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FORUM ARTICLE

Evaluating the post-release efficacy of invasive plant biocontrol by insects: a comprehensive approach

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Abstract We propose a comprehensive program to evaluate the post-release phase of biocontrol programs that use insect herbivores to control invasive plant species. We argue that any release should be done in randomized release and non-release sites and should be followed up by well-replicated sampling and experimental protocols that evaluate the degree of success or failure. These follow-up studies should include landscape scale monitoring across relevant habitat gradients of (1) the abundance of the biocontrol agent, (2) the impact of the biocontrol agent on the target plant species, (3) the potential for non-target effects, and (4) the response of native species and communities to a reduction in the invasive species. We also argue that (5) experimental reductions of the biocontrol agent are required to eliminate the chance that the putative impact of the biocontrol agent is not confounded with other causes. Finally, we describe six scenarios, informed largely by a community ecology perspective, in which a biocontrol agent may decrease the abundance or vigor of the target plant species but not lead to successful control where native communities re-establish. We classify these failure scenarios as either direct or indirect effects of the invasive plant species: Native Source Limitation, Static Competitive Hierarchies, Novel Weapons, Trophic Shifts, Invasive Engineering and Associated Invasives. Overall, we argue that well replicated and landscape-scale post release monitoring programs are required not only to evaluate critically the degree of success and failure of biocontrol programs worldwide but also to provide insights into improving future biocontrol efforts.

Keywords Biological control · Competition · Herbivory · Host density · Insect · Non-target effects · Post-release monitoring · *Lythrum salicaria*

Introduction

Biological control offers the potential for powerful, cost-effective management of invasive plant species and has claimed a limited number of successes worldwide, though many more failures (Crawley 1989; Julien and Griffiths 1998; McFadyen 1998, 2000). Crawley (1989) noted more than 15 years ago that the degree of success in biocontrol is rarely quantified in a rigorous manner. Remarkably, this situation has not improved (Thomas and Reid 2007). Despite 215 new invertebrate biocontrol programs (novel agent-plant associations within an invaded region) that were initiated between 1991 and 1996 (Julien and Griffiths 1998), only a relatively small number of studies have evaluated the impacts of established biocontrol agents on

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host-plant abundance in the field (e.g. Dhileepan et al. 2000; Blossey and Skinner 2000; Story et al. 2000; Clark et al. 2001; Dhileepan 2001; Mico and Shay 2002; Roduner et al. 2003; Landis et al. 2003; Lindgren 2003; Seastedt et al. 2003; Kok et al. 2004; Lesica and Hanna 2004; McConnachie et al. 2004; Paynter 2005; Butler et al. 2006; Cornett et al. 2006; Grevstad 2006; Story et al. 2006; Dhileepan 2007; Ireson et al. 2007). In total, these 20 papers evaluated 20 different insect species that successfully established on just 10 different invasive plant species. For comparison, the 215 new programs documented by Julien and Griffiths (1998) comprised 58 plant species and 119 biocontrol agents, at least 70% of which successfully established populations in the new region.

We suggest that biocontrol assessments should not only be conducted with more regularity, but also with more experimental rigor than has often been the case. Although eight of the 20 studies we cite did utilize control plots, only three authors (Lesica and Hanna 2004; Butler et al. 2006; Dhileepan 2001; 2007) used a randomized design that would allow a meaningful statistical test in the classical sense (sensu Hurlbet 1984) of the magnitude and significance of biocontrol effects on host plant abundance. Additionally, few biocontrol assessments have used protocols that would permit evaluation of environmental factors (e.g., soil fertility or rainfall) related to a release program's degree of success or failure across the landscape (Dhileepan 2001; Lesica and Hanna 2004; Butler et al. 2006). Theory predicts that herbivore impact will vary substantially based upon abiotic gradients, particularly fertility (Power 1992; Grover 1997; Chase et al. 2000), and biotic gradients, such as host density (Carson et al. 2004; Long et al. 2003; Carson and Root 2000). Finally, research regarding the community and ecosystem consequences of successfully controlling a formerly widespread and abundant invasive is often lacking (Denslow and D'Antonio 2005; Thomas and Reid 2007). From our sample, nearly half of the 20 studies neglected to measure a single response by the surrounding vegetation to biocontrol releases.

