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Successes We May Not Have Had: A Retrospective Analysis of Selected Weed Biological Control Agents in the United States

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In this paper, we describe five successful classical biological weed control agents released in the United States. For each of the five arthropod species, we compared data from prerelease studies that experimentally predicted the agent's host range with data collected postrelease. In general, experimental host range data accurately predicted or overestimated risks to nontarget plants. We compare the five cases with insects recently denied for introduction in the United States and conclude that none of the discussed agents would likely be approved if they were petitioned today. Three agents would be rejected because they potentially could attack economic plants, and two because of potential attack on threatened or endangered plants. All five biocontrol agents have contributed significantly to the successful management of major weeds with no or minimal environmental risk. We believe that the United States may miss opportunities for sustainable and environmentally benign management of weeds using biological control if the regulatory framework only considers the *risks* of agents as potential plant pests and treats any host-range data regarding economic or threatened and endangered species as a binary decision (i.e., mandates rejection if there is any chance of feeding or development). As a way forward we propose the following: (1) the addition of risk and benefit analyses at the habitat level with a clear ranking of decision-making criteria as part of the U.S. Department of Agriculture Animal and Plant Health Inspection Service Technical Advisory Group's evaluation process of biocontrol agents; (2) recognition of the primacy of realized host range data for potential agents that considers the insect's host selection behavior instead of emphasizing fundamental host range data during release evaluations, and (3) development of formalized postrelease monitoring of target and nontarget species as part of the release permit. These recommendations may initially be advanced through reassessment of current policies but may in the longer term require the implementation of dedicated biocontrol legislation.

Key words: Biological control of weeds, host range, non-target attack, risk assessment, introduction policy.

Prerelease testing of classical weed biological control agents aims to quantify risks to nontarget species and assess the benefits (damage inflicted on the target weed by an agent) of introducing the biocontrol agent to a new environment. Host-range testing includes delimiting both the fundamental and the realized host ranges of herbivorous arthropods. The fundamental host range comprises all plant species on which the organism can complete its life cycle, whereas the realized host range comprises those plant species the organism actually uses under natural field conditions (Schaffner 2001). The fundamental host range is determined using no-choice tests in which a herbivore is exposed to one plant species at a time, usually under confined laboratory or common garden conditions without being able to exhibit its normal host-selection behavior. In contrast, the realized host range is determined with choice tests under field cage or natural field conditions, in which herbivores are able to choose from among the target weed and other possible host plants. Multiple case studies demonstrate that a herbivore's realized host range under field conditions is always narrower than its fundamental host range (e.g., Blossey et al. 2001; Center et al. 2007; Cristofaro et al. 2013; Dudley and Kazmer 2005;

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McFadyen et al. 2002; Medal and Cuda 2010; Paynter et al. 2004; Pratt et al. 2009; see additional examples in Wapshere 1989). To our knowledge, there is not a single case using appropriate host-range testing protocols where the opposite result has been demonstrated.

Recently, decisions about releases made by the U.S. Department of Agriculture Animal Plant Health Inspection Service (USDA APHIS, the regulatory agency responsible for biological control introductions) have been weighted more on the fundamental host range of a potential agent and seemingly ignore the realized host range. This conservative approach is a safe one, because there are no known examples of agents that attack plants outside their fundamental host range (Paynter et al. 2004, Pemberton 2000, van Klinken and Edwards 2002). However, here we argue that implementing it as the sole criterion for release decisions significantly overestimates potential risks associated with the release of candidate agents. Doing so limits the number of agents available for release, and consequently reduces the prospects for successful control (van Wilgen et al. 2013).

To present our arguments, it is first important to understand the biology of host use under no-choice and choice conditions. A plant species might be able to support development of a potential agent under no-choice conditions but not be attacked in the field for several reasons. These include but are not limited to the following: life-history traits or the host selection behavior of the agent that typically act as filters (e.g., visual or olfactory host location and identification cues that are bypassed under confined conditions), the availability of preferred host plants (i.e., the target weed or weeds), the ability of the agent to disperse and forage for preferred host plants, and a low probability for the agent to encounter nontarget plant species. Low encounter rates may result from asynchronies of phenologies of the nontarget plant and the biological control agent or little or no overlap between geographic distributions or habitat requirements of nontarget plant species and the biological control agent, or a combination of both (Briese 2004; Schaffner 2001; van Klinken and Edwards 2002; Wapshere 1989). The fundamental host range of an agent is a genotypic trait that can relatively easily be determined experimentally, whereas the realized host range is how the fundamental host range is expressed within a particular environment and is therefore influenced by specific environmental conditions, such as the relative availability of hosts (Louda et al. 2005b; Sheppard et al. 2005; van Klinken and Edwards 2002).

A recent case highlights the importance of considering the biological differences between fundamental and realized host ranges. The weevil *Ceratapion basicorne* (Illiger) was petitioned for release to control *Centaurea solstitialis* L., yellow starthistle. It was recommended for release by the Technical Advisory Group (TAG), an expert committee representing federal agencies in the United States, other organizations, and the countries of Mexico and Canada, that advises USDA APHIS, but the insect was not approved for release. The reason given for the negative decision by USDA APHIS was that "… this insect may negatively impact a United States crop plant (safflower)" and was likely based on data showing that under no-choice conditions, the weevil's fundamental host range included safflower (*Carthamus tinctorius* L.) (Smith 2007), a crop plant grown for oil production. However, in tests examining the realized host range of the weevil, safflower was not attacked during five open-field experiments (three included in the petition and two conducted subsequently (Cristofaro et al. 2013; Rector et al. 2010; Smith et al. 2006). In addition, *C. basicorne* has never been reported from safflower in their shared native Eurasian range (Cristofaro et al. 2013). It is unclear whether or how realized host-range data for the weevil were considered in the decision process or whether these data were weighed against the fundamental host range data (L. Smith, personal communication). The decision to deny the release of *C. basicorne* was unexpected, since the guidelines in the TAG reviewer manual explicitly emphasize consideration of realized host range data (USDA 2000, p 4-3-5). In contrast, the decision appears more reflective of a zero-tolerance standard in respect to *any* potential utilization by a candidate agent on agriculturally or economically used plant species under no-choice laboratory conditions. This case exemplifies the uncertainty that exists among biocontrol scientists regarding the definition and quantification of risks associated with biocontrol introductions that are applied during the regulatory decision process. To our knowledge, there are currently no guidelines for risk assessments, though these would be important if the petitioner is to define additional research in order to address concerns raised by regulatory authorities during the introduction process.

