

Indirect nontarget effects of host-specific biological control agents: Implications for biological control

Dean E. Pearson^{a,b,*}, Ragan M. Callaway^b

^a Rocky Mountain Research Station, USDA Forest Service, Missoula, MT 59807, USA

^b Division of Biological Sciences, University of Montana, Missoula, MT 59812, USA

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Abstract

Classical biological control of weeds currently operates under the assumption that biological control agents are safe (i.e., low risk) if they do not directly attack nontarget species. However, recent studies indicate that even highly host-specific biological control agents can impact nontarget species through indirect effects. This finding has profound implications for biological control. To better understand the causes of these interactions and their implications, we evaluate recent case studies of indirect nontarget effects of biological control agents in the context of theoretical work in community ecology. We find that although particular indirect nontarget effects are extremely difficult to predict, all indirect nontarget effects of host specific biological control agents derive from the nature and strength of the interaction between the biological control agent and the pest. Additionally, recent theoretical work suggests that the degree of impact of a biological control agent on nontarget species is proportional to the agent's abundance, which will be highest for moderately successful control agents. Therefore, the key to safeguarding against indirect nontarget effects of host-specific biological control agents is to ensure the biological control agents are not only host specific, but also efficacious. Biological control agents that greatly reduce their target species while remaining host-specific will reduce their own populations through density-dependent feedbacks that minimize risks to nontarget species.

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1. Introduction

Classical biological control is based on the enemy release hypothesis. This hypothesis states that exotic species become pests in new environments by escaping the influence of those natural enemies that suppressed their populations in their native range (Crawley, 1997; Keane and Crawley, 2002). Thus, the strategy behind classical biological control is to reestablish top-down control by reintroducing the natural enemies of the pest into its new range. This has been the conceptual underpinning of

classical biological control for over 100 years and it continues to be today (Hajek, 2004; Van Driesche and Bellows, 1996). Although a variety of natural enemies may help control a pest in its native range, not all potentially effective natural enemies will serve as safe biological control agents in a pest's new environment. In particular, natural enemies with broad host ranges are unlikely to provide the surgical precision we desire in biological control, because they may attack important nontarget organisms in the new environment and become exotic pests in their own right (Follett and Duan, 2000; Harris, 1990; Howarth, 1991; Louda et al., 1997; Simberloff and Stiling, 1996; Wajnberg et al., 2001). As a result, biological control programs

* Corresponding author. Fax: +1 406 543 2663.

E-mail address: dpearson@fs.fed.us (D.E. Pearson).

emphasize host specificity in selecting agents for introduction to avoid these undesirable nontarget effects. The outcome has been that biological control operates under the assumption that nontarget effects arise only when biological control agents directly attack nontarget species, or conversely that host-specific biological control agents are safe (we define safe as low risk or safe enough for introduction).

Although the importance of host specificity for the safety of biological control should not be understated (e.g., Louda et al., 1997), perhaps it has been overstated (e.g., Hoddle, 2004a). The emphasis on host specificity has diverted attention from other potential sources of risk to nontarget species that has contributed, at least in part, to certain biocontrol strategies like the “lottery approach” (Myers, 1985) which may unnecessarily elevate nontarget risk, especially indirect nontarget risk. The lottery approach is a multiple release strategy in classical biological control that promotes the deployment of multiple host-specific biological control agents for each target pest (Hokkanen and Pimentel, 1984; McEvoy and Coombs, 2000; Myers, 1985). This approach places great emphasis on host specificity of individual agents, but does not weigh efficacy as heavily in this process (McEvoy and Coombs, 2000; Sheppard, 2003). This lack of emphasis on efficacy derives from the assumption that the most effective agent or combination of agents will emerge from the milieu of introductions. The biological control of spotted knapweed (*Centaurea maculosa* Lam.) provides a classic example of the lottery approach. Thirteen species of biological control agents have been introduced for the control of spotted knapweed (Lang et al., 2000), and the pool of agents that are sufficiently host specific to warrant introduction may be exhausted (Müller-Shärer and Schroeder, 1993). Thus, the entire suite of host specific biological control agents may have been introduced for this weed. Although there is currently little indication of successful control of spotted knapweed (Maddox, 1982; Müller-Shärer and Schroeder, 1993), in other cases where the lottery approach has been successful, it is often only one or two of several released agents that end up ultimately effecting control (Denoth et al., 2002; Forno and Julien, 2000; McFadyen, 2003; Myers, 1985). For example, in the classical success story of klamath weed (*Hypericum perforatum* L.), three agents were introduced, but success was attributed to only one of these (Huffaker and Kennett, 1959).

The lottery approach is only one of several multiple-release strategies in biological control (Harris, 1991; Sheppard, 2003), but it is the one that has been most criticized because relative to other multiple-release approaches it depends the most on chance and the least on explicit knowledge of community interactions in the introduction of multiple biological control agents for each target weed (McEvoy and Coombs, 1999, 2000;

Myers, 1985; Myers et al., 1989; Sheppard, 2003; Strong and Pemberton, 2000). The result of multiple-release strategies in general and the lottery approach in particular is that exotic organisms intentionally introduced for classical biological control exceed the number of exotic pests targeted for control (Hokkanen and Pimentel, 1984; McEvoy and Coombs, 1999; Myers, 1985). Although the introduction of any individual agent will present some risk to nontarget species, the degree of risk will increase with increasing numbers of agents. If host specificity does not sufficiently ensure the safety of biological control agents, multiple-release strategies like the lottery approach that emphasize numbers of agents over agent efficacy may present undue risks toward nontarget species. Here, we apply recent advances in community ecology theory to two recent case studies of community interactions in biological control to evaluate the implications of indirect nontarget effects of host-specific biological control agents for the practice of biological control.

2. Theory addressing nontarget effects of host-specific biological control agents

Application of community ecology theory to biological control suggests that there are many ways in which biological control agents can indirectly impact nontarget organisms. For example, Holt and Hochberg (2001) identified five general scenarios based on community modules (sets of interactions described by three to six strongly interacting organisms) through which biological control agents could indirectly affect nontarget species (Fig. 1). Four of these scenarios involve an indirect effect that is mediated through a direct attack by the biological control agent on a nontarget species, i.e., these scenarios depend on some aspect of host infidelity by the biological control agent. This is reassuring because, in theory, contemporary biological control strategies that ensure a high degree of host specificity should safeguard against most of these indirect nontarget effects (this assumes screening is effective at predicting host range, but see Louda et al., 2003). However, one scenario (Fig. 1E), referred to as “enrichment” by Holt and Hochberg (2001), only requires the presence of a generalist natural enemy capable of exploiting the biological control agent. In this case, the biological control agent can be an extreme specialist on the target weed and still profoundly impact other organisms in the systems where they have been introduced. If the biological control agent becomes sufficiently abundant, this interaction can be strong enough to subsidize populations of generalist natural enemies and indirectly affect other organisms attacked by that natural enemy. We believe that such indirect nontarget effects are of particular concern because they are not currently guarded against. This is