Better quantitative field tests of biocontrol efficacy are also essential for documenting risks to non-target species (Simberloff and Stiling 1996; Thomas and Willis 1998; Louda et al. 1997; Cory and Myers 2000; Arnett and Louda 2002; Louda and O'Brien 2002; Louda et al. 2003; Pearson and Callaway 2003). Our focus in this critique is on assessing the efficacy of biocontrol agents on their target plant species, rather than assessing the extent of non-target feeding; however, we emphasize the importance of incorporating sufficiently long-term, landscape-scale monitoring on non-target species into any biocontrol release program. Increasing rigor in pre-release agent testing has resulted in fewer negative impacts on non-target plant species (McFadyen 1998), the most susceptible of which tend to be those most closely related to the invasive species (Pemberton 2000). Nevertheless, monitoring for non-target impacts should extend for multiple generations because host shifts can evolve with increased exposure to non-host species (e.g. Bush 1969; Gould 1979; Carroll and Boyd 1992; Louda et al. 2003), and because indirect impacts of biocontrol agents on non-target species are unlikely to be seen immediately post release (Pearson and Callaway 2005).

Overall, if we cannot evaluate when, where, and under what conditions a biocontrol agent is effective, we have little means by which to weigh the costs and benefits of introductions. This is particularly important given that multiple insects have often been released to control an invasive when a single biocontrol species might have sufficed (McEvoy and Coombs 1999; Dhileepan et al. 2000; Clark et al. 2001; Roduner et al. 2003) and given the substantial expense of widespread releases of insects with little impact (McFadyen 1998). Although many have emphasized the importance of post-release monitoring (McFadyen 1998; Grodowitz 1998; Blossey and Skinner 2000; Landis et al. 2003; Hoffman and Moran 1998; Blossey 1995; Lindgren 2003), none to date have offered a comprehensive protocol that includes randomized release and control sites, the critical step required to isolate and quantify the effects of biocontrol agents using a classical statistical approach.

Historically, evaluations of biological control programs have focused on responses at the individual or population level (establishment of biocontrol agents or responses by the invasive species), even though management goals generally include some expectation that the native flora will rebound to pre-invasion levels. Although greenhouse and cage trials provide some insights into the community level effects of biocontrol agents, most such studies cannot take into account how in situ levels of predation, competition, and abiotic factors may cause biocontrol failures in natural systems (Adair and Holtkamp 1999; Wheeler and Center 2001). We argue that well replicated, randomized field studies are needed that (1) rigorously evaluate the impact of biocontrol agents on target species and how this impact varies regionally across important environmental gradients and (2) use well replicated, long-term monitoring of plant community response to better understand the reasons for biocontrol failure (e.g., the invasive remains dominant) and biocontrol success (e.g., re-establishment of the native community) across the landscape.

These sorts of comprehensive evaluations are rare (Thomas and Reid 2007) but are needed to evaluate carefully why so many release efforts fail or, conversely, to understand why some releases are so successful. Admittedly, there are many definitions of success in regards to biocontrol (Syrett et al. 2000). Our view is that successful biocontrol programs will depress invasive plant populations enough to permit the re-establishment of native plant communities. Ours differs from other definitions of success—such as slowing the rate of invasion or combining management with more intensive approaches (e.g. herbicides plus biocontrol)—because the focus here is on restoring native communities using field techniques that are not labor-intensive and are therefore practicable against expansive invasive populations. This protocol can still be applied to evaluating biocontrol success for weeds of agricultural systems (particularly multi-species pastures), with the caveat that quantifying responses by the surrounding native vegetation would obviously be irrelevant (cf. component 5, below).

Below, we outline a protocol for rigorous biocontrol evaluation and follow that with a discussion of six scenarios that could lead to biocontrol failure. The six scenarios are informed largely from a community ecology perspective and therefore, as with the protocol itself, they are most relevant for biocontrol of invasive species. These scenarios are valuable avenues for troubleshooting biocontrol failures and for investigating mechanisms by which an invasive species may still be able to outcompete co-occurring vegetation and remain abundant in spite of the successful biocontrol agent.