Here, we argue that focusing solely on the fundamental host range of potential agents, though safe, will reduce the benefits of biological control as a management option for invasive plant control. We first present an overview of the regulatory process in the United States. Then, to support our argument, we present five case studies of successful arthropod biological control agents of herbaceous weeds in rangeland, wetlands, and cropping systems in North America that likely would not be permitted for release today based solely on their fundamental host range. Our selection criteria were that (1) the released agent is, at least locally, successfully controlling the target weed and (2) after a review of host-range testing and field data, we believe that the agent would not be permitted for release if petitioned today although it can be considered environmentally safe. This paper does not attempt to review all existing cases that may fit the above criteria, but instead uses the selected case studies to discuss criteria applied during the permitting process of classical weed biocontrol agents in the United States. For each of the selected cases, we address the question of whether the agent caused any predicted or unpredicted nontarget attack on other plant species by comparing results of prerelease studies (predicted host range) with postrelease studies (realized host range) using all available data. We then try to provide rationales outlining why we believe that the agents would not be released if petitioned today. The cases are described from oldest to most recent release date of respective agents. We summarize commonalities of the case studies, discuss changes in safety standards and risk perception and provide recommendations that would assure environmental safety standards of the regulatory process for biological control agent introductions in the United States while at the same time ensuring classical biological weed control as a viable management strategy for invasive plants.

Overview of the Current Regulatory Process for the Introduction of Weed Biological Control Agents in the United States

The federal agency responsible for coordinating the assessment of petitions for permits to import and release nonnative herbivores as biological control agents of noxious weeds, and subsequently issuing those permits, is USDA APHIS, operating under the regulatory authority contained in the Endangered Species Act of 1973 (16 U.S.C. 1531 et. seq.), National Environmental Policy Act of 1970 (42 U.S.C. 4321 et seq.), Plant Protection Act of 2000 (7 U.S.C 7701 et. seq.), Coastal Zone Management Act of 1972 (16 U.S.C. 1451 et. seq.), and Executive Order 13112 (64 CFR 6184) for Invasive Species of 1999. In the United States, all movement, including the importation and release into the environment of biological control organisms of noxious weeds, is regulated by the Plant Protection Act, which also provides the Secretary of Agriculture with the authority to regulate "any enemy, antagonist, or competitor used to control a plant pest or noxious weed."

Procedures outlined in the National Environmental Policy Act need to be followed primarily because issuing a permit allowing for the introduction and release of a biological control agent constitutes an action by a federal agency (USDA APHIS) that has the potential to negatively impact the human environment. In addition, the Endangered Species Act applies to weed biological control agent introductions because it is possible that the introduction of a nonindigenous plant herbivore could potentially pose a risk or have direct or indirect adverse effects on federally listed threatened or endangered species or habitats (16 U.S.C. 1531 et. seq.). The U.S. Department of Interior's Fish and Wildlife Service (USFWS) is charged with the protection of threatened and endangered species from *any* potential adverse effects and thus it has the authority to oppose the introduction of a weed biological control agent if there are reasons for concern.

Researchers develop and submit petitions for permits to release biological control agents of exotic weeds. USDA APHIS provides guidance on petition format to ensure that all required information is included and meets minimum quality standards (USDA 2000). The petition summarizes target weed and agent biology, agent host range, and the expected impact of the agent on the target weed and identifies any potential adverse effects to the environment that could arise as a result of the proposed release. The petition is submitted to the TAG for Biological Control Agents of Weeds, a committee convened by USDA APHIS with representatives appointed to represent the interests of 17 cooperating agencies, countries, and organizations, including most U.S. federal agencies involved in land management (Cofrancesco and Shearer 2004). The members of the TAG, who may also be biocontrol practitioners, review petitions themselves and can also exercise the option of seeking further input from intra-agency subject experts. Reviews are then discussed and summarized by the chair of the TAG and a recommendation for or against the release of the agent is forwarded to USDA APHIS. USDA APHIS considers the recommendation from the TAG during its decision-making process, although the agency has no obligation to do so. If the TAG recommends the release of the agent, the next stage is mandatory consultations with tribal nations and the USFWS (outlined under Section 7 of the Endangered Species Act). If USDA APHIS has cause to believe that issuing a permit that will allow for the importation and subsequent environmental release of an agent poses a risk to U.S. agricultural interests (according to the Plant Protection Act), or to federally listed threatened or endangered species (according to the Endangered Species Act), then the agency is legally obliged to decline approval of the permit. If the petition fails to garner support during mandatory tribal or USFWS consultations, the review process will typically be aborted. For petitions receiving support of the TAG, USDA APHIS, tribal nations, and the USFWS, USDA APHIS will provide an Environmental Assessment (EA) as is required by the National Environmental Policy Act. If the agency concludes that nationally there is a finding of no significant impact to the environment, a permit applying to all 48 mainland states will be issued to legally allow for the release of the agent.

Case Studies

Hypericum perforatum **(L.), St. Johnswort.** St. Johnswort is a perennial herb of Eurasian origin introduced to Australasia and North America, where it developed into a major weed in prairie ecosystems, rangelands, cropping

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systems, and open forests (Jensen et al. 2002; Piper 2004). Between 1945 and 1979, seven insect biological control agents were released for the control of St. Johnswort in North America (Julien and Griffiths 1998). The leaf beetle *Chrysolina quadrigemina* Suffrian was introduced in 1945. Both adults and larvae feed externally on the leaves and can defoliate plants (Piper 2004). The beetle proved to be the most important single agent that contributed to the successful control of St. Johnswort. In California alone, infestations of more than 800,000 ha (2 million acres) were reduced to less than 1% of that area (Huffaker 1967; Huffaker and Kennett 1959), accruing more than $20 million in savings for the agricultural industry between 1953 and 1959 (DeBach and Rosen 1991). In most arid regions in south-central British Columbia, *C. quadrigemina* reduced the weed to less than 2% of the prerelease levels, and it was effective in reducing the weed to negligible levels at release sites in southern Ontario (Jensen et al. 2002).

Prerelease host-specificity tests for *C. quadrigemina* concentrated mostly on screening economic plant species in distantly related families (Currie and Garthside 1932; Holloway 1948). However, before introduction into Canada in 1952, additional tests were conducted with seven species in the genus *Hypericum*: five natives and two introduced ornamentals (Smith 1958). Feeding occurred on all *Hypericum* species, and *C. quadrigemina* was able to complete its life cycle on two of the natives (*Hypericum frondosum* Michx. and *Hypericum moserianum* Luquet ex André) and on the introduced ornamental *Hypericum calycinum* L. used extensively in landscaping (Smith 1958). It therefore came as no surprise when, in the 1970s, the beetle was found attacking *H. calycinum* and the native North American *Hypericum concinnum* Benth. in several counties in California (Andres 1985).