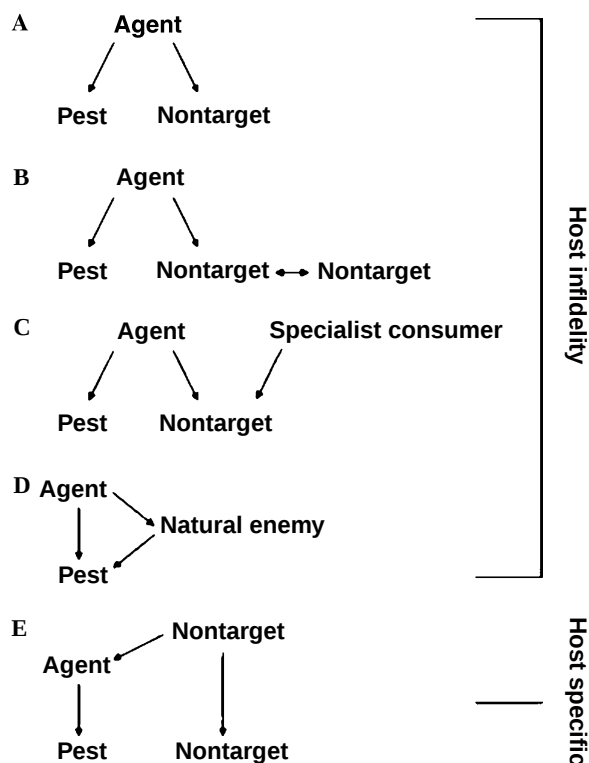


Fig. 1. Community modules showing pathways for nontarget effects of biological control agents (after Holt and Hochberg, 2001). The first four interactions resulting in nontarget effects (A–D) involve host infidelity on the part of the biological control agent, but the last nontarget effect can occur for even highly host-specific biological control agents. Interactions are named as follows (see Holt and Hochberg, 2001): (A) shared predation, (B) mixed predation and competition, (C) exploitative competition, (D) intraguild predation, and (E) enrichment or food–web interaction. Arrows indicate consumption except in (B) where the double-sided arrow indicates competition.

primarily because indirect nontarget effects that arise from biological control agents with broad host ranges are well documented (Follett and Duan, 2000; Wajnberg et al., 2001), but only a handful of studies have recently begun to evaluate the potential viability and significance of indirect nontarget effects arising from host-specific biological control agents (Pearson and Callaway, 2003). Though these studies are currently few, they help to illustrate the nature and extent of the problems associated with indirect nontarget effects of host-specific biological control agents.

3. Empirical evidence for indirect nontarget effects of host-specific biological control agents

We recently examined empirical evidence for indirect nontarget effects of host-specific biological control agents and identified three categories of indirect nontarget effects that can arise from highly host-specific control agents (Pearson and Callaway, 2003). These categories include: (1) ecological replacement, (2) compensatory

responses, and (3) food–web interactions (Fig. 2). This last category equates with the enrichment scenario described by Holt and Hochberg (2001; Fig. 1E), but the other two categories are not yet recognized by their framework. We briefly introduce these concepts here (Fig. 2) and provide examples of compensatory responses and food–web interactions to illustrate the implications of these indirect nontarget effects for the practice of biological control.

3.1. Ecological replacement

Ecological replacement occurs when an established invader replaces displaced native species in such a way that other native species become dependent on the invader. Nontarget effects occur when successful control of the invader deleteriously impacts the nontarget native species that have come to depend on it (Fig. 2A).

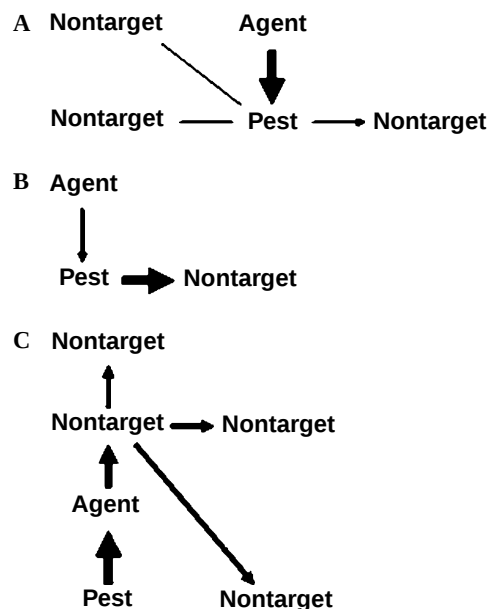


Fig. 2. Community modules depicting pathways for indirect nontarget effects of host-specific biological control agents. (A) Ecological replacement: agent is host specific and strongly suppresses the target weed thereby releasing suppressed natives, but this also weakens dependencies that have developed between the weed and other native species thereby negatively impacting these nontarget species. (B) Compensatory response: agent is host specific and the overall interaction between the biological control agent and the weed is top-down, but the target pest is only weakly impacted, because it displaces the negative impacts onto nontarget species through compensatory responses. (C) Food–web interaction: agent is host-specific, but the overall interaction between the biological control agent and the pest is strongly bottom-up so that the biological control agent becomes superabundant and then serves to subsidize other natural enemies in the system. These natural enemies then translate this subsidy into significant interactions with other nontarget species. Arrow direction indicates direction of the dominant interaction and the weight indicates the strength of the interaction. Lines without arrows in (A) simply indicate some sort of dependence.

Biological control under conditions of ecological replacement can result in undesirable indirect nontarget effects, but this is because the targeted pest has become important or desirable with regard to some aspect of its ecology, not because a biological control agent has misbehaved or otherwise failed. For example, saltcedar (*Tamarix* spp.) is a serious invasive pest in the southwestern United States which has replaced native trees and shrubs in many riparian areas (DeLoach et al., 2000). The southwestern willow flycatcher (*Empidonax traillii extimus* [Phillips]), which is an endangered subspecies of the willow flycatcher, normally nests in willows (*Salix* spp.), but in some areas where willows have been replaced by saltcedar, the flycatcher now nests in the saltcedar (Sogge, 2000). The proposed biological control program for saltcedar was initially held up due to concerns that successful control of the invader would leave the flycatcher without nesting habitat in some areas (DeLoach et al., 2000). However, this program has resumed after careful examination of the risks and assessment of potential mitigation on behalf of the flycatcher. Avoiding the unintended indirect nontarget effects associated with ecological replacement involves careful assessment of the target weed and its community interactions before introductions are made. We see the issue of ecological replacement as it relates to biological control as more of a policy issue than a problem with the ecological understandings of biological control. We are more concerned here with the ecological aspects of deploying biological control.