A 5-step comprehensive protocol for monitoring the efficacy of biocontrol agents

A comprehensive protocol for evaluating to what degree a biocontrol program is effective should have the following 5 components, expanded below: (1) The biocontrol agent should be released in randomly selected sites (release sites) that are paired with non-release sites (control sites) in a replicated manner, stratified across relevant temporal and spatial biotic and abiotic gradients. (2) The abundance of the invasive plant species should be quantified in release and non-release sites prior to any releases and periodically thereafter. (3) The abundance of the biocontrol agent should be quantified on host plants in release and non-release sites. (4) The biocontrol agents should be experimentally suppressed on target plants in replicated subplots arranged in a stratified random manner within release and non-release sites. (5) The response of the associated plant community should be quantified in release and non-release sites prior to any releases and periodically thereafter.

(1) The biocontrol agent should be released in randomly selected sites (release sites) that are paired with non-release sites (control sites) in a replicated manner, stratified across relevant temporal and spatial biotic and abiotic gradients. Biocontrol experts need to know both whether the biocontrol agent established and where was it most successful. A large body of theory predicts that the impact of herbivores (introduced or not) will vary along landscape-scale gradients in site productivity (see reviews by Power 1992; Grover 1997; Chase et al. 2000). If so, then the release of biocontrol agents should be done in a stratified random manner in replicated sites across these broad fertility or precipitation gradients. This will allow biocontrol experts to determine in what parts of the habitat biocontrol is likely to work. Other relevant landscape-scale features or gradients may include soil type, slope, or aspect but will depend on the natural history of the invasive species in question.

Biotic gradients should also be considered if possible, including the local abundance of the host (see component 2) and the diversity and abundance of co-occurring native plant species and other exotic plant species (see component 5; Goeden and Louda 1976; Pratt et al. 2003; Hunt-Joshi et al. 2005). The key is to try to identify or quantify the factors that are likely to correlate with or cause variation in the impact of the biocontrol agent. Overall, the selection of relevant factors should consider the potential for interactions among the invasive, the biocontrol agent, co-occurring species, and their relationship to prominent habitat features.

Highly dispersive herbivores present an additional challenge to the identification of paired release and non-release sites. Some biocontrol agents can disperse tens of kilometers per year (e.g. Chen et al. 2005), potentially colonizing populations originally identified at non-release sites. Therefore, the greater the rate of herbivore movement across the landscape, the further apart sites will need to be, and appropriate biotic and abiotic assessments should be conducted to ensure paired sites are as similar as possible. However, determining the efficacy of herbivores when non-release sites have been colonized is still possible with this protocol, simply by controlling statistically for herbivore abundance and time since herbivore establishment. Non-release site monitoring will also inform the dispersal abilities of released biocontrol.

(2) The abundance of the invasive plant species should be quantified in release and non-release sites prior to any releases and periodically thereafter. Prior to release, standard methods should be used to quantify the abundance and vigor (e.g., height, rosette size, etc) of the invasive in randomly selected, replicated, and preferably permanent sampling plots in as many release and non-release sites as possible (Evans and Landis 2007). These plots can then be periodically recensused to evaluate if and to what degree the biocontrol agent caused a reduction in the target species and whether this varied with host abundance or vigor or both. Indeed, there is growing evidence that the negative impact of either introduced or native phytophagous insects

increases substantially with host concentration (Carson et al. 2004). If so, then we may only see biocontrol agents controlling invasives in a small number of very dense locations or patches, potentially leaving stands where the invasive remains in lower abundance but is still the dominant or co-dominant species in the community.

If there are paired release and non-release sites (component 1, above), then plant abundance assessments repeated over time will help determine whether declines in the invasive plant population are due to herbivore pressure from the biocontrol agent versus other causes, such as generalist herbivory, intraspecific competition or interspecific competition (reviewed in Simberloff and Gibbons 2004). Simultaneous declines in both release and non-release sites would be suggestive of an invasive species' decline due to factors unrelated to the biocontrol agent itself.