In subsequent postrelease studies with *H. calycinum*, *H. concinnum*, and two additional native North American species, *Hypericum anagalloides* Cham. & Schlecht and *Hypericum scouleri* Hook. subsp. *scouleri* [= *Hypericum formosum* Kunth var. scouleri (Hook.)], beetles were able to complete development on all four nontargets in no-choice laboratory tests; *H. concinnum* and *H. scouleri* supported similar adult emergence rates as *H. perforatum* (Andres 1985). An impact experiment also showed that larval feeding by *C. quadrigemina* can reduce plant size of *H. concinnum.* And finally, two of the native *Hypericum* species (*H. concinnum* and *H. anagalloides*) and to a lesser extent, *H. calycinum*, were accepted for oviposition in an open-field test (Andres 1985).

However, *C. quadrigemina* has not been reported attacking *H. anagalloides* and *H. scouleri* in the field, which might be due to different habitat preferences of these two natives and the target weed *H. perforatum* (Andres 1985). Despite reports of nontarget attack by *C. quadrigemina*, *H. concinnum,* which commonly occurs sympatrically with *H. perforatum*, has remained common in those Californian communities to which it is native (Andres 1985). Although *H. calycinum* was in some instances severely defoliated, reports of nontarget attack declined with time (Andres 1985), probably because of a decrease in the target weed density and subsequent beetle abundance. Thus, despite the nontarget attack, which was predictable from experimental testing, the introduction of *C. quadrigemina* contributed greatly to the control of the target weed and had no measurable long-term negative effect on either the native *Hypericum* species or the horticultural industry.

Considering only the original host-specificity data presented *C. quadrigemina* would not be permitted for release today, simply because none of the native congeners of *H. perforatum* were tested. When considering the test data collected after the release of the beetle in the United States, it is doubtful that a release permit for *C. quadrigemina* would be granted, because larvae developed equally well on at least one commercially grown *Hypericum* species and several native *Hypericum* species as on the target weed. In addition, all nontarget *Hypericum* species tested were accepted to some degree for oviposition under open-field conditions. A recent report reviewing the biological control program against St. Johnswort in New Zealand came to the same conclusion (Groenteman et al. 2011), i.e., that *C. quadrigemina* (and its congener *Chrysolina hyperici* Förster) would not have been approved for introduction into New Zealand under current risk assessment protocols in that country. The authors write: "Had this happened, NZ would have missed out on one of its greatest biocontrol success stories, despite there being no evidence for subsequent impact on the populations of indigenous congeners."

***Convolvulus arvensis* L., Field Bindweed.** Field bindweed is a perennial vine native to Eurasia that was introduced into North America during the 18th century. The plant can form dense, tangled mats that may reduce crop production by as much as 60% (Littlefield 2004). In 1998, U.S. crop losses due to field bindweed infestations were estimated to exceed $377.8 million annually (Boldt et al. 1998). In 1989, the gall-forming mite *Aceria malherbae* Nuzzaci was introduced to North America for the biological control of field bindweed and 4 yr later, in 1993, also for control of hedge bindweed, *Calystegia sepium* (L.) R. Br. Nymphs and adults of the mite suck on plant sap, leading to gall formation on leaves and stem tips, which stunts plants and reduces flowering (Littlefield 2004).

Quantitative field data on the effectiveness of *A. malherbae* are limited. In Texas, bindweed biomass has been reduced by over 95% in many areas, primarily on roadsides, highway medians, and yards; there has been less success in cultivated row crops (Smith et al. 2010). At some release sites in Wyoming, bindweed populations have decreased to innocuous levels within 4 to 5 yr following the release of the mite (J. L. Baker, personal communication). In Oregon, the mite is spreading and reducing bindweed biomass by 90% (Smith et al. 2010). In Canada, the mite has also shown good biological control potential; however, there is considerable variation among release sites with regard to levels of establishment and impact, which may partly be explained by differences in environmental conditions (McClay and De Clerck-Floate 2002a). Completely galled plants are severely stunted where the mite is well established (McClay and De Clerck-Floate 2013).

In prerelease studies conducted under quarantine conditions in the United States, a total of 43 test plant species were evaluated, 22 in the family Convolvulaceae and the remaining species in 20 different plant families (Rosenthal and Platts 1990). The test plants included two threatened and endangered listed species: *Calystegia peirsonii* (Abrams) Brummitt, and *Calystegia stebbinsii* Brummitt, and four subspecies of other *Calystegia* spp., which were considered rare or endangered. The mite was able to reproduce and sustain populations on all nine *Calystegia* species tested, including the above-mentioned federally listed species (Rosenthal and Platts 1990). Considering these results, it is highly unlikely that the gall mite would be permitted for release in 2014 based on the mandated responsibility of the USFWS to protect threatened and endangered listed species under the Endangered Species Act. Rosenthal and Platts (1990) argued that "Benefits from the possible control of *C. arvensis* in North America must be contrasted with any harm due to possible attacks on native plants" and regarding the potential attack on threatened and endangered species, that "such species that occur at low levels of abundance are less subject to attack because of the density dependent manner in which biological control agents work. Thus, there is relatively little chance of actual encounter and impact on rare *Calystegia* species and subspecies."

In subsequent experiments with one native *Convolvulus* and three native *Calystegia* species in field plots between 2005 and 2007, galling was observed on all plants, although the severity and frequency of galling was much lower on the *Calystegia* species when compared to *C. arvensis*, and live mites were only found on two of the three native species exposed (R. Hansen, personal communication). These tests were conducted by attaching mite-infested field bindweed to test species, constituting a no-choice test under field conditions. The results also suggested that the mites may not be able to successfully overwinter on the nontarget plant species in Colorado or that aerially dispersing mites in spring did not successfully colonize nontarget plants (Smith et al. 2010).

Since nearly all of the native *Calystegia* species on which the gall mite is able to develop are geographically limited to the state of California, which has denied any release of the mite, no nontarget effects on *Calystegia* species have been reported there to date. This result demonstrates the potential value and effectiveness of geographical restrictions on releases for some agents where dispersal is limited.

***Lythrum salicaria* L., Purple Loosestrife.** Purple loosestrife is a perennial wetland plant introduced from Eurasia to North America in the early 1800s. It is capable of forming continuous stands that can displace native vegetation with significant ecological impacts on wetlands (see references in Blossey et al. 2001). Five biological control agents were released against purple loosestrife between 1992 and 1994. Among these, two defoliating leaf beetles, *Galerucella calmariensis* L. and *Galerucella pusilla* Duftschmid, are particularly effective. Both larvae and adults feed on leaves and buds and can defoliate plants (Piper et al. 2004). The biomass at several purple loosestrife stands in Oregon and Washington has been reduced by 90%; after several years of repeated defoliation, plant size decreased while plant mortality increased (Piper et al. 2004). In Manitoba, nearly 100% control of purple loosestrife has been achieved at many release sites (Lindgren et al. 2002). In Michigan, *G. calmariensis* caused 100% defoliation of purple loosestrife, which resulted in reduced stem heights by up to 85% and reduced plant cover by up to 95% accompanied by an increase in nontarget plant species richness (Landis et al. 2003).