3.2. Compensatory responses

Compensatory responses can cause deleterious indirect nontarget effects by host-specific biological control agents when an agent's attack elicits a response from the target species that actually increases its negative impact on nontarget species or shifts its impact to other nontargets (Fig. 2B). Compensatory effects may occur when a damaged plant increases relative growth rates and competitive effects (Ramsell et al., 1993), induces the production of chemicals that might harm neighbors (Siemens et al., 2002), or stimulates the release of root exudates (Hamilton and Frank, 2001). Plant compensatory responses to herbivory are quite common (Crawley, 1989; Trumble et al., 1993), and there are numerous examples of compensatory responses of exotic plants to mechanical clipping (Callaway et al., 2001, unpublished; Gerlach and Rice, 2003) and to insects used as biological control agents (Islam and Crawley, 1983; Julien et al., 1987; Katovich et al., 1999; Müller, 1989; Steinger and Müller-Shärer, 1992), but it is not clear how often compensation results in negative effects on neighbors. Ramsell et al. (1993) showed that *Tipula paludosa* Meigen feeding on *Lolium perenne* L. actually increased its negative impacts on *Rumex obtusifolius* L. due to a

compensatory response to root grazing. Over-compensation to clipping was reported for the invasive *Centaurea solstitialis* by Gerlach and Rice (2003), suggesting the potential for this weed to increase its negative effects under herbivory, and Callaway et al. (unpublished) showed that clipping *C. solstitialis* did increase its negative impacts on native and naturalized California grasses, but acknowledged that clipping differs from herbivory in many regards. Callaway et al. (1999) and Ride-nour and Callaway (2003) found that application of the biological control agent *Agapeta zoegana* L. (Lepidoptera: Tortricidae) to its host plant spotted knapweed did not reduce biomass or fecundity in spotted knapweed, but instead caused significant reductions in reproduction and trends toward reduced biomass in neighboring Idaho fescue (*Festuca idahoensis* Elmer). Thus, the extent to which compensatory responses might result in indirect nontarget effects of biological control introductions is not yet clear given the limited research. However, given the variability in the nature and strength of compensatory responses of plants to herbivory (Crawley, 1989; Trumble et al., 1993), it is likely that indirect effects of biological control agents that do occur through compensatory responses would be highly variable and difficult to predict.

3.3. Food-web interactions

Food-web interactions can arise when generalist consumers or other generalist natural enemies exploit a host-specific biological control agent (Figs. 1E and 2C). If the biological control agent is sufficiently abundant, this interaction can result in a subsidy that significantly elevates the consumer's populations. Such a subsidy can translate to indirect effects on nontarget species through food-web interactions via the consumer.

For example, the gall flies (*Urophora affinis* (Frauenfeld) and *U. quadrifaciata* (Meigen), Lepidoptera: Tortricidae) introduced to North America to control spotted knapweed (Müller-Shärer and Schroeder, 1993) have become extremely abundant (Harris, 1980) and are now exploited by many native consumers (Story et al., 1995). Earlier studies indicated that exploitation of this resource by the native deer mouse (*Peromyscus maniculatus* Wagner) significantly altered deer mouse diets with potential to elevate mouse populations in knapweed-invaded grasslands (Pearson et al., 2000). This finding spawned a recent debate in *Conservation Biology* about the sufficiency of host specificity as a safeguard against nontarget effects (Hoddle, 2004a,b; Louda and Stiling, 2004). In question, in part, was whether gall flies simply served as an extra food resource for mice or whether gall flies actually functioned as a subsidy that elevated mouse populations and with them the potential for indirect nontarget effects. New research that was in press during this debate establishes that *Urophora* food subsidies

actually double or triple mouse populations by increasing overwinter survival of mice in knapweed-invaded habitats (Ortega et al., 2004). Additional studies have since corroborated this result (Pearson and Callaway, unpublished; D.E. Pearson unpublished data). This increase in deer mouse populations is very significant and significantly increases the potential for gall flies to indirectly affect other nontarget species through food–web interactions (Pearson and Callaway, 2003). In fact, Pearson and Callaway (unpublished) show that gall fly food subsidies to mice have tripled the prevalence of the Sin Nombre virus, a hantavirus that causes hantavirus pulmonary syndrome in humans (Childs et al., 1994). Their study area covered over 1600 km², but the affected area likely includes a much larger region of knapweed-infested habitats in several western states and provinces. Additional research suggests that as spotted knapweed invades native grasslands, gall fly subsidies to deer mice indirectly increase deer mouse seed predation and reduce recruitment in native plants already directly impacted by spotted knapweed (Pearson, unpublished data).

Native species are not the only nontarget organisms susceptible to impacts of biological control food–web interactions. Biological control agents themselves can also be affected. *Coleomegilla maculata* De Geer is an aggressive predator of *Galerucella pusilla* Duft. and *Galerucella californiensis* L., two biological control agents introduced against purple loosestrife (*Lythrum salicaria* L.) (Landis et al., 2003). Thus, *C. maculata* is a shared natural enemy between these two agents that has the potential to affect their relative abundance through apparent competition—a special case of food–web interactions that arises when an organism affects the abundance of a potential competitor by subsidizing a shared enemy (Holt, 1977). Although host specificity in weed biological control guards against negative effects of apparent competition that arise from the biological control agent becoming the shared natural enemy between a target weed and nontarget plants, it does not guard against apparent competition occurring through higher trophic interactions involving natural enemies that attack the biological control agent. Recent surveys monitoring introductions of *G. californiensis* and *G. pusilla* indicate that *G. californiensis* established successfully at 100% of 24 release sites whereas *G. pusilla* failed to establish at any of these release sites (Landis et al., 2003). Although differential establishment of the two conspecifics could be due to intrinsic differences in abiotic interactions or direct competition between the two agents, it is quite possible that apparent competition plays a role. *C. maculata* is a strong predator of both species (Sebolt and Landis, 2004). If *G. californiensis* is better able to suffer this predation, it may indirectly contribute to the demise of *G. pusilla* by subsidizing the *C. maculata* attack on *G. pusilla*.

Given the frequency with which biological control agents are exploited by natural enemies in the

introduced range (e.g., Goeden and Louda, 1976; Julien and Griffiths, 1998; Kluge, 1990; Müller and Goeden, 1990; Nuessly and Goeden, 1984; Pearson et al., 2000; Pratt et al., 2003; Reimer, 1988; Sebolt and Landis, 2004; Story et al., 1995), food–web interactions are likely a common outcome of the establishment of host-specific biological control agents. For example, Nuessly and Goeden (1984) documented intensive predation by the house mouse (*Mus musculus* L.) on the stem-boring moth (*Coleophora parthenica* Meyrick) introduced for the biological control of Russian thistle (*Salsola australis* R. Brown) in California. This system is highly reminiscent of the knapweed–gall fly–deer mouse system described above. However, as in virtually all cases of biotic interference with biological control agents, the emphasis of Nuessly and Goeden was on evaluating the effect of the mouse on the control agent not the effect of the control agent on the mouse and other nontarget organisms. Biological control agent–food–web interactions appear to be widespread, but their implications are poorly understood largely because their impacts are virtually unexplored.

