resources such as hosts, mates, or microhabitats. Negative effects of one control organism on another's demography may include a decrease in reproduction or an increase in mortality or emigration. For example, weevils *Larinus minutus* Gyllenhal. (Coleoptera: Curculionidae) at high density interfere with access to the flower heads of diffuse knapweed (*Centaurea diffusa*) by the gall fly species *Urophora affinis* and *U. quadrifasciata* (Coombs, unpublished observations). The implications of these interactions for the dynamics of interacting populations in this system are unknown.

3.2.3 One control organism reduces the resources available to another (exploitation competition)

It is generally assumed that there nothing to fear if one control organism reduces host resources available to another; the likely outcome is a reduced host equilibrium. Most definitions of biocontrol assume that it is desirable to reduce pest equilibrium levels while retaining sufficient stability in the pest-enemy interaction to prevent the host from sporadically re-emerging as a pest. Contrary to conventional wisdom, there is mounting evidence that competition among control organisms can reduce control success. First, one control organism can undermine the establishment of another organism species. Briese (1997) reports that the leaf-defoliator *Chrysolina quadrigemina* (Suffrian) (Coleoptera: Chrysomelidae) may have inhibited the establishment of another, more effective control organism, root-borer *Agrilus hyperici* (Liro) (Coleoptera: Buprestidae), by inducing boom-and-bust fluctuations in populations of the target weed *Hypericum perforatum* L. (Clusiaceae) in Australia. If the order in which control agents are established is important for their eventual success, then we should try to predict the interactions that will occur between potential control agents, as well as their likely individual impact on the weed, in the country of introduction, as currently practiced in New Zealand (Syrett et al. 1996). Second, one established control organism may undermine the effectiveness of another, more effective control organism. Woodburn (1996) reports that early, aggregated attack on thistle seed heads by a univoltine, seed-feeding weevil, *Rhinocyllus conicus* Frölich (Coleoptera: Curculionidae) hindered control of nodding thistle *Carduus nutans* L. (Asteraceae) in Australia by decreasing the numerical response of a more promising agent, a bivoltine tephritid seed fly *Urophora solstitialis* (Linnaeus) (Diptera: Tephritidae). Also, plant changes induced by one herbivore species may protect plants against a second, potentially more damaging species. An example can be found in recent studies involving plant-feeding mite species. Grape vines in the San Joaquin Valley of California are protected from the highly virulent Pacific mite *Tetranychus pacificus* McGregor by early inoculation with the more benign Willamette mite *Eotetranychus willametti* (McGregor) (Karban and English-Leob 1990, Karban et al. 1991, Karban et al. 1997). Plant pathologists have found similar cases in which "vaccination" with relatively benign pathogens reduces the negative impact of virulent viral, bacterial, and fungal pathogens (van Loon et al. 1998). In a similar way, releasing ineffective control organism species in weed control programs may induce plant resistance that reduces the impact of more virulent control organism species.

Precautionary measures for avoiding antagonistic interactions among control organisms have been offered but seldom followed. Almost 30 years ago, Zwölfer (1973) devised a prescription under the "balanced competition hypothesis" based on certain assumptions about the nature of competition and coexistence of control organisms operating side by side within the same seed head, and how the inferior competitor might respond if released from competition: If a trade-off exists between colonization and competition abilities (e.g. strong competitors are poor colonizers), then introduce the inferior intrinsic competitor first, knowing that if the result is unsatisfactory, the superior intrinsic competitor can be introduced later. The prescription was seldom followed (in part because it is not always easy to determine which species is likely to play which role in a given environment). Harris (1989, 1990) offers another recommendation based on metabolic source-sink relationships assumed to regulate resource allocation within plants. He suggests that there are seven guilds of phytophagous insects feeding in the seed-heads of knapweeds (*Centaurea* spp.) and other species in the Asteraceae subfamily Cynareae. The guilds in approximate order of attack on the flower-heads are: (1) the formation of woody galls, (2) receptacle feeding, (3) formation of non-woody ovary galls, (4) ovary feeding, (5) formation of achene galls, (6) feeding on well developed but still soft achenes, (7) feeding on mature achenes and preying on insect species in the previous guilds. He suggested that seed destruction is maximized by establishing a biological control systems with a single species from each of the following three guilds: (1) woody gall former, (4) ovary feeder, (6) feeder on well developed by still soft achenes. He assumes that (1) the primary control organism should be woody gall former because the gall that it induces acts as a strong metabolic sink capable of draining resources from the whole plant, (2) it is best to avoid adding competitors or facultative carnivores that might undermine the primary control-organism's effectiveness. Contrary to this parsimonious prescription of 3 species in 3 guilds, the actual biological control system for knapweeds in North America now contains 13 insect species in 6 guilds.