Prerelease studies were conducted with 47 test plant species in Europe (Blossey et al. 1994) and with 15 species in containment facilities in the United States (12 of which were identical with species tested in Europe) (Kok et al. 1992). Under no-choice conditions, both *Galerucella* species fed and laid eggs on the native North American *Lythrum alatum* Pursh. (winged loosestrife) and *Lythrum californicum* Torr. & Gray, the European *Lythrum hyssopifolia* L., the ornamental *Lagerstroemia indica* L. (crepe myrtle), and the native North American *Decodon verticillatus* (L.) Ell. (swamp loosestrife). In no-choice larval transfer tests, both beetle species developed to adulthood on *L. alatum* and the European *Lythrum virgatum* L. (which is taxonomically very similar to *L. salicaria*). In addition, *G. calmariensis* successfully developed on the native North American *Ammannia auriculata* Willd. and *Ammannia latifolia* L. during tests conducted in Europe.

Two open-field tests were conducted with *L. alatum* and *D. verticillatus* in Europe prior to release (Blossey et al. 1994). In the first test, plants were exposed to beetles that had overwintered and were beginning to lay eggs. Under these conditions, no feeding or oviposition was recorded on the two test plant species. In the second test, plants were exposed to newly emerged adults of the F1 generation.

Under these conditions, all purple loosestrife control plants were completely defoliated and an estimated 30 to 40% of the leaf surface of the two nontarget plant species was consumed (Blossey et al. 1994).

Based on these results, it was predicted that limited nontarget attack by newly emerging F1 adults might occur, but that attack would be restricted to *L. alatum* and *D. verticillatus* (Blossey el al. 1994). Subsequent postrelease monitoring determined that the mass emergence of newly emerged F1 *Galerucella* adults also resulted in unpredicted, localized, short-term (temporal) attack on at least two completely unrelated plants (*Rosa multiflora* Thumb. and *Potentilla anserina* L.), but this was transitory in nature and disappeared as loosestrife populations declined (Blossey et al. 2001). As predicted, similar transitory adult feeding also occurred on the two closely related native North American species, *L. alatum* and *D. verticillatus* (Blossey et al. 2001; Corrigan et al. 1998). A few egg masses were found on *L. alatum*, but no late instars were observed to develop on this plant in the field (Corrigan et al. 1998), in contrast to results from larval-transfer tests in the laboratory reported above.

The California Department of Food and Agriculture (CDFA) initially refused to permit the release of beetles in California because no-choice test results in quarantine (Kok et al. 1992) showed substantial feeding and oviposition (especially by *G. calmariensis*) on *Lagerstroemia indica* (crepe myrtle), an economically important nursery plant and popular ornamental. The CDFA asked biocontrol researchers in Oregon to clarify the potential for nontarget damage to this plant. Schooler et al. (2003) established a replicated field experiment in 1996 (4 yr after release of the beetles), in which *L. indica* and purple loosestrife were placed at increasing distances from a purple loosestrife stand heavily attacked by *Galerucella* spp. Extensive defoliation of *L. indica* was limited to within 30 m (98 ft) and approached zero at about 50 m from the beetle front. At each distance, damage was lower for *L. indica* than for purple loosestrife. The authors concluded that the two *Galerucella* species would only have minimal, short-term effects on populations of crepe myrtle because the plant is unsuitable for beetle development, has little geographic overlap with purple loosestrife, and non-target attack decreased with increasing distance from purple loosestrife stands harboring beetles. Based on these results, both *Galerucella* species were permitted for release in northern California. Until 2010, the beetles established at least at one location in northern California where no crepe myrtle occurred (M. Pitcairn, personal communication). Once beetles disperse to more southern locations where crepe myrtle does occur, follow-up surveys will be conducted (M. Pitcairn, personal communication).

The experiments leading to the final approval for release of the beetles in California were only possible because releases had already taken place in other states, which enabled field experiments assessing the realized host range. Today, the damage to a widely used ornamental and concerns of the State of California about release would probably prevent a release permit for the *Galerucella* spp. in the United States.

***Linaria* spp., Toadflaxes.** Yellow toadflax, *Linaria vulgaris* Miller, and Dalmatian toadflax, *Linaria dalmatica* (L.) Miller (syn: *Linaria genistifolia* subsp. *dalmatica*), were introduced as ornamentals from eastern Europe in the second half of the 19th century and they, along with hybrids (Ward et al. 2009), are now widespread across North America (Nowierski 2004). *Linaria* species are avoided by cattle and reduce the productivity of infested rangelands. Yellow toadflax is also a problem in cultivated lands that has increased with the adoption of low-till cultivation practices (McClay and De Clerck-Floate 2002b). Between 1962 and 1996, six biological control agents were released for the control of Dalmatian toadflax, yellow toadflax, or both in North America (De Clerck-Floate and Harris 2002; Wilson et al. 2005). A recent molecular study (Toševski et al. 2011) has shown that the stem-boring weevil *Mecinus janthinus* Germar, first released in North America in 1991, is actually composed of two closely related species, *M. janthinus* from *L. vulgaris* and the cryptic *Mecinus janthiniformis* Toševski & Caldara from the *L. genistifolia–L. dalmatica* complex in southeastern Europe. *Mecinus janthiniformis* is now credited with successfully controlling Dalmatian toadflax in the northwestern United States and British Columbia (Schat et al. 2011; Van Hezewijk et al. 2010; Weed and Schwarzländer 2014). The larvae of this weevil mine in the stems and in spring, emerging adults feed on host-plant shoot tips, leading to a complete suppression of flowering and seed production, and severe stunting of shoots (De Clerck-Floate and Harris 2002). Recent studies on the landscape scale showed that toadflax patches decreased in density and became more fragmented over time, with 15% of patches disappearing completely due to *M. janthiniformis* (Van Hezewijk et al. 2010) and that the weevil had a direct negative effect on the stem-density growth rate of *L. dalmatica* patches (Weed and Schwarzländer 2014). Recently, large population increases of *M. janthinus* and reductions in toadflax densities have been reported at some sites of *L. vulgaris* in Canada and the United States (A. McClay, J. Milan, and S. Sing, personal communications).