4. Safeguarding against indirect nontarget effects of host-specific biological control agents

These examples show that host specificity alone does not ensure the safety of biological control programs as previously argued (Frank, 1998; Hoddle, 2004a). Moreover, they indicate that the nature of indirect nontarget effects that can arise from even highly host-specific biological control agents are such that they simply cannot be ignored. This conclusion has serious implications for biological control and raises the crucial question of whether or not indirect nontarget effects of host specific biological control agents can be predicted well enough to screen for them or if a better understanding of the types of interactions that result in indirect nontarget effects will allow us to avoid deleterious outcomes by designing around them.

Predictability has historically been an important element for safeguarding against nontarget effects. In the case of weed biological control, knowledge of the host range of the natural enemy is utilized to develop screening tests to determine the degree of host specificity of biological control agents and identify potentially at-risk nontarget species (Briese, 2003; McEvoy, 1996; Wapshere, 1974). This approach has clearly reduced the risks associated with biological control agents introduced for weed control (Pemberton, 2000), but the key to employing this technique has been the predictability associated with host-range expansion that has allowed testing to focus on a finite number of prospective alternative hosts without having to test all nontarget species present in the new environment (Briese, 2003; Pemberton, 2000).

Examination of the *C. maculosa*–*Urophora* spp. and *C. maculosa*–*A. zoegana* examples suggests that specific indirect nontarget effects are highly unpredictable. It is extremely unlikely that one would anticipate at the outset of these introductions that gall flies would elevate the prevalence of hantavirus via subsidies to deer mouse populations or that *A. zoegana* would increase the negative effect of *C. maculosa* on *F. idahoensis*. In general, predicting specific indirect nontarget effects seems unlikely. However, understanding the process by which these interactions occur may allow us to more effectively guard against the types of pathways that can lead to these indirect nontarget effects.

Based on the theoretical and empirical evidence presented above, there are only two basic pathways currently recognized by which indirect nontarget effects can arise from host-specific biological control agents, and both are driven by the interaction between the biological control agent and the weed (Fig. 2). Better understanding of the components of this critical interaction may help improve our ability to avoid indirect nontarget effects while simultaneously increasing the success of biological control. Food-web interactions are one route to indirect nontarget effects of host-specific biological control agents that has been identified by both theoretical and empirical research (Fig. 2C). As illustrated by the *C. maculosa*–*Urophora* spp. case study, food-web subsidies depend on an interaction between the biological control agent and the weed that translates into an overall bottom-up effect (Pearson and Callaway, 2003). That is to say, the effect of the weed on the biological control agent is stronger than the effect of the biological control agent on the weed so that the overall outcome is an increase in the biological control agent instead of a decrease in the weed. This situation creates conditions ripe for subsidies to other food-web elements via generalist natural enemies that are capable of exploiting both the biological control agent and other organisms in the system because the overall interaction is bottom-up rather than top-down as intended. Equally important is the strength of this interaction. For example, in the *C. maculosa*–*Urophora* spp. case even though the direction of the interaction is bottom-up, if the interaction between *C. maculosa* and *Urophora* spp. were weak (i.e., *C. maculosa* only very weakly subsidized *Urophora* spp.) the indirect effects of gall flies would rapidly attenuate. Mice would eat gall flies, but gall flies would not be sufficiently abundant to subsidize mouse populations and indirect effects passing through mice to other species would be negligible.

The second route by which indirect nontarget effects can arise from host-specific biological control agents is through compensatory responses (Fig. 2B). This type of indirect nontarget effect has not yet been recognized by theoretical work in biological control, but is illustrated by the empirical example of *C. maculosa* and *A. zoegana*.

In this case, the direction of the interaction appears to be top-down as intended (Müller-Shärer, 1991), but the weed is able to compensate by displacing the negative impact of the biological control agent, thereby increasing the negative effects on the recipient organism. Interaction strength appears to be key here as well. Although *C. maculosa* seems able to displace the negative impacts of *A. zoegana* in the current scenario, if the impact of *A. zoegana* on *C. maculosa* could be increased, it seems likely that eventually *C. maculosa* would no longer be able to compensate and successful control would be achieved. In general, if the biological control agent is strong enough (e.g., it kills or nearly kills the plant outright), it is unlikely that the plant will be able to compensate for the attack.

Thus, disregarding issues of ecological replacement as policy problems, we currently recognize two pathways by which host-specific biological control agents can cause indirect impacts on nontarget species: (1) compensatory responses (Fig. 2B), which are top-down in nature and (2) food-web subsidies (Fig. 2C), which are bottom-up in nature. These examples indicate that the nature of the biological control–weed interaction (top-down versus bottom-up) and the strength of this interaction are both very important aspects determining the potential for indirect nontarget effects of host-specific biological control agents. This information is valuable for isolating the source of indirect nontarget effects arising from host-specific biological control agents to identify the species likely to be at risk, but how do we predict the potential degree of impacts expected?

Theoretical work suggests that indirect effects arising from biological control agents will be proportional to the agent's abundance (Holt and Hochberg, 2001). This means, indirect nontarget effects will be closely linked to the biological control agent's success. Unsuccessful biological control agents that are not effective at establishing or exploiting their host in the new environment will not become sufficiently abundant to threaten nontarget species. Highly successful biological control agents will over-exploit the target species with a resultant reduction in their own numbers and associated risks to nontarget species (Holt and Hochberg, 2001). In contrast, biological control agents of intermediate success, that effectively establish and exploit their host without greatly reducing its populations, are the agents most likely to reach high equilibrium densities in the introduced range and present the greatest risks to nontarget species (Holt and Hochberg, 2001). The implication here is that efficacy is the key to understanding and predicting indirect nontarget effects of host-specific biological control agents. Highly effective host specific biological control agents will present low risk to nontarget species. So long as the agents do not host-switch, they will reduce their own numbers through a density-dependent feedback as they reduce the target species. Even if the biological control

agent becomes superabundant in the initial process of establishment, which increases its potential indirect nontarget impacts, as long as the biological control agent is ultimately successful, these indirect nontarget effects should be ephemeral (exceptions could include extirpation of a nontarget species or other permanent impacts during the abundant phase). Classical biological control successes such as klamath weed in California, USA and prickly pear (*Opuntia* spp.) in Australia and elsewhere very effectively illustrate this phenomenon (DeBach et al., 1976; Huffaker and Kennett, 1959). Efficacy therefore is not only important for biocontrol success, it is also important for ensuring the safety of biological control.