(3) The abundance and impact of the biocontrol agent should be quantified on host plants in release and non-release sites. To link the release of the biocontrol agent to the decline of the target species, it is essential to demonstrate that the biocontrol agent was not only present but also numerous enough to sufficiently damage the host. For example, we found that the percent leaf damage on the invasive wetland species purple loosestrife (*Lythrum salicaria*) caused by an introduced leaf-feeding beetle, (*Galerucella calmariensis*) varied substantially across 46 release sites in New York, Ohio, and Pennsylvania, USA (Fig. 1). The amount of damage caused would rarely have been sufficient to allow the formerly dominant native cattails (*Typha latifolia*) to re-establish in invaded wetlands (Bunker 2004).

This phenomenon is not limited to purple loosestrife biocontrol. McClay and Balciunas (2005) list 13 insect biocontrol agents that frequently occur in high abundances where released but have little or no effect on their target weeds. Reasons for these apparent disparities include invasives that are not seed-limited, biocontrol agents that feed on non-essential plant tissues, and damage that occurs too late in the season to affect reproductive output of the invader. Although McClay and Balciunas make a well-reasoned argument that the efficacy of potential biocontrol agents should be assessed prior to release (in addition to host-specificity testing), we contend that such an assessment must also be conducted post-establishment.

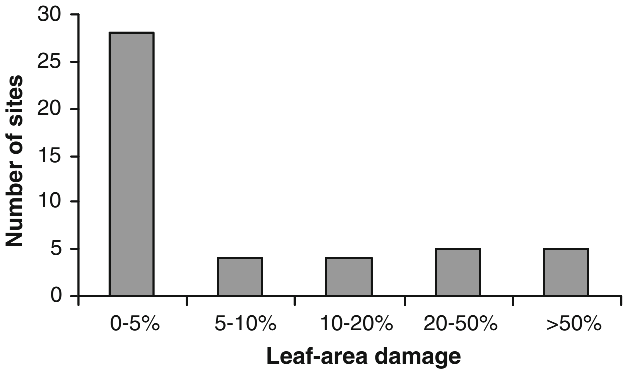

Fig. 1 The percent leaf area damaged on purple loosestrife (*Lythrum salicaria*) caused by the chrysomelid beetle *Galerucella calmariensis* at 46 wetland sites in Pennsylvania and New York, USA. Percent damage was estimated visually on at least 36 randomly selected individuals by comparing damage on leaves to a template of artificial (paper) leaves with multiple classes of damage (Carson and Root 2000)

As a final point, it will be important to determine if and how fast the biocontrol agent is colonizing and establishing in non-release sites and thus potentially impacting host plant populations. The creation of metapopulation or source-sink dynamics may increase biocontrol effectiveness (Murdoch et al. 1995), as would unaided dispersal and establishment of the biocontrol agent on a widespread invasive species. Conversely, exceptional dispersers may experience Allee effects in daughter populations, leading to a post-establishment lag before substantial impacts on the target species are observed and, at least in theory, decreasing biocontrol effectiveness throughout the agent's introduced range (Fagan et al. 2002; Jonsen et al. 2007).

(4) The biocontrol agents should be experimentally suppressed on target plants in replicated subplots arranged in a stratified random manner within release and non-release sites. To unequivocally demonstrate that the biocontrol agent caused the demise of the invasive, experimental reductions of herbivores on the invasive via hand removals, netting or insecticide should be conducted using appropriate techniques at multiple release sites (Dhileepan 2007). Siemann et al. (2004) recently described the pros and cons of various exclusion techniques. Using experimental reductions dramatically reduces the chances of confounding putative reductions in the target species caused by the biocontrol agent with other causal agents that might reduce the abundance of the invasive plant such as natural successional changes or region-wide outbreaks of disease, drought, or fire. If the impact of the biocontrol agent varies among release sites, site factors such as fertility, disturbance regime, plant species composition, consumer abundance, or host abundance can be used as covariates in any analysis. We recognize that these exclusion manipulations will be infeasible or difficult in many cases, but coupling this manipulative approach with observations of herbivore abundance (component 3) provides an exceptionally rigorous means of attributing population declines in the host species to herbivore activity.