Prerelease studies with *M. janthiniformis* (then named *M. janthinus*) collected from *L. genistifolia* in Macedonia were conducted in Europe with 38 test plant species, 22 in the former family Scrophulariaceae (Jeanneret and Schroeder 1992), which has recently been revised (Albach et al. 2005). A recent comprehensive study on the phylogeny of toadflaxes suggests that the native North American

Nuttallanthus is most probably nested within the genus *Linaria* (Fernandez-Mazueco et al. 2013). The emphasis of the original test-plant list was on ornamentals, and only nine native North American species were tested, one in the tribe Antirrhineae (to which the target weed belongs) and eight in other tribes. Jeanneret and Schroeder (1992) concluded that the host range of *M. janthiniformis* (then named *M. janthinus*) was restricted to the genus *Linaria* and did not develop on snapdragon, *Antirrhinum majus* L., an important ornamental in North America. These results, however, were based primarily on adult feeding and oviposition tests using cut shoots and on a limited number of larval transfer tests (Jeanneret and Schroeder 1992). Subsequent no-choice tests with additional native plant species in 2000 and from 2010 to 2011 using potted plants, have shown that *M. janthinus* and *M. janthiniformis* are able to develop to the adult stage on two native species in tribe Antirrhineae, i.e., *Sairocarpus virga* (A. Gray) D.A. Sutton (= *Antirrhinum virga* A. Gray) and *Nuttallanthus canadensis* (L.) D.A. Sutton [= *Linaria canadensis* (L.) Mill.], which is listed as endangered in Ohio (Toševski et al. 2012). *Mecinus janthinus* collected from *L. vulgaris* developed to the mature larval stage on three additional native species: *Sairocarpus nuttallianus* (Benth. ex A. DC.) D.A. Sutton, *Neogaerrhinum strictum* (Hook. & Arn.) Rothm. (= *Antirrhinum kelloggii* Greene), and *Maurandella antirrhiniflora* (Humb. & Bonpl. ex Willd.) Rothm. (= *Maurandya antirrhiniflora* Humb. & Bonpl. ex Willd.) (Gassmann et al. 2002; Toševski et al. 2012). A population of *Mecinus* from Russia, which could have been *M. janthinus* or *M. janthiniformis*, also developed on *Sairocarpus multiflorus* (Pennell) D.A. Sutton (= *Antirrhinum multiflorum* Pennell) under no-choice conditions (Gassmann et al. 2002). In a postrelease multiple-choice field cage test conducted in Bozeman, MT, in 2001 with insects that were most probably *M. janthiniformis,* where *S. virga*, *S. multiflorus*, and *N. strictum* were exposed, only *S. virga* supported the development of a single adult *Mecinus.* The mean offspring per stem was 0.06 on *S. virga* vs. 0.95 on *L. dalmatica* (Gassmann et al. 2002), suggesting that in presence of the target weed, *S. virga* is not a preferred host. In a postrelease evaluation of the potential for nontarget attack by *M. janthiniformis*, only feeding and oviposition scars, but no development, were found on the native *Nuttallanthus texanus* (Scheele) under no-choice conditions (Breiter and Seastedt 2007).

Initially, the State of California refused to permit release of *M. janthiniformis* (named at that time *M. janthinus*), because of concerns about native Scrophulariaceae in that state. However, in 2008, a release of 1,400 *M. janthiniformis* weevils was made in California in a rapidly expanding infestation of *L. dalmatica* nearly 644 km (400 mi) distant from the closest known location of *S. virga* (Villegas 2009). Results to date are that the weevil has not moved out of the release location, and no attack has been seen on any *Sairocarpus* (= *Antirrhinum)* spp. at that location (L. Smith, personal communication). However, *M. janthiniformis* has recently been sighted in northern California, most likely immigrating inadvertently from populations in southern Oregon (Villegas et al. 2011).

In 2014, *M. janthiniformis* would not be approved for release. With advances in host-range testing methodologies and inclusion of native species in test lists, the test list used in the 1980s would be considered incomplete, and justifiably so. Subsequent testing on additional species, mostly native to North America, indicated that the fundamental host ranges of *M. janthinus* and *M. janthiniformis* comprise several nontarget plants, all members of the same tribe, Antirrhineae, as the targets *L. vulgaris* and *L. dalmatica*. Given that the fundamental host range of *M. janthiniformis* also includes a state-listed rare species (*N. canadensis* in Ohio), a release permit would likely be denied today. Additional testing under multiple-choice conditions and postrelease monitoring is required to determine the realized host ranges of both *Mecinus* species.

***Solanum viarum* Dunal, Tropical Soda Apple.** Tropical soda apple is native to South America and was first reported in southern Florida in 1988 (Mullahey et al. 1993). Since then it has spread very rapidly throughout Florida and into other southern states, where it invades rangelands, pastures, and natural areas (Mullahey et al. 1996). Dense patches of *S. viarum* reduce cattle stocking rates and limit their movement, and serve as reservoirs for pests of Solanaceae crops (Diaz et al. 2014). Exploration for biological control agents of *S. viarum* began in 1994 in its area of origin and in 2003, the leaf-feeding beetle *Gratiana boliviana* Spaeth was introduced into Florida (Medal and Cuda 2010). Both larvae and adults feed on the leaves of *S. viarum* and can completely defoliate plants, resulting in reduced growth and fruit production (Diaz et al. 2014; Overholt et al. 2009). Up to a 90% decline in the density of *S. viarum* has been observed in high-density populations only 2 to 3 yr after beetle releases (Overholt et al. 2010). Percentage of cover of *S. viarum* decreased from an initial level of 80 to 90% to 5 to 10%, 2 yr after release (Medal et al. 2008). A preliminary economic analysis suggests that the release of *G. boliviana* reduced the management costs of *S. viarum* by approximately 50% statewide, resulting in potential statewide savings of $3 to 8 million annually (Salaudeen et al. 2012).

During prerelease multiple-choice host-specificity tests, 123 plant species (including 25 species in the genus *Solanum*) in 35 families were exposed to *G. boliviana* under quarantine conditions (Medal et al. 2002). Adults fed on four test species and laid eggs on two: the introduced weed *Solanum torvum* Swartz and the crop *Solanum melongena* L. (eggplant). An average of 68 eggs were found on *S. viarum,* but only 0.2 eggs were found on eggplant, suggesting it is a marginal host (Medal et al 2002). In no-choice larval-transfer tests, no development occurred on any of the 21 nontarget test plant species exposed under quarantine conditions in Florida, but a few larvae did develop to the adult stage on eggplant in tests conducted in Argentina (Medal et al. 2002). This triggered a field survey of 30 unsprayed eggplant fields in the native range of *G. boliviana* (Argentina, Brazil, Paraguay, and Uruguay) between 1997 and 2000 (Medal et al. 2002). No larvae or adults of *G. boliviana* were found in any of the fields surveyed. In addition, a large open-field test was established in Argentina in 2000, exposing two popular varieties of eggplant to the beetles, with no feeding, oviposition, or development observed on eggplant (Gandolfo et al. 2007). The prediction therefore was that it would be highly unlikely that *G. boliviana* would attack eggplant after release (Gandolfo et al. 2007).