For the case of host-parasitoid interactions, momentum is building once again to obtain a mathematical understanding of what consequences antagonistic interactions among control organisms might have for biocontrol (May and Hassell 1981, Kakehashi et al. 1984, Briggs 1993, Briggs et al. 1993). These investigations are relevant to weed biocontrol because many insects that feed on plants (e.g. seed-slaying insects) have life styles analogous to parasitoids (Price 1980), in which a female lays an egg on a host and the larvae develops by feeding on the body of the host. Briggs (1993) develops two versions of a stage-structured, delay-differential equation model of two parasitoids attacking different developmental stages of a single host species. She found realistic situations in which the best competitor is not necessarily the parasitoid that produces the lowest adult host density and the combination of two parasitoid species may yield higher host density than that achieved by the single most effective parasitoid. This suggests that the lowest host density may be achieved in biological control by the release of only the most effective control organism rather than multiple control-organism species.

In summary, the tide of opinion seems to be turning against the long-standing, laissez-faire policy of introducing multiple control-organism species, leaving them to sort it out for themselves which single one or combination is best for biological control. Most studies to date are based on direct effects on individual plants. To weigh the implications of antagonistic interactions among control organisms for weed control, future studies should attempt to measure and model both direct and indirect effects on the plant responses at individual, population, and metapopulation levels.

3.3 One pest is replaced by another pest that can be even harder to control.

If control of one weed leads to its replacement by another weed not susceptible to the control organism, then we are faced with a continuing cost of control and little benefit. This has happened in a number of cases. Control of water hyacinth *Eichhornia crassipes* (Martius) Soms-Laubach (Pontederiaceae) led to its replacement in many areas by water lettuce *Pistia stratiotes* Linnaeus (Araceae) (O'Brien 1995). Control of purple loosestrife *Lythrum salicaria* L. (Lythraceae) is leading to its replacement in many areas by reed canary grass *Phalaris arundinacea* L. (Poaceae) (Thompson et al. 1987). In Australia, control of a susceptible genotype of rush skeletonweed *Chondrilla juncea* Linnaeus (Asteraceae) led to its replacement by another, more resistant one (Burdon et al. 1981). Managing weed biological control often means managing plant succession (Luken 1990). There have been very few attempts to monitor plant succession following successful biological weed control (McEvoy et al. 1991) since the pioneering study of Klamath weed *Hypericum perforatum* L. that appeared nearly 40 years ago (Huffaker and Kennett 1959). There have been even fewer attempts to manage plant succession as part of a biological control program. Control of ragwort *S. jacobaea* in western Oregon led to replacement of ragwort by perennial grasses (McEvoy et al. 1991) and the reappearance of a rare native plant, the hairy-stemmed checker mallow *Sidalcea hirtipes* Hitchc. (Malvaceae) (Gruber and Whytemare 1997). In other cases, recolonization by the desired suite of species may be slow and unreliable because desired species are no longer in the vicinity and dispersal over long distances can be limited. Natural colonization may have to be supplemented by interventions such as removing plants or their parts, changing resource availability, changing propagule availability and using animals to remove weed biomass (Luken 1990). It is unfortunate that today applied ecologists concerned with managing ecological succession (Luken 1990) and those managing biological weed control (Harley and Forno 1992) take little notice of each other. Investigating the role of biological control in ecological restoration can provide important insights into the way that ecological communities are assembled and ecosystems function, and add another weapon to restoration-ecology’s armory.

3.4 Control organisms introduced to promote environmental and economic health end up undermining it by harming non-target organisms.