5. Deliberate community assembly

The ultimate intent of biological control is deliberate community assembly (sensu Holt and Hochberg, 2001). Whenever we introduce biological control agents we do so with the intent of achieving a specific outcome in terms of community interactions. Although all multiple release strategies share this common goal, they differ in their routes to achieving it. Multiple release strategies represent a continuum in biological control that ranges from the lottery approach at one extreme to deliberate community assembly at the other, with the cumulative stress model and others somewhere in between (Harris, 1991; Myers, 1985; Sheppard, 2003). Strategies like the lottery and cumulative stress models rely on chance and the assumption that multiple host specific biological control agents will have additive or synergistic effects with regard to their overall impact on the weed. However, multiple agents are just as likely to increase the chances of antagonistic interactions like competition or intra-guild predation among biological control agents (e.g., Ehler and Hall, 1982; Story et al., 1991; Wang and Messing, 2003; Woodburn, 1996) that can undermine effective control while increasing risk to nontarget species. Deliberate community assembly requires an understanding of the ecology and biology of the weed as well as the biological control agent to select, and introduce the minimal number of agents while maximizing control. The importance of these understandings are being increasingly recognized in biological control (Briese, 2004; Hinz and Schwarzlaender, 2005; Sheppard, 2003), and recent studies in weed biological control have begun to show how knowledge of the relative sensitivities of a weed's life-cycle transitions can indicate which natural enemy attacks are most likely to be effective (McEvoy and Coombs, 1999, 2000; McEvoy et al., 1993). These studies have begun to pave the way toward deliberate community assembly as a minimalist multiple release strategy in biological control and recent biological control programs are increasingly moving in this direction (Blossey et al.,

1996; Briese and Zapater, 2002; Briese et al., 2002). Recent findings regarding nontarget effects in biological control (Pearson and Callaway, 2003) argue now more than ever for shifting multiple-release strategies away from lottery-style approaches toward more deliberate community assembly by minimizing agent numbers and reducing redundancy while attempting to maximize efficacy of a few select agents through greater knowledge of the weed and prospective biocontrol agents.

6. Host specificity versus efficacy

Given that host specificity and efficacy are both critical for safe and effective biological control, it is of interest to revisit the question of whether these two goals are biologically at odds with each other. Degree of host specificity is seen as an indication of highly coevolved relationship between natural enemy and host (Allee et al., 1949) and some have argued that this coevolved process undermines the efficacy of the natural enemy (Hokkanen and Pimentel, 1984; Pimentel, 1963). If this is true, evolution may tend to deny us the best ecological combination for biological control—those organisms that serve as both highly host specific and highly efficacious agents. Certainly the huge success of myxoma virus in controlling European rabbits illustrates just how effective new natural enemy–host associations can be (Moore, 1987). However, the risks associated with implementing biological control based on new natural enemy–host associations are deemed too great to accept given that this practice involves introducing natural enemies that are sufficiently generalist that they are willing to establish on new host species (Goeden and Kok, 1986). Moreover, older and more coevolved associations can also be very successful as noted for *Chrysolina* control of klamath weed (Huffaker and Kennett, 1959; Syrett et al., 2000). The question then arises, what conditions cause biological control agents derived from older coevolved associations to at times be so virulent? We need to better understand how and when mechanisms such as conditions in the new environment or escape from natural enemies by the biological control agent are likely to facilitate successful control (Colautti et al., 2004; Hinz and Schwarzlaender, 2005) if we are to use this understanding to engineer more predictable and successful biological control. In particular, better understanding of the potential tradeoffs between host specificity and efficacy is critical given the need for maximizing both of these factors for safe and effective biological control.

7. Efficacy testing

The notion of elevating efficacy standards for biological control introductions to the level of those standards

currently applied to host-specificity testing seems onerous indeed given the current costs, time, and effort required for host-specificity testing (Van Driesche and Bellows, 1996). However, recent theoretical work suggests that by turning this process around, time and costs, might actually be saved in the testing process over current approaches. McClay and Balciunas (2005) suggest that because efficacy testing can be much simpler than host specificity testing (it involves testing only one natural enemy–plant interaction per natural enemy instead of many), it can actually function as a fast, effective method for reducing the list of control agents being tested for introduction. Even if such a method is only crudely applied, it could provide a more objective means of prescreening for efficacy before host-specificity testing that could be systematically applied and formally evaluated. Under a deliberate community assembly approach, agents that test poorly for efficacy simply would not get evaluated further because they are rejected for release. Evaluating weed life-cycle transitions (McEvoy and Coombs, 1999; McEvoy et al., 1993) can also reduce the list of species that need to be tested for host specificity by screening out organisms unlikely to effect control over the weed. For example, seedhead flies may be inappropriate for species that are not seed limited (Myers and Risley, 2000; Stanley, 2005). Although, efficacy tests in the laboratory and in the field in the native range will never provide a fail-safe predictor for the outcomes of complex community interactions in the new environment, using efficacy testing to drive biological control agent selection is consistent with a deliberate community assembly approach to biological control that focuses on fewer more efficacious control agents that will reduce risk to nontarget species and increase chances for successful biological control.

8. Defining success

The conclusion that indirect nontarget effects arising from host-specific biological control agents are linked to biocontrol success has important ramifications for how successful control is defined. From a theoretical perspective, successful biological control is defined based on a threshold of economic or ecological impact and therefore is dichotomous (Van den Bosch and Messenger, 1973). However, in practice, the definition of successful biological control has evolved into a rather continuous concept including different degrees of partial control being variously identified as success (Gurr and Wratten, 2000; McFadyen, 1998). This has resulted in a general lack of agreement on a common definition of successful control that has contributed to the widely divergent estimates of biological control success seen in the literature (e.g., DeLoach, 1991; McFadyen, 1998; Williamson, 1996). However, as pointed out by McEvoy

(1996) and Syrett et al. (2000), it is important to appropriately assess costs when evaluating biocontrol success. If one considers that a partially successful control agent that provides marginal financial or ecological returns from a minor reduction in weed populations may simultaneously have disproportionately strong impacts and costs associated with its nontarget effects, then the notion of partial success must be reevaluated in this context. If moderately successful agents hold the greatest potential risk to indirect nontarget species (Holt and Hochberg, 2001), this understanding must be incorporated in the evaluation of success to develop more objective standards for quantifying biological control success.

9. Future directions

Additional work is needed to advance our understandings of how weed and natural enemy biology and ecology determine not only biological control success, but also community-level outcomes of biological control introductions so that we can begin to more predictably engineer community outcomes resulting from these introductions (e.g., McEvoy and Coombs, 1999; McEvoy et al., 1993). For example, little is known about compensatory responses of weeds or invertebrate pests to biological control agents. More work is needed in the realm of efficacy testing and evaluation of sensitivities of weed life-cycle transitions to determine to what extent such information can serve to better filter out weak agents that offer little chance for successful control (McClay and Balciunas, 2005). Biological control agents as a whole should be evaluated with regard to efficacy versus potential indirect nontarget risks to determine if certain biological control groups or strategies that have low efficacy also have high potential risks for indirect nontarget effects. If certain categories of biological control agents have low efficacy, high potential risks, or both, these groups should be considered for exclusion from future biological control programs. Finally, we need to expand on our understanding of potential tradeoffs between host specificity and efficacy if we are to determine how to best maximize both of these factors in the agents we choose.