After 7 yr of postrelease monitoring, *S. viarum* has been replaced by other plant species and no nontarget effects have been observed, even on congeners of the weed such as the nonnative *Solanum tampicense* Dunal (wetland nightshade) and *S. torvum* (Turkey berry) that were growing intermixed with or in close proximity to *S. viarum* (Medal et al. 2008). Several thousand acres of eggplants, including organic production, are being grown in Florida statewide, and there have been no reports of any damage or feeding on eggplant by *G. boliviana,* despite the statewide distribution of the beetle in Florida (Diaz et al. 2014; J. Medal, personal communication).

Given that oviposition and development, though limited, occurred on a commercially important crop (eggplant) in pre-release host-specificity tests, we conclude that in the absence of criteria that specify tolerable risk levels, *G. boliviana* would not be permitted for release today.

Summary and Discussion

Pre- vs. Postrelease Data for Our Five Case Studies. The biological control agents discussed in the five case studies were released in the United States as long as 68 and as recently as 12 yr ago. All have contributed to the sustainable and environmentally benign management of their respective target weeds. For the three agents for which postrelease data on nontarget attack was available, predictions of potential nontarget effects based on prerelease or postrelease host-specificity testing were accurate or overestimated attack potential (*C. quadrigemina* for St. Johnswort, *Galerucella* spp. for purple loosestrife, and *G. boliviana* on tropical soda apple). In addition, the documented nontarget attack was transitory (decreased with time), decreased with distance from the weed infestation or following its successful control (e.g. *Galerucella* spp. for purple loosestrife; Corrigan et al. 1998; Schooler et al. 2003), or both. The only case in which nontarget attack occurred on plant species unrelated to the target weed that was not predicted prerelease occurred after outbreaks of the biological control agent, and these effects were only transitory (i.e., *Galerucella* spp. for purple loosestrife; Blossey et al. 2001). For cases in which nontarget attack persisted, there are no reported population-level effects (*C. quadrigemina* on *H. concinnum*; Andres 1985), and the ornamental *H. calycinum* is still grown and marketed. The other two agents discussed (*A. malherbae* and *M. janthiniformis*) have so far not reached or have not been reported in areas where the respective nontarget plants occur (California). In the case of *M. janthiniformis,* nontarget attack on one native species, *S. virga,* is possible.

For the three agents for which either prerelease open-field tests (*Galerucella* spp. and *G. boliviana*) or postrelease open-field tests and field host range data (*C. quadrigemmina*) showed that nontarget attack did not have any major economical or environmental effects, we believe that agents would be safe for release if petitioned today. For the two cases in which testing was inadequate, i.e., did not include a sufficient number of native plants (*M. janthiniformis*) or conclusive open-field test data (*A. malherbae*), results of respective tests would need to be awaited to better define the realized host range prior to making a decision. In sum, after reviewing all available data, it is our assessment that the release of the discussed agents has resulted in a net benefit to the U.S. economy and environment.

Would They Be Released Today? We believe that for the illustrated cases the agents would not be approved if petitioned today. In three cases, this would be because of potential or confirmed attack on economically important plant species (*Hypericum calycinum, Lagerstroemia indica, Solanum viarum*), and in two cases, because of potential attack on rare, protected, or threatened and endangered plant species (*Nuttallanthus canadensis* and *Calystegia* spp.) (Table 1). We base our assessment on the reasoning provided for the denial of issuance of a release permit for *C. basicorne* (L. Smith, personal communication). Similar to the *C. basicorne* case, with regard to realized host-range data, two additional leaf beetles petitioned as biological control agents for tropical soda apple, *Gratiana graminea* Klug and *Metriona elatior* Klug, with a host range very similar to that of the released *G. boliviana* (Bredow et al. 2007; Medal et al. 1999, 2010), were not recommended for release by the TAG (USDA APHIS 2014; J Medal, personal communication). This is surprising, because *G. graminea* has a narrower fundamental host range than *G. boliviana* with an average of 86 eggs laid on tropical soda apple and only 0.1 on eggplant and no larval development observed on eggplant whatsoever (Medal et al. 2010).

Improvement of Environmental Safety and Risk Standards in Foreign Exploration and Biocontrol Regulation.

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Table 1. Factors that could have prevented biological control agents discussed in case studies from being approved for release in the United States today, applying current policies and regulations.

Target weed/biological control agent	Year of release in the United States	Attack on economic plant	Attack on T&E[a] species	Objection by individual state
St. Johnswort/*Chrysolina quadrigemina*	1945	X		
Field bindweed/*Aceria malherbae*	1989		X	X
Purple loosestrife/*Galerucella* spp.	1992	X		X
Dalmatian toadflax/*Mecinus janthiniformis*	1996		X	X
Tropical soda apple/*Gratiana boliviana*	2002	X		

[a] Abbreviation: T&E, threatened and endangered.

We did not include the seed-head–feeding weevil *Rhinocyllus conicus* Frölich, released in 1968 in the United States for the control of invasive thistles in the genus *Carduus*, as a case study in our paper, because it does not fit our second selection criteria (i.e. that the agent would not be permitted for release today *although it can be considered environmentally safe*). Firstly, *R. conicus* has since its release been found associated with the population decline of two native North American *Cirsium* species, *Cirsium canescens* Nutt. and *Cirsium pitcheri* (Torr. ex Eaton) Torr. & A. Gray, listed as threatened in the United States (Louda et al. 2005a), and secondly, *R. conicus* was collected during original foreign exploration efforts from plant species in four different genera (*Carduus, Cirsium, Onopordum* and *Silybum*; Zwölfer 1967), clearly demonstrating that the weevil is oligophagous.

The case of *R. conicus* illustrates how environmental safety standards in classical weed biological control have evolved since the 1960s. The National Environmental Policy Act and the Endangered Species Act were signed into law in 1970 and 1973, respectively, marking a societal shift in the perception of native fauna and flora and outlawing damage to threatened and endangered plant species in the United States. In hindsight, the release of *R. conicus* would be a clear violation of that law. However, the original host-specificity tests conducted for the weevil in the 1960s reflect the predominant agricultural values of the time and consequently only included one native North American *Cirsium* species, and that species was only included in adult feeding trials (Gassmann and Louda 2001). The assessment of the potential effects of *R. conicus* on native North American species was not a requirement of testing procedures at the time (Gassmann and Louda 2001). Today, the seed-head weevil would not even be selected as a potential biological control agent, given its oligophagous feeding habit. Also, in 2014, it is standard practice to only test a single source agent population rather than specimens collected from several host plant species over a large spatial scale as was done with *R. conicus*. Limited prerelease testing of native plant diversity also occurred in *C. quadrigemina* and *M. janthiniformis* (see case studies), again illustrating the change in socioeconomic values over time (Briese 2004). Even until the early 1990s, the emphasis of host-specificity testing was to ensure that species of economic importance were not attacked by a potential agent even if these species were completely unrelated to the target weed (also see Fowler et al. 2004). Systematic inclusion of native North American species in test plant lists has dramatically changed in the last 15 to 20 yr, partially in response to the Endangered Species Act but also because of efforts to better predict the realized host range in North America, using the actual species that could be affected. Similarly, technological advancements that were unavailable at the time some agents were initially tested, especially the increasing availability of molecular genetic tools, have improved our understanding of phylogenetic relationships of target weeds and native North American flora in many weed biological control programs (see Gaskin et al. 2011 for a review). Consequently, some released biological control agents were never tested against the full range of native plant species closely related to the target weed, and were introduced into the United States only to be found attacking native species in later host-range tests (e.g., *M. janthiniformis* for Dalmatian toadflax). In some instances in which native plant species were attacked during tests, the respective agents were still released, either because attack was judged to be transitory (e.g., *Galerucella* spp. for purple loosestrife) or because benefits from control of the weed were judged to outweigh the risk of harm to native plant species (e.g., *Aceria malherbae* for field bindweed; see Rosenthal and Platts (1990).