(5) The response of the associated plant community should be quantified in release and non-release sites prior to any releases and periodically thereafter. A sometimes

unstated goal of biological control is to reduce the invasive species so that the native community returns with similar species composition, diversity, and function. The emphasis of biocontrol assessment is usually at the individual or population level (i.e. the response of the target species), but community- and ecosystem-level responses arguably provide the ultimate measure of biocontrol success in most natural systems. Despite their presumed importance, few assessments of biocontrol success have quantified community or ecosystem responses to biocontrol introductions (Denslow and D'Antonio 2005). In particular, if the native plant community does not recover a biocontrol program may not be considered entirely successful. Consequently, desirable characteristics of the given plant community should be assessed before and after biocontrol release in any assessment program. Biocontrol practitioners might consider using uninvaded reference sites with similar habitat characteristics where pre-invasion vegetation data is unavailable. These reference sites could serve as a yardstick to determine whether native species diversity and composition approaches pre-invasion conditions following release. These reference sites, of course, are not true controls and hence any conclusions reached must be interpreted with caution.

Six scenarios leading to biocontrol failure: a community ecology perspective

As noted in the 5 components above, even if the introduced herbivore is common and significantly decreases the abundance of an invasive, the native community may fail to return, show a significant time lag, or re-assemble with a different complement of species. Here, concepts from community ecology provide insights into invasive species management using biocontrol, and the history of biocontrol introductions and invasive species management in general can enhance our understanding of community ecology. We discuss six possible scenarios by which an invader decreases in abundance with no concomitant increase in native vegetation. Five of these six scenarios can be broadly categorized as either *direct* or *indirect* effects by the invading plant species. The first three scenarios result from direct effects: Native Source Limitation, Static Competitive Hierarchies, and Novel Weapons. The next two scenarios result, respectively, from indirect effects mediated through the biotic or the abiotic environment: Trophic Shifts and Invasive Engineering. The sixth scenario, Associated Invasives, does not group neatly as either a direct or indirect effect but could result from either process.

(1) Native source limitation: Seabloom et al. (2003) have shown that the major limitation to restoring native vegetation in California is dispersal-limited native species. Additions of native seeds have resulted in the successful establishment of those species, many of which are now known to outcompete the exotic grasses that dominate many of those plant communities (Corbin and D'Antonio 2004). Due to sparse populations and local extinctions of the native flora, biocontrol of the dominant invaders may not allow a shift from exotic-dominated to native-dominated vegetation. Human-induced dispersal therefore becomes a necessary component of restoration efforts, even with successful biocontrol. It is currently unknown how important dispersal limitation is for native flora recovery in other exotic-dominated plant communities.

The *relative* abundance of native propagules can also become a limiting factor, either when the invader experiences strong storage effects or when seed set reductions due to biocontrol are minimal (e.g., Parker 2000). Storage effects are likely to be extremely important, since the seed bank under a monotypic exotic canopy will tend to be biased against native plant regeneration. Demographic studies on invasive species have provided valuable insights into which life stage is most susceptible to herbivore damage by highlighting to what extent seed set must be diminished for successful control of the target species. These results can be disheartening. Parker (2000) calculated that seed set on *Cytisus scoparius* would have to be reduced by over 99% in prairies to result in successful control, whereas observed herbivore pressure from the biocontrol agent *Apion fuscirostre* (Coleoptera: Curculionidae) only reduced seed set by 50% (Parker 2000). Elsewhere, seed set reductions on *C. scoparius* after up to 7 years in the presence of *A. fuscirostre* were comparable and always under 75% (Parker 2000). This example and others like it (e.g., Shea and Kelly 1998), emphasize the importance of utilizing biocontrol agents that are capable of sufficiently targeting susceptible life stages of the plant.