10. Conclusions

The fact that host-specific biological control agents can deleteriously impact nontarget species has profound implications for biological control and multiple release strategies like the lottery approach. The lottery approach has been challenged on the grounds that (1) it is risky to introduce more biological control agents than are

necessary to achieve effective control and (2) multiple biological control agents can just as well negatively affect the outcome of biological control as result in additive or synergistic interactions as intended (McEvoy and Coombs, 2000; Myers, 1985; Myers et al., 1989; Pearson and Callaway, 2003; Strong and Pemberton, 2000). Until now, the assumption that host-specific biological control agents are safe has helped to sustain multiple release approaches like the lottery approach despite these attacks. However, recognition of the fact that serious indirect nontarget effects can arise from even the most host-specific biological control agents changes the rules of the game. Host specificity is necessary, but it is not a sufficient criterion for the safe release of biological control agents. The relationship between biocontrol efficacy and risk to nontarget species suggests that efficacy of biological control agents may be as important as host specificity for safe and effective biological control. To address the problem of indirect nontarget effects of host-specific biological control, multiple release strategies will need to shift further toward a deliberate community assembly approach that minimizes numbers of agents and agent redundancy, while maximizing efficacy through better knowledge of biocontrol agent and weed interactions.

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References

- Allee, W.C., Emerson, A.E., Park, O., Park, T., Schmidt, K.P., 1949. Principles of Animal Ecology. W.B. Saunders, Philadelphia.
- Blossey, B., Malecki, R.A., Schroeder, D., Skinner, L., 1996. A biological weed control program using insects against purple loosestrife (*Lythrum salicaria*) in North America. In: Moran, V.C., Hoffmann, J.H. (Eds.), Proceedings of the IX International Symposium on Biological Control of Weeds. University of Cape Town, South Africa, pp. 351–356.
- Briese, D.T., 2004. Weed biological control: applying the science to solve seemingly intractable problems. *Aust. J. Entomol.* 43, 304–317.
- Briese, D.T., 2003. The centrifugal phylogenetic method used to select plants for host-specificity testing of weed biological control agents: can and should it be modernized? In: Spafford-Jacob, H.S., Briese, D.T. (Eds.), Improving the Selection, Testing and Evaluation of Weed Biological Control Agents. CRC for Australian Weed Management, Tech. Ser. 7, pp. 23–34.
- Briese, D.T., Zapater, M., 2002. A strategy for the biological control of blue heliotrope (*Heliotropium amplexicaule*). In: Spafford Jacob, H., Dodd, J., Moore, J.H. (Eds.), Proceedings of the 13th Australian Weeds Conference. Plant Protection Society of WA, Perth, pp. 394–397.
- Briese, D.T., Petit, W., Swirepik, A., Walker, A., 2002. A strategy for the biological control of *Onopordum* spp. Thistles in south-eastern Australia. *Biocontrol Sci. Tech.* 12, 121–137.
- Callaway, R.M., DeLuca, T.H., Belliveau, W.M., 1999. Biological-control herbivores increase competitive ability of *Centaurea maculosa*. *Ecology* 80, 1196–1201.
- Callaway, R.M., Newingham, B., Zabinski, C.A., Mahall, B.E., 2001. Compensatory growth and competitive ability of and invasive weed are enhanced by soil fungi and native neighbors. *Ecol. Lett.* 4, 1–5.
- Childs, J.E., Ksiazek, T.G., Spiropoulou, C.F., Krebs, J.W., Morzunov, S., Maupin, G.O., Gage, K.L., Sarinsky, J., Ensore, R., Frey, J., Peters, C.J., Nichol, T.S., 1994. Serologic and genetic identification of *Peromyscus maniculatus* as the primary rodent reservoir for a new hantavirus in the southwestern United States. *J. Infect. Dis.* 169, 1271–1280.
- Colautti, R.I., Ricciardi, A., Grigorovich, I.A., MacIsaac, H.J., 2004. Is invasion success explained by the enemy release hypothesis. *Ecol. Lett.* 7, 721–733.
- Crawley, M.J., 1989. Insect herbivores and plant population dynamics. *Annu. Rev. Entomol.* 34, 531–564.
- Crawley, M.J., 1997. Plant Ecology. Blackwell Scientific, London.
- DeBach, P., Huffaker, C.B., McPhee, A.W., 1976. Evaluation of the impact of natural enemies. In: Huffaker, C.B., Messenger, P.S. (Eds.), Theory and Practice of Biological Control. Academic Press, New York, pp. 255–285.
- DeLoach, C.J., 1991. Past successes and current prospects in biological control of weeds in the United States and Canada. *Nat. Areas J.* 11, 129–142.
- DeLoach, C.J., Caruthers, R.I., Lovich, J.E., Dudley, T.L., Smith, S.D., 2000. Ecological interactions in the biological control of saltcedar (*Tamarix* spp.) in the United States: toward a new understanding. In: Spencer, N.R. (Ed.), Proceedings of the X International Symposium on Biological Control of Weeds, July 4–14, 1999. Montana State University, Bozeman, pp. 819–873.
- Denoth, M., Frid, L., Myers, J.H., 2002. Multiple agents in biological control: improving the odds? *Biol. Control* 24, 20–30.
- Ehler, L.E., Hall, R.W., 1982. Evidence for competitive exclusion of introduced natural enemies in biological control. *Environ. Entomol.* 11, 1–4.
- Follett, P.A., Duan, J.J., 2000. Nontarget Effects of Biological Control. Kluwer Academic Publishers, Boston, MA.
- Forno, I.W., Julien, M.H., 2000. Success in biological control of aquatic weeds by arthropods. In: Gurr, G., Wratten, S. (Eds.), Biological Control: Measures of success. Kluwer Academic Publishers, Boston, MA, pp. 159–188.
- Frank, J.H., 1998. How risky is biological control? *Comment. Ecol.* 79, 1829–1834.
- Gerlach Jr., J.D., Rice, K.J., 2003. Testing life history correlates of invasiveness using congeneric plant species. *Ecol. Appl.* 13, 167–179.
- Goeden, R.D., Kok, L.T., 1986. Comments on a proposed “new” approach for selecting agents for the biological control of weeds. *Can. Entomol.* 118, 51–58.
- Goeden, R.D., Louda, S.M., 1976. Biotic interference with insects imported for weed control. *Annu. Rev. Entomol.* 21, 325–342.
- Gurr, G., Wratten, S., 2000. Biological Control: Measures of success. Kluwer Academic Publishers, Boston, MA.
- Hamilton III, E.W., Frank, D.A., 2001. Can plants stimulate soil microbes and their own nutrient supply? *Ecology* 82, 2397–2402.
- Hajek, A.E., 2004. Natural Enemies: An Introduction to Biological Control. Cambridge University Press, Cambridge, UK.
- Harris, P., 1980. Effects of *Urophora affinis* Frfld. and *U. quadrifasciata* (Meig.) (Diptera: Tephritidae) on *Centaurea diffusa* Lam. and *C. maculosa* Lam. (Compositae). *Z. Angew. Entomol.* 90, 190–210.
- Harris, P., 1990. Environmental impact of introduced biological control agents. In: Mackauer, J., Ehler, L.E., Roland, J. (Eds.), Critical Issues in Biological Control, Intercept. Andover, Hants, UK, pp. 289–300.