Consequences of Nontarget Attack. Even in cases where nontarget attack does occur after the release of a biological control agent, this is not necessarily detrimental for the nontarget plant on a population level. As two of our case studies (St. Johnswort and purple loosestrife) and numerous other studies have shown, nontarget attack is often transitory and does not persist in time or ceases with

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distance from agent outbreaks (Andres 1985; Blossey et al. 2001; Julien and Griffiths 1998; McFadyen et al. 2002; Schooler et al. 2003; Suckling and Sforza 2014). This kind of attack is often referred to as "spillover" and is functionally a form of apparent competition, since it generally only occurs at high agent densities and in presence of the target weed, i.e., the attack ceases with the reduction of the target weed density.

A recent review on the magnitude of nontarget impacts from classical weed biocontrol agents found that the vast majority of introduced agents (> 99%) have had no known significant adverse effect on nontarget plants thus far (Suckling and Sforza 2014). For the cases for which impact could be quantified (n = 140), and where impacts were detected, the majority (91.6%) were categorized as minimal or minor in magnitude with no known adverse long-term impact on nontarget plant populations. The only two cases in which moderate to massive negative direct impacts occurred were from *R. conicus* on native North American *Cirsium* species (see above) and from the moth *Cactoblastic cactorum* (Berg) (Suckling and Sforza 2014). *Cactoblastic cactorum* was introduced from South America to Australia in the 1920s and then to southern Africa, where it contributed to the spectacular control of invasive *Opuntia* species (Zimmermann et al. 2010). From 1957 onward, it was unfortunately also released on islands in the Caribbean, from where it spread naturally or accidentally through the plant-nursery trade to Florida. It is now threatening numerous native, economically used, and culturally important *Opuntia* species in the southern United States (Zimmermann et al. 2010). Certainly, the introduction of *C. cactorum* in the Caribbean would not be permitted today because of the risk of attack on nontarget native opuntias.

However, there are also cases in which initial nontarget attack resulted in a net positive effect for the nontarget species. The flea beetle *Aphthona nigriscutis* Foudras, released for the control of leafy spurge, *Euphorbia esula* L., attacked the native *Euphorbia brachycera* Engelm. [=*Euphorbia robusta* (Engelm.) Small ex Britton & A. Br.], in mixed stands of both plants (Baker et al. 2004). In the first year of postrelease monitoring (1999), 87% of *E. brachycera* plants showed feeding damage by flea beetle adults and mortality of plants with heavy feeding was 36%. However by 2002, when leafy spurge cover had declined from more than 50% to less than 6%, the *E. brachycera* population increased from 31 to 542 plants, of which less than 3% showed any feeding damage. Hence, the biological control agent had a large net beneficial impact on the native nontarget species and the indirect beneficial effect increased with decreasing target weed densities. A similar scenario has been described for the nontarget attack of the moth *Neurostrota gunniella* Busck released for control of *Mimosa pigra* L. on the native *Neptunia major* in Australia (Taylor et al. 2007; Q. Paynter, personal communication).

Unfortunately, due to limited resources, postrelease monitoring for nontarget attack is not systematically being conducted and has mostly focused on the individual plant level (e.g., Taylor et al. 2007; Willis et al. 2003; but see Van Hezewijk et al. 2010; Weed and Schwarzländer 2014). More long-term studies, such as the ones described above, are desperately needed to better understand if and how direct nontarget attack results in negative or potentially positive population-level consequences and to distinguish sustained from transitory nontarget feeding.

Recommendations

Develop Criteria for Risk and Benefit Assessments. In the United States, the Plant Protection Act does not specify guidelines on how to define and quantify risks of biological control agents to crops other than stating that a biological control agent "may not be a plant pest." This limited legislative guidance has likely resulted in some of the confusion among researchers regarding the implementation of policy for management activities such as biological control (also see Miller and Aplet 2005). The risks of biological control are considered under multiple laws with policies that emphasize the consideration and mitigation of risk to crops (under the Plant Protection Act), risk to the environment (under the National Environmental Protection Act), or risk to threatened and endangered organisms (under the Endangered Species Act). Through the EA, the regulatory process as currently implemented also considers the risk of an invasive species itself to crops, the environment, or threatened and endangered species as well as the consequences of "no action." However, there exists currently no formally outlined risk analysis including the likelihood of nontarget attack to occur and its magnitude in the evaluation process (Sheppard et al. 2003). In addition, USDA APHIS currently has no mandate to *weigh* these potential risks against the potential benefits of releasing the agent. Instead, if a potential risk to a crop, or *any* risk to a threatened and endangered species is found, the agent is most likely not being released. The selected case studies illustrate that, historically, a broader interpretation of regulations may have been possible. Initially, we recommend a reassessment of current policy to enable the consideration of both benefits and risks of all management activities, including biological control and nonactions, focused at a habitat level, rather than for individual species of concern as is done now. Ideally, such a reexamination should include the formal addition of risk–benefit analyses with a ranking of decision-making criteria as part of the TAG's evaluation of test plant lists when a biological control project is initiated, rather than waiting until the process has moved to an EA consultation stage. This would assist petitioners in the preparation of data sets for the petition; the agencies they represent, which would be able to allocate limited resources effectively; and the regulatory agency, which could be assisted in the development of an EA-like document by the petitioners and the agencies they represent.