Releasing more and more control organisms challenges the capacity of monitoring efforts, increasing the likelihood that target and nontarget effects go undetected. There are several well documented examples where classical weed biocontrol has inadvertently harmed non-target species. Recent studies document actual effects on non-target species for the cases of both officially sanctioned control organisms – such as *C. quadrigemina* beetles on a groundcover in California (Andres 1985), *T. jacobaeae* caterpillars on ornamental and native plants in Oregon (Diehl and McEvoy 1990), *R. concicus* beetle larvae on native thistles in western North America (Turner et al. 1987, Louda et al. 1997) – as well as unsanctioned control organisms arriving accidentally in North America – *Cactoblastis cactorum* Bergroth (Lepidoptera: Pyralidae) caterpillars on native cacti in Florida (Bennett and Habeck 1995, Pemberton 1995, Simberloff and Stiling 1996a). Based on a worldwide review of recorded instances of damage to non-target plants by biological control organisms (McFadyen 1998), about 3 in 95 control organism species in the western continental USA have attacked native nontarget plant species so far. These cases illustrate the dangers inherent in releasing oligophagous control organisms with relatively broad host ranges into environments with many potential non-target species within the known host range. Oligophagous is used to refer to insects feeding on a number of plant species, usually in different genera within one plant family (Bernays and Chapman 1994). Faced with the possibility of harmful non-target effects that already range in severity from transient to persistent attack, what is the probability of escalation to population suppression, local population extinction, species endangerment, species extinction, and community and ecosystem effects in the future? The most important uncertainties that remain have to do with forecasting control organism movement, evolution, and indirect effects, plus refining estimates of the severity, probability, and consequences of non-target effects (McEvoy 1996, Secord and Kareiva 1996).

A rule of thumb in biocontrol favors target organisms that are taxonomically distinct from other plants (McClay 1989, Peschken and McClay 1995). In practice, this rule is often violated as indicated by the large number of other species, hybrids and infraspecific taxa within genera of target species for the western USA (Fig. 3). It would be prudent to anticipate and monitor potential effects in plant genera that contain native plant species in western North America, including *Centaurea**, *Cirsium**, *Cynoglosum**, *Euphorbia**, *Hieracium*, *Hypericum**, *Lepidium*, *Linaria**, *Lythrum**, *Potentilla*, *Salvia**, and *Senecio** for which control organisms are either already established (*) or releases are planned in the near future (Fig. 3). This precautionary measure would improve the ability of researchers to predict severity and likelihood of harmful interactions between control organisms and non-target species. It would increase the confidence of regulatory authorities that host range and environmental safety can be reliably predicted from protocols based on host plant records, phylogenetic analysis, genetic screening, plus host range tests in the lab and field.

Two case studies involve oligophagous control organisms imported and released in environments containing many native plants (potential nontargets) related to the target plant. The cinnabar moth *T. jacobaeae* was introduced to North America in 1959 to control ragwort *S. jacobaea* (Asteraceae). Host specificity testing prior to importing the cinnabar moth into Canada established the "physiological host range" by showing that the larvae of the cinnabar moth can feed and develop in the laboratory on plants species in the tribe Seneceonae (Bucher and Harris 1961), notably species in the genera *Senecio* and *Erechtites*. The genus *Senecio* is a treasure trove of native species containing 162 species, hybrids, and infraspecific taxa in North America (Fig. 3) (USDA 1997). Field observations 30 yr after initial release of the cinnabar moth in North America confirm that "the ecological host range" includes other species in the genus *Senecio* including other exotic weeds (*S. vulgaris* L., *S. sylvaticus* L.), horticultural plants (*S. bicolor* ssp. *cineraria* (DC.) Cater), and at least one native species in genus *Senecio* (*S. triangularis* Hook, S.) (Diehl and McEvoy 1990). Turning to the second example, the weevil *R. conicus* was imported to control musk thistle *Carduus nutans,* Italian thistle *C. pycnocephalus* L., milk thistle *Silybum marianum* (L.) Gaertner in North America (Andres and Rees 1995, Goeden 1995b, Goeden 1995a). The larvae of *R.*