- Harris, P., 1991. Invitation paper (C.P. Alexander fund): classical bio-control of weeds: its definition, selection of effective agents, and administrative-political problems. *Can. Entomol.* 123, 827–849.
- Hinz, H., Schwarzlaender, M., 2005. Comparing invasive plants from their native and exotic range: what we can learn for biological control? *Weed Technol.* 18, 1533–1541.
- Hokkanen, H., Pimentel, D., 1984. New approach for selecting biological control agents. *Can. Entomol.* 116, 1109–1121.
- Hoddle, M.S., 2004a. Restoring balance: using exotic species to control invasive exotic species. *Conserv. Biol.* 18, 38–49.
- Hoddle, M.S., 2004b. The strength of biological control in the battle against invasive pests: a reply. *Conserv. Biol.* 18, 38–49.
- Holt, R.D., 1977. Predation, apparent competition, and the structure of prey communities. *Theor. Pop. Biol.* 12, 197–229.
- Holt, R.D., Hochberg, M.E., 2001. Indirect interactions, community modules and biological control: a theoretical perspective. In: Wajnberg, E., Scott, J.K., Quimby, P.C. (Eds.), *Evaluating Indirect Effects of Biological Control*. CABI Publishing, Wallingford, UK, pp. 13–38.
- Howarth, F.G., 1991. Environmental impacts of classical biological control. *Annu. Rev. Entomol.* 36, 485–509.
- Huffaker, C.B., Kennett, C.E., 1959. A ten-year study of vegetational changes associated with biological control of Klamath weed. *J. Range Manage.* 12, 69–82.
- Islam, Z., Crawley, M.J., 1983. Compensation and regrowth in ragwort (*Senecio jacobaea*) attacked by cinnabar moth (*Tyria jacobaeae*). *J. Ecol.* 71, 829–843.
- Julien, M.H., Griffiths, M.W., 1998. *Biological Control of Weeds: A World Catalogue of Agents and their Target Weeds*. CABI Publishing, Wallingford, UK.
- Julien, M.H., Bourne, A.S., Chan, R.R., 1987. Effects of adult and larval *Cyrtobagous salviniae* on the floating weed *Salvinia molesta*. *J. Appl. Ecol.* 24, 935–944.
- Katovich, E.J.S., Becker, R.L., Ragsdale, D.W., 1999. Effect of *Galerucella* spp. on survival of purple loosestrife (*Lythrum salicaria*) roots and crowns. *Weed Sci.* 47, 360–365.
- Keane, R.M., Crawley, M.J., 2002. Exotic plant invasions and the enemy release hypothesis. *Trends Ecol. Evol.* 4, 164–170.
- Kluge, R.L., 1990. Prospects for the biological control of trifid weed, *Chromolaena odorata*, in South Africa. *S. Afr. J. Sci.* 86, 229–230.
- Lang, R.F., Richard, R.D., Parker, P.E., Wendel, L., 2000. Release and establishment of diffuse and spotted knapweed biocontrol agents by USDA, APHIS, PPQ, in the United States. *Pan-Pac. Entomol.* 76, 197–218.
- Landis, D.A., Sebolt, D.C., Haas, M.J., Klepinger, M., 2003. Establishment and impact of *Galerucella californiensis* L. (Coleoptera: Chrysomelidae) on *Lythrum salicaria* L. and associated plant communities in Michigan. *Biol. Control* 28, 78–91.
- Louda, S.M., Arnett, A.E., Rand, T.A., Russell, F.L., 2003. Invasiveness of some biological control insects and adequacy of their ecological risk assessment and regulation. *Conserv. Biol.* 17, 73–82.
- Louda, S.M., Kendall, D., Connor, J., Simberloff, D., 1997. Ecological effects of an insect introduced for the biological control of weeds. *Science* 277, 1088–1090.
- Louda, S.M., Stiling, P., 2004. The double-edged sword of biological control in conservation and restoration. *Conserv. Biol.* 18, 50–53.
- Maddox, D.M., 1982. Biological control of diffuse knapweed (*Centaurea diffusa*) and spotted knapweed (*Centaurea maculosa*). *Weed Sci.* 30, 76–82.
- McClay, A., Balciunas, J.K., 2005. The role of pre-release efficacy assessment in selecting classical biological control agents for weeds—applying the Anna Karenina principle. *Biol. Control* 35, 197–207.
- McEvoy, P.B., 1996. Host specificity and biological pest control. *BioScience* 46, 401–405.
- McEvoy, P.B., Coombs, E.M., 1999. Biological control of plant invaders: regional patterns, field experiments, and structured population models. *Ecol. Appl.* 9, 387–401.
- McEvoy, P.B., Coombs, E.M., 2000. Why things bite back: unintended consequences of biological weed control. In: Follett, P.A., Duan, J.J. (Eds.), *Nontarget Effects of Biological Control*. Kluwer Academic Publishers, Boston, MA, pp. 167–194.
- McEvoy, P.B., Rudd, N.T., Cox, C.S., Huso, M., 1993. Disturbance, competition, and herbivory effects on ragwort *Senecio jacobaea* populations. *Ecol. Monogr.* 63, 55–75.
- McFadyen, R.E., 1998. Biological control of weeds. *Annu. Rev. Entomol.* 43, 369–393.
- McFadyen, R.E., 2003. Does ecology help in the selection of biocontrol agents? In: Spafford-Jacob, H.S., Briesse, D.T. (Eds.), *Improving the Selection, Testing and Evaluation of Weed Biological Control Agents*. CRC for Australian Weed Management, Tech. Ser. 7, pp. 5–10.
- Moore, N.W., 1987. *The Bird of Time*. Cambridge University Press, Cambridge, UK.
- Müller, H., 1989. Growth pattern of diploid and tetraploid spotted knapweed, *Centaurea maculosa* Lam. (Compositae) and effects of the root mining moth *Agapeta zoegana* (L.) (Lepidoptera: Cochyliidae). *Weed Res.* 29, 103–111.
- Müller-Shärer, H., 1991. The impact of root herbivory as a function of plant density and competition, survival, growth, and fecundity of *Centaurea maculosa* in field plots. *J. Appl. Ecol.* 28, 759–776.
- Müller-Shärer, H., Schroeder, D., 1993. The biological control of *Centaurea* spp. in North America: do insects solve the problem? *Pestic. Sci.* 37, 343–353.
- Müller, H., Goeden, R.D., 1990. Parasitoids acquired by *Coleophora parthenica* (Lepidoptera: Coleophoridae) ten years after its introduction into southern California for the biological control of Russian thistle. *Entomophaga* 35, 257–268.
- Myers, J.H., 1985. How many insects are necessary for successful biological control of weeds. In: Delfosse, E.S. (Ed.), *Proceedings of the VI International Symposium on Biological Control of Weeds*, August 19–25, 1984. Vancouver, BC, Agriculture Canada, Ottawa, pp. 77–82.
- Myers, J.H., Higgins, C., Kovacs, E., 1989. How many insect species are necessary for biological control of insects? *Environ. Entomol.* 18, 541–547.
- Myers, J.H., Risley, C., 2000. Why reduced seed production is not necessarily translated into successful weed biological control. In: Spencer, N.R. (Ed.), *Proceedings of the X International Symposium on Biological Control of Weeds*. Montana State University, Bozeman, pp. 569–581.
- Nuessly, G.S., Goeden, R.D., 1984. Rodent predation on larvae of *Coleophora parthenica* (Lepidoptera: Coleophoridae), a moth imported for the biological control of Russian thistle. *Environ. Entomol.* 13, 502–508.
- Ortega, Y.K., Pearson, D.E., McKelvey, K.S., 2004. Effects of exotic plant invasion and introduced biological control agents on native deer mouse populations. *Ecol. Appl.* 14, 241–253.
- Pearson, D.E., Callaway, R.M., 2003. Indirect effects of host-specific biological control agents. *Trends Ecol. Evol.* 18, 456–461.
- Pearson, D.E., McKelvey, K.S., Ruggiero, L.F., 2000. Non-target effects of an introduced biological control agent on deer mouse ecology. *Oecologia* 122, 121–128.
- Pemberton, R.W., 2000. Predictable risk to native plants in weed biological control. *Oecologia* 125, 489–494.
- Pimentel, D., 1963. Introducing parasites and predators to control native pests. *Can. Entomol.* 95, 785–792.
- Pratt, P.D., Coombs, E.M., Croft, B.A., 2003. Predation by phytoseiid mites on *Tetranychus linearis* (Acari: Tetranychidae), an established weed biological control agent of gorse (*Ulex europaeus*). *Biol. Control* 26, 40–47.