In the longer term we propose that legislation may be amended to include risk–benefit analysis mechanisms in the biocontrol introduction process in the United States as has been done successfully in New Zealand and Australia (Barratt and Moeed 2005; Cullen and Delfosse 1985; Hill et al. 2013; Sheppard et al. 2003). Both exotic plant pests and biological weed control are regulated under the authority of the Plant Protection Act and the jurisdiction of USDA APHIS. A regulatory framework that addresses simultaneously the management of exotic plant pests and biological weed control could be developed that would provide great synergistic efficiencies and transparency, and would enable science-based decisions (Sheppard et al. 2003). The procedural framework currently used in New Zealand under that nation's Environmental Protection Authority most closely matches these criteria (for details see Barratt and Moeed 2005; Sheppard et al. 2003). An important component of the New Zealand Environmental Protection Authority is that its decisions have a judicial basis, which cannot be overruled or challenged (e.g., by lawsuits). Similar to New Zealand, Australia passed a Biological Control Act in 1984, which legislates a regulatory process to ensure decisions in cases where there are conflicting interests (Cullen and Delfosse 1985; McFadyen 1998). Common to both countries is the creation of legislation specifically tailored toward classical biological control, which facilitates both the effective implementation and regulation of this management tool.

Realized vs. Fundamental Host Range. It appears that for the case of *C. basicorne* and the tropical soda apple agents that were not recommended for release (*G. graminea* and *M. elatior*), results of open-field tests or their field host range in the native range (realized host range) were not considered or weighted in importance relative to feeding, oviposition, or development data under no-choice conditions (fundamental host range). Both the case studies discussed in this paper and other experimental results (Center et al. 2007; Clement and Cristofaro 1995; Frye et al. 2010; Pratt et al. 2009) have emphasized the value of multiple-choice cage or open-field tests in the country of origin (prerelease) to accurately predict the realized host range of biological control agents postrelease. Even if nontarget plant species are attacked by an agent in experimental open-field tests, the plants are not necessarily utilized in the field, since lack of geographical or habitat overlap might prevent the co-occurrence of the plant and the agent (see *H. anagalloides* and *H. scouleri* in St. Johnswort case) (Andres 1985; Briese 2004).

An approach that has been used to specifically validate prerelease host specificity data and predictions are common gardens in the area of introduction, where test plant species that were expected to be potentially attacked were exposed under seminatural conditions together with the respective target weed to the agent (Center et al. 2007; Frye et al. 2010; Pratt et al. 2009). Results of these experiments have shown that prerelease predictions on the risk of potential nontarget attack were accurate to conservative, i.e., overestimating risk (Center et al. 2007; Frye et al. 2010; Pratt et al. 2009). These experiments are also much more cost-effective than large-scale postrelease monitoring surveys and can be conducted right after release, without waiting for the agent to establish and reach outbreak densities. However, they do not replace postrelease monitoring efforts (see below).

We believe that the incorporation of realized host range data from common garden or open-field experiments in the country of origin needs to be recognized if not prioritized in the introduction process. These experiments should explicitly be weighted more heavily in risk benefit analyses and release decisions for biological control agents. Multiple-choice experiments and studies explicitly investigating the host selection behavior of candidate agents consider the host-finding abilities and needs of candidate biocontrol agents without which nontarget attack is extremely unlikely to occur. If in the future only the fundamental host ranges of potential agents were to be considered as part of a zero-tolerance for risk decision-making the number of available biological control agents would decline dramatically (also see Sheppard et al. 2005). To our knowledge, there are no examples for biological control agents that have a wider host range than that demonstrated in multiple-choice field tests (Blossey et al. 2001; Clement and Cristofaro 1995; Paynter et al. 2004; Pratt et al. 2009).

Formalize Postrelease Monitoring as Part of Permitting Process. Multiple reviews of biological control have reiterated the need for postrelease monitoring to confirm effectiveness or lack thereof of released biocontrol agents, assess potential nontarget plant use and, generally to validate prerelease host-range testing results (Blossey et al. 1994; Fowler et al. 2004; McFadyen 1998; Sheppard et al. 2005). The only systematic nationwide survey for potential nontarget effects of weed biological control agents that we are aware of has been conducted in New Zealand, and it covered 21 of the 30 agents established by 2004 in that country (Paynter et al. 2004; Waipara et al. 2009). Repeating a similar effort in the United States is unrealistic, considering the size of the country and the large number of target weeds and released agents (118 agents released for 53 weeds at this time; R. Winston, personal communication). However, smaller monitoring efforts, targeting an individual weed or group of related weeds or agent taxa, may be feasible. Recent efforts to include all available nontarget data in the revised fifth edition of Biological Control of Weeds: A Worldwide Catalogue of Agents and Their Target Weeds (Winston et al. *in press*) is also a positive step forward.

From a regulatory point of view we recommend a mandated requirement for organizations granted release permits to conduct follow-up studies on release impacts and first-order nontarget interactions. Postrelease monitoring, including that of nontarget attack, is currently required in every release permit granted; however, the extent to which that monitoring occurs is not always clear. Thus, we recommend development of a standardized reporting system that requires the releasing organizations to provide follow-up monitoring data in the public domain. Better postrelease data would also help test the case for the safety and efficacy of biological control as a management strategy, address concerns about the lack of data on the fate of exotic insect releases, and facilitate evaluations of future agents.

Conclusions

Biological weed control has significantly advanced as a scientific discipline since the 1950s when *Chrysolina* was released for the control of St. Johnswort and subsequently honored for its success by a monument raised in California. But we recognize that biological control is an irreversible action and for that reason there is such careful review and oversight of the decision to release exotic organisms in all countries in the world that utilize biological control. A consistent argument in favor of other management activities such as mechanical control or herbicides is that they are reversible whereas biological control is not. Although it is true that other management activities can be halted, it is certainly not true that if they are stopped, the habitat will revert to some sort of better, let alone native, state. Once an invasive plant species has moved into the habitat, restoration is extremely difficult and the habitat is often irrevocably changed. Herbicides themselves can have longer-term residual effects that, for instance, limit the regeneration of native plants (e.g., Wagner and Nelson 2014). Biological weed control, conducted with prudence, overall has a long history of safe and effective implementation around the world (Blossey et al. 2001; McFadyen 1998; Paynter et al. 2004; Pemberton 2000; Suckling and Sforza 2014). Similarly, herbicides can be effective if used appropriately. A key difference between management strategies appears to be that biological control is being held to a higher ecological impact standard than other control tactics, with recent emphases on nontarget effects or secondary trophic effects or even food web effects. It is striking that the oversight of other management strategies for invasive plants does not routinely include consideration of nontarget or habitat-level effects, which have become common in biological control programs. The recommended implementation of an overall risk–benefit approach would consider all management options using the same criteria and result in better decision-making. The reviewed case studies and regulatory systems for biological weed control in other countries demonstrate that it is possible to reliably balance the risks, costs, and benefits of biological weed control. In a time of ever-shrinking resources, biological control remains one of the more cost-effective and the only truly sustained means for the management of exotic invasive plants in the United States. It would be unfortunate to lose biological control as an option in our management toolbox.

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