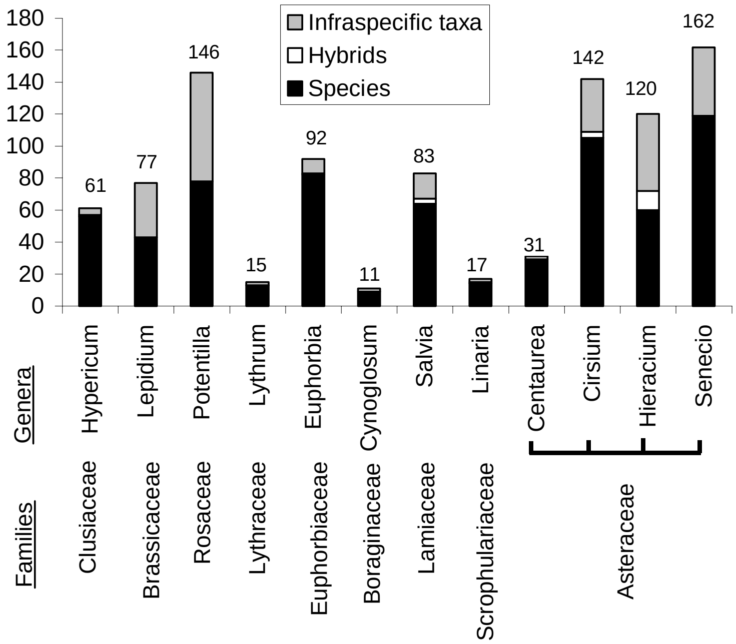

Fig. 3. Taxa with high diversity indicated by the number of plant species, hydrids, and infraspecific taxa in target plant genera and families for biological weed control programs in western USA (CA, OR, WA, ID). It would be prudent to anticipate and monitor potential nontarget effects in these plant genera because they contain many native plant species.

conicus can feed and develop in seed heads of plants in four thistle genera (*Carduus*, *Cirsium*, *Silybum*, and *Onopordum*) found in North America with the tribe Cardueae (family Asteraceae) (Zwölfer and Harris 1984). The genus *Cirsium* contains many native plants among the 142 species, varieties and infraspecific taxa found in North America (Fig. 3). In a recent, influential paper, Louda et al. (Louda et al. 1997) claim that *Silybum* and *Onopordum* are native North American genera, but the sole North American representatives of these genera are of Eurasian origin (USDA 1997).

What are the lessons to be learned from this experience? First, the fundamentals of host specificity as a criterion for judging safety in biological weed control remain sound. Host specificity depends on attributes of the control organism, the recipient environment, and the organism by environment interaction. The cinnabar moth *T. jacobaeae* has a broad host range with the potential to feed and develop on species in the genus *Senecio* that contains many native species in North America. The weevil *R. conicus* has a broad host range with the potential to feed and develop on species in four genera of thistles (*Carduus*, *Silybum*, *Onopordum*, *Cirsium*) that occur in North America, and only *Cirsium* contains species native to North America. The same insect that is a hazard in North America is safely used in New Zealand, where there are no native thistles. Second, although the species is the operational unit of host specificity testing, new control organism genotypes with different potentials require independent screening. After screening one genotype of *R. conicus*, other genotypes of this species with different host ranges were introduced without additional screening (Peter Harris, personal communication). Third, impacts on nontargets should be monitored and assessments updated accordingly. A Precautionary Approach would recommend suspending redistribution and range expansion of *R. conicus* and *T. jacobaea* in North America while impacts of on target and nontarget organisms are being reassessed. This recommendation is being ignored: the cinnabar moth was recently transported from Oregon and released in Montana by the USDA Forest Service with few questions asked, and even fewer answers given, about risk to potential nontarget plants. The USDA Plants Data Base lists 42 taxa in the genus *Senecio* for Oregon and 41 taxa for Montana (USDA 1997). There should be a tacit moratorium barring redistribution of problem control organisms until scientists have assessed the damage and regulators can agree on new rules.

There is also the risk of introducing contaminating or misidentified species along with "approved" agents. Balciunas and Villegas (1999) reconstruct how the false peacock fly *Chaetorellia succinea* (Costa) (Diptera: Tephritidae) was accidentally released along with the true peacock fly *Ch. australis* Hering on yellow starthistle *Centaurea solstitialis* L. (Asteraceae) in southwest Oregon in 1991 and then redistributed to several states. At the time of release, *Ch. succinea* did not have approval for release granted by the regulatory authority U.S. Department of Agriculture's Animal and Plant Health Inspection Service (USDA-APHIS). Brief host-range tests conducted on the false peacock fly in Europe showed that it would not attack safflower, *Carthamus tinctorius*, a close relative of yellow starthistle. However, the false peacock fly can hybridize with *Ch. carthami*, a minor pest of safflower in the Middle East. The false peacock fly is now more abundant, more widely distributed across California, and more damaging to seeds of the target host than the true peacock fly. Now, after the fact, the host range of the false peacock fly and the probability and severity of damage to commercial safflower varieties are being evaluated.

4. AVOIDING REVENGE EFFECTS

We earlier recommended that the best away to avoid revenge effects is to adopt a precautionary approach and to follow simple guidelines for decision making under uncertainty (McEvoy and Coombs 1999). The Precautionary Principle (O'Riordan and Cameron 1994) applied to Classical Biological Control decisions has four parts.