(2) Novel weapons: Another situation that can make biocontrol success less likely occurs when exotic species use "novel weapons" that facilitate invasion and persistence (Bais et al. 2003; Callaway and Aschehoug 2000; Callaway and Ridenour 2004). Novel weapons are generally biochemical exudates released by exotic plants that can seriously impair native plant species and disrupt soil microbial communities (Callaway and Ridenour 2004). In these cases, the biocontrol agent will only work if it sufficiently negates the effect these allelochemicals. In at least one case, damage by a biocontrol agent increased allocation to these allelopathic weapons (Callaway et al. 1999; Ridenour and Calloway 2003).

(3) Static competitive hierarchies: In a particularly challenging scenario, biocontrol agents may reduce the density or size of the invasive species but the invasive species continues to be dominant because it remains the

superior competitor; thus competitive hierarchies remain unchanged or static. This situation could be fairly common and depends upon the mechanism of competition. For example, an invasive species may be the superior resource competitor because it reduces the quantity of the shared limiting resource (e.g., nitrogen or light) to a level where native competitors cannot persist (Tilman 1982; Grover 1994, 1997). If so, then an introduced specialist will only allow displacement by native plant species if the herbivore damages the invasive sufficiently to make native species superior resource competitors than invasive species (for the underlying theory see Tilman 1982; Holt et al. 1994; Grover 1994, 1997). In this case, the success of biocontrol will depend on the competitive ability of the native species and the indirect impact of the biocontrol agent on the limiting resource.

If competitive ability and relative abundance of native species varies substantially across the landscape, then the efficacy of the biocontrol agent may vary substantially as well. Thus, knowing how community composition changes may be important in explaining landscape scale patterns of success or failure. In cases where the biocontrol agent does not cause massive mortality of the invasive but only reduces its density or vigor to a lesser degree, success may only occur when native plant species that are good resource competitors are found growing with the invasive species.

(4) Trophic shifts: In this indirect effect on native vegetation, the invasive species interacts with the surrounding biotic environment to change the likelihood of native plant reestablishment. It does this by altering other trophic levels (e.g., mutualists, pathogens, herbivores, parasitoids, and predators) affecting the persistence of native species. If such a shift has occurred, simply reducing the abundance of the invasive via biocontrol may be inadequate.

For example, soil microflora vary in host specificity, with different plant species culturing contrasting soil microbial communities; these communities may then enhance the performance of the dominant plant species (Klironomos 2002; Bever 2003; Ravit et al. 2003). If invasives persist in dense stands for many years, there can be a loss of microbial species over time (Kourtev et al. 2002; Mummey and Rillig 2006; Van der Putten et al. 2007). For example, leachates from the invasive *Alliaria petiolata* (garlic mustard) inhibit arbuscular mycorrhizal spore germination (Roberts and Anderson 2001), reducing mycorrhizal colonization and tree seedling performance (Stinson et al. 2006). Diverse and specific microbes may be necessary for a diverse native community to reform. Indeed, in grasslands, a high arbuscular mycorrhizal fungal diversity supports greater plant diversity (Van der Heijden et al. 1998).

Similarly, specialist pollinators associated with native species may be lost when invasives become abundant and widespread. Despite the paucity of relevant long term pollinator studies (Williams et al. 2001), there is evidence that pollinator diversity and composition changes following a change in dominant vegetation (Archer 1989). If so, pollinators associated with invasive taxa may replace native pollinators, leading to a major reduction in native plant species fitness. Additionally, native pollinators may preferentially pollinate exotics thereby perpetuating invasions and delaying or inhibiting native species recovery (Brown et al. 2002, Ghazoul 2002, 2004).

Finally, major changes in herbivore diversity and abundance can occur following the spread of an invasive species (e.g. Lau and Strauss 2005). If these herbivores were integral to the functioning and structure of native communities, then this could be inimical to the return of the natural vegetation. This would become particularly important in circumstances where an abundant exotic plant causes increases in generalist herbivore populations (apparent competition sensu Holt et al. 1994), however the strength and persistence of such shifts due to species invasions are generally unknown.

(5) Invasive engineering: The indirect effect of an invasive species on native vegetation via interactions with the abiotic environment is considered invasive engineering. Here, the invasive species sufficiently alters the abiotic environment to such a degree that native species fail to sufficiently recover. In this case, these invasive species may be considered ecosystem engineers (Jones et al. 1994, 1997; Crooks 2002). Examples include wetland invasives permanently altering hydrology or legumes permanently altering fertility (Vitousek et al. 1987; Crooks 2002; Symstad 2004).