- Ramsell, J., Malloch, A.J.C., Whittaker, J.B., 1993. When grazed by *Tipula paludosa*, *Lolium perenne* is a stronger competitor of *Rumex obtusifolius*. *J. Ecol.* 81, 777–786.
- Reimer, N.J., 1988. Predation on *Liothrips urichi* Karny (Thysanoptera: Phlaeothripidae): a case of biotic interference. *Environ. Entomol.* 17, 132–134.
- Ridenour, W.M., Callaway, R.M., 2003. Root herbivores, pathogenic fungi, and competition between *Centaurea maculosa* and *Festuca idahoensis*. *Plant Ecol.* 169, 161–170.
- Sebolt, D.C., Landis, D.A., 2004. Arthropod predators of *Galerucella californiensis* L. (Coleoptera: Chrysomelidae): an assessment of biotic interference. *Environ. Entomol.* 33, 356–361.
- Sheppard, A.W., 2003. Prioritizing agents based on predicted efficacy: beyond the lottery approach. In: Spafford-Jacob, H.S., Briese, D.T. (Eds.), *Improving the Selection, Testing and Evaluation of Weed Biological Control Agents*. CRC for Australian Weed Management, Tech. Ser. 7, pp. 11–22.
- Siemens, D., Garner, S., Mitchell-Olds, T., Callaway, R.M., 2002. The cost of defense in the context of competition. *Brassica rapa* may grow and defend. *Ecology* 83, 505–517.
- Simberloff, D., Stiling, P., 1996. How risky is biological control? *Ecology* 7, 1965–1974.
- Sogge, M.K., 2000. Breeding season ecology. In: Finch, D.M., Stoleson, S.H. (Eds.) *Status, Ecology, and Conservation of the Southwestern Willow Flycatcher*. United States Department of Agriculture, Forest Service, Rocky Mountain Research Station, General Technical Report RMRS-GTR-60, pp. 57–70.
- Stanley, A.G., 2005. Evaluating the effectiveness of biological control: spotted knapweed, seed head gallflies, predacious mice, and environmental variation. Ph.D. Dissertation, University of Washington, Seattle, WA.
- Steinger, T., Müller-Shärer, H., 1992. Physiological and growth responses of *Centaurea maculosa* (Asteraceae) to root herbivory under varying levels of interspecific competition and soil nitrogen availability. *Oecologia* 91, 141–149.
- Story, J.M., Boggs, K.W., Good, W.R., Harris, P., Nowierski, R.M., 1991. *Metzneria paucipunctella* Zeller (Lepidoptera: Gelechiidae) a moth introduced against spotted knapweed its feeding strategy and impact on two introduced *Urophora* spp. (Diptera: Tephritidae). *Can. Entomol.* 123, 1001–1008.
- Story, J.M., Boggs, K.W., Good, W.R., White, L.J., Nowierski, R.M., 1995. Cause and extent of predation on *Urophora* spp. larvae (Diptera: Tephritidae) in spotted knapweed capitula. *Environ. Entomol.* 24, 1467–1472.
- Strong, D.R., Pemberton, R.W., 2000. Biological control of invading species-risk and reform. *Science* 288, 1969–1970.
- Syrett, P., Briese, D.T., Hoffmann, J.H., 2000. Success in biological control of terrestrial weeds by arthropods. In: Gurr, G., Wratten, S. (Eds.), *Biological Control: Measures of Success*. Kluwer Academic Publishers, Boston, MA, pp. 189–230.
- Trumble, J.T., Kolodny-Hirsch, D.M., Ting, I.P., 1993. Plant compensation for herbivory. *Annu. Rev. Ent.* 38, 93–119.
- Van den Bosch, R., Messenger, P.S., 1973. *Biological Control*. Intext Educational Publishers, New York, NY.
- Van Driesche, R.G., Bellows Jr., T.S., 1996. *Biological Control*. Chapman & Hall, New York, NY.
- Wang, X., Messing, R.H., 2003. Intra- and interspecific competition by *Fopius arisanus* and *Diachasmimorpha tryoni* (Hymenoptera: Braconidae), parasitoids of tephritid fruit flies. *Biol. Control* 27, 251–259.
- Wapshere, A.J., 1974. A strategy for evaluating the safety of organisms for biological weed control. *Ann. Appl. Biol.* 77, 201–211.
- Wajnberg, E., Scott, J.K., Quimby, P.C., 2001. *Evaluating Indirect Effects of Biological Control*. CABI Publishing, Wallingford, UK.
- Williamson, M., 1996. *Biological Invasions*. Chapman & Hall, New York.
- Woodburn, T.L., 1996. Interspecific competition between *Rhinocyllus conicus* and *Urophora solstitialis*, two biocontrol agents released in Australia against *Carduus nutans*. In: Moran, V.C., Hoffmann, J.H. (Eds.), *Proceedings of the IX International Symposium on Biological Control of Weeds*. University of Capetown, South Africa, pp. 409–415.