- First, potential harm to non-target organisms can arise from the release of biological control organisms.
- Second, actual harm to non-target organisms of sufficient magnitude and severity has occurred to warrant new principles for conducting biological control introductions.
- Third, the burden of proof for showing that new control organisms are necessary, safe, and effective rests with those proposing the activity.
- Fourth, the process of applying the precautionary principle must be open, informed and democratic and must include potentially affected parties. It must also involve an examination of the full range of alternatives, including no action.

Our foregoing review of revenge effects suggests that the practice of biocontrol currently falls short of general standards set by others (Ludwig et al. 1993) for decision making under uncertainty: "we must consider a variety of plausible hypotheses about the world; consider a variety of possible strategies; favor actions that are robust to uncertainties; hedge; favor actions that are informative; probe and experiment; monitor results; update assessments and modify policy accordingly; and favor actions that are reversible." The next efforts in weed biocontrol should combine prospective approaches, aimed at detailing the likely impacts that would arise from a proposed activity, and retrospective approaches, aimed a quantifying the actual impacts of the activity (Osenberg and Schmitt 1996).

Our prescription for avoiding revenge effects boils down to treating new control organisms as "guilty until proven innocent": presume each new control organism species is unnecessary, unsafe, and ineffective until it is shown, beyond a reasonable doubt, to be necessary, safe, and effective. Troubles arise when noble but narrowly focussed goals enter the complex interactions that make up nature and society. Unable to foresee which complexities need attention, we forge ahead, always expecting the best. In the USA, politics presently trumps policy: agency infighting, confusion about how to bring biosecurity policy in line with statutory authority, and regulatory uncertainty compound the problem of overseeing the growing global market for biocontrol organisms (OTA - U.S. Congress Office of Technology Assessment 1993, OTA - U.S. Congress Office of Technology Assessment 1995). For biocontrol of weeds, it is too dramatic to claim, like Chicken Little, that harm caused to date by weed control organisms approaches ecological disaster. A tingid bug *Teleonemia scrupulosa* Stål (Hemiptera: Tingidae) caused local problems on a crop -- but with effects localized by time, space, and crop variety (Harris 1988) -- this is nothing like the ecological disaster that Miller and Aplet (1993) have alleged. It is equally misleading to brush aside concerns about possible environmental harm in the name of restoring public confidence, claiming like Voltaire's Dr. Pangloss that we already live in the best of all possible regulatory worlds. This adds one more version of a revenge effect, when official comments meant to shore up public confidence (Soper 1992) end up undermining it. Given the nature and magnitude of the actual risks and the inevitable costs of regulation, the challenge is to determine what kinds of oversight mechanisms are needed. Inadequate or misdirected oversight mechanisms may leave potentially serious risks unaddressed, while unwarranted regulatory burdens create disincentives to innovation that diminish the availability of important new techniques or products (Barton et al. 1997). Nevertheless, it should be possible to find a balance in biocontrol oversight mechanisms without the polarizing influence of Chicken Little or Dr. Pangloss.

CONCLUDING REMARKS

The practice of weed biocontrol currently resembles a lottery in which more and more control organisms are added to speed the discovery of the few that are effective. Practicing biocontrol as if it were a lottery fuels runaway importation rates; creates needless complexity, redundancy, and risk; distracts scientific attention from monitoring and evaluation; and stunts the development of more parsimonious alternatives. Biocontrol under the Lottery Model leads to four kinds of revenge effects: (1) Scarce resources are diverted from more profitable alternatives for managing pests, (2) One control organism undermines another, more effective control organism, leading to increase in pest density, (3) One pest is replaced by another pest that can be even harder to control, (4) Control organisms introduced to promote environmental and economic health end up undermining it by harming non-target organisms.

Advances in understanding, prediction, and management of biocontrol could be made in two ways. The first way is through more timely and informative post-release evaluation of impacts on target and nontarget organisms. Currently biocontrol scientists often have very limited knowledge of the factors that limit effectiveness of control organisms, and much of that knowledge is subjective. For monitoring and evaluation of biocontrol programs, it is useful to recognize stages in the development of biocontrol (release, establishment, increase and spread of control organisms, suppression of the target organism, and plant succession replacing the weed with other plants), and then analyze progress step by step. The second way is through experimental screening of each control organism for effectiveness as well as safety prior to release and making educated guesses about effectiveness based on expert intuition, data bases, and experimental and mathematical models. Given the uncertainties involved in biocontrol, the best way to avoid revenge effects is to adopt a precautionary approach and to follow simple guidelines for decision making under uncertainty.

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