Invasive plant species may alter the abiotic environment to such a degree that even if a biocontrol agent substantially reduces host density, native species may be very slow to return, fail to return altogether, or the new community that forms does not resemble the former native community. In this case, the invasive engineers a new system over time, with major ecosystem-level consequences (reviewed by Crooks 2002). It is important to note here that in cases where invasives have re-engineered the ecosystem, additional post-release ecosystem monitoring that was not described here will be required (e.g., nutrient or hydrological cycles).

(6) Associated invasives: This scenario results from the invasive species being replaced by co-occurring exotic species. In these cases, the “secondary” exotic species spreads rapidly into the area previously dominated by the former invasive species, preventing native vegetation from returning (e.g., Pickart et al. 1998; Symstad 2004). One striking example of this dynamic was reported by Campbell and McCaffrey (1991) on biocontrol of Klamath weed (*Hypericum perforatum*). At most sites in northern Idaho

successful biocontrol by *Chrysolina quadrigemina* (Coleoptera: Chrysomelidae), *C. hyperici*, and *Agrilus hyperici* (Coleoptera: Buprestidae) is followed by the establishment of invasive populations of *Centaurea* spp. and *Bromus* spp. As this scenario only requires an association—not necessarily an interaction—between multiple exotic species, control of each potential secondary invader may require a unique management approach.

Conclusions and summary

We recognize that the comprehensive monitoring program we have outlined will require a commitment of both time and money. These resources will likely be a small percent of the overall expenditures of any major biocontrol program. We are not the first to call for efficacy assessments of biocontrol agents (e.g. McClay and Balciunas 2005), but we have striven to outline rigorous guidelines for carrying out post-release assessments that focus on both population- and community-level responses. We recognize limited resources may force biocontrol practitioners to choose a subset of the recommendations proposed here; regardless, we believe that a strong emphasis on post-release monitoring is a necessary component of biocontrol introductions.

Our emphasis on adherence to the principles of randomization, replication, and experimental controls is rooted in a background of empiricism and traditional experimental design, sensu Hurlbert (1984). Alternatives to the classical statistical approach (e.g. Burnham and Anderson 1998; Gelman et al. 2004) are gaining in utility and will also provide valuable insights, particularly where manipulative experiments are impossible or where additional data are available prior to the manipulation. However, we feel that experimental suppression of the biocontrol agent and quantification of the surrounding vegetation before and after biocontrol releases are essential components of a cause-and-effect assessment.

In terms of failed biocontrol releases, the six scenarios we have presented are meant to provide a community-based framework within which to place future investigations. Information on community-level responses to biocontrol programs are lacking despite a long history of biocontrol agent releases. Although suppression of an invasive plant population is a pre-requisite to successful biocontrol, it may not be sufficient to allow eventual recovery of native vegetation. The community perspective is useful not only for assessing when "success" has been attained, but also for troubleshooting biocontrol failures. This approach may be vital for understanding why biocontrol success is so variable, and it can provide valuable insights for adaptive management in situations where biocontrol failure is imminent.

By separating our six scenarios into those due to direct and indirect effects, we have also tried to emphasize the importance of indirect effects as potential explanations for invasive success and biocontrol failure. Recent trends in the literature suggest the popularity of this view. A search for ecological papers using the terms "indirect effect" and "invasive" or "exotic" using ISI Web of Knowledge yielded 95 references published between 1994 and 2006. Of these, over 75% were published between 2002 and 2006. Apparently, the research community as a whole has begun to see the importance of indirect effects for understanding the dynamics of species invasions. We wish to emphasize the importance of indirect effects specifically as they relate to understanding the reasons for biocontrol success or failure.

We have outlined a comprehensive program for post-release evaluation of insect biocontrol programs and have presented six scenarios that may result in biocontrol failure. We consider this a starting point from which to design such programs and debate differing perspectives regarding biocontrol assessment. We welcome further dialogue and critique regarding changes and improvements to this approach.

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