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HOW SAFE IS WEED BIOLOGICAL CONTROL? A GLOBAL REVIEW OF DIRECT NONTARGET ATTACK

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abstract
This review summarizes all known direct nontarget attack (NTA) cases of intentionally released or actively redistributed weed biological control agents, in order to allow for an objective risk-benefit analysis when choosing the most appropriate method for controlling invasive plants. Of 457 agents inten-

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tionally released until 2008, 60 (13.1%) have been recorded attacking nontarget species in the field. Of 1517 releases made using the 457 agent species, 122 (8.0%) resulted in NTA. Both proportions have declined over time. Three-quarters of all NTA cases occurred on plant species in the same family as the target weed. Approximately one-half of NTA cases were predicted/predictable. In the majority of unpredicted *cases (93.5%), the respective nontarget plant species had not been tested prerelease. There were only four cases of "false negatives" (less than 1%), where the impacted plant species* had *been tested prerelease and deemed not at risk.*

The incidences of unpredicted nontarget attack of intentionally released weed biocontrol agents decreased over time and this trend is thought to continue with scientific advancements. What is most needed is more systematic postrelease monitoring to compare with prerelease host range testing to further advance the predictability of host use of biocontrol agents.

Introduction

THE introduction and naturalization of plant species outside their native range is likely to intensify with continuing globalization and increasing international trade (van Kleunen et al. 2015). Although only a very small percentage of naturalized plant species become invasive (Williamson and Fitter 1996), the ones that do can have severe negative effects on individual vital parameters of native species (Pyšek et al. 2012), species richness and diversity (Gerber et al. 2008; Hejda et al. 2009), agriculture and forest production, nutrient and fire cycles, water availability, and recreation and tourism (Charles and Dukes 2007; Beck et al. 2008b; Pyšek et al. 2012). The sum of these negative effects can reduce ecosystem services, ultimately impacting people's livelihoods (Shackleton et al. 2007; Mwangi and Swallow 2008; Haji and Mohammed 2013).

Complex interactions of invasive plants with their invaded habitats have created significant management challenges. Conventional control methods, including mechanical control (e.g., hand pulling, tillage) and chemical applications, have long been used in agricultural settings (Kelton and Price 2010). These control strategies are, however, often not feasible or economically sustainable for the management of exotic plants on vast tracts of private or publically owned lands, including terrain in difficult-to-access, remote areas and/or containing sensitive vegetation (Culliney 2005; Sheley et al. 2011). Conventional control methods are also increasingly restricted or prohibited altogether, for example, along or close to bodies of water (European Commission 2000; Federal Water Pollution Control Act 2002; Queensland Government 2013). Classical biological control (CBC) is another method to manage exotic invasive plants by reuniting natural enemies (biological control agents) from the invasive plant's native range with the respective plant in its introduced range. Since its first application more than 150 years ago (Goeden 1988), CBC has proven that it can be a cost-effective and sustainable control method for exotic invasive plants, with some spectacular successes in a variety of environments (Room et al. 1981; Bangsund et al. 1999; Culliney 2005; de Lange and van Wilgen 2010; Van Driesche et al. 2010; Clewley et al. 2012; Suckling 2013).

During the last 20 years, studies have, however, also shown that some releases of weed biological control agents resulted in negative direct effects on native plant species (Zimmermann et al. 2000; Louda and O'Brien 2002; Louda et al. 2005), and may also cause negative indirect effects (Carvalheiro et al. 2008; Pearson and Callaway 2008). Although these are unintended and unfortunate outcomes of the application of biological control, it should not be entirely surprising since *all* methods of invasive plant control influence both the abiotic and biotic components of the ecosystem to which they are applied (DiTomaso 1997). Studies have documented negative effects of chemical and physical control on populations of native plants, bacteria and fungi, invertebrates and vertebrates in both terrestrial and aquatic ecosystems, soil structure (including erosion), ecosystem functions through accumulation and transport and, most importantly, human health (DiTomaso 1997; Sheley and Denny

2006; Crone et al. 2009; Gasnier et al. 2009; Sheley et al. 2011; Helander et al. 2012; Mesnage et al. 2013; Séralini et al. 2014; Wagner and Nelson 2014). Despite these findings, it is CBC that has come under particular scrutiny in recent years. For example, regardless of stringent and rigorous host-specificity tests, obtaining approval for the introduction of new biological weed control organisms is becoming increasingly difficult, especially in the United States (e.g., Hinz et al. 2014). Therefore, in order to allow for an objective risk-benefit analysis when choosing the most appropriate method for controlling invasive plants, an in-depth analysis of the frequency and extent of nontarget effects of CBC is warranted.

Previous efforts reviewing and summarizing direct nontarget attack (NTA) caused by biological weed control agents exist, but they are outdated (Blossey et al. 2001), restricted in their geographic scope (Funasaki et al. 1988; Pemberton 2000; Fowler et al. 2004; Paynter et al. 2004), or emphasized only one group of organisms such as fungal pathogens (Barton 2012). The latest review by Suckling and Sforza (2014) focused on the magnitude of NTA and, consequently, was restricted to a subset of cases for which such information was available. This review is the first effort to globally summarize *all* known NTA cases of intentionally released weed biological control agents.

This review has three goals. First, to provide a global summary of instances of direct NTA caused by intentionally released or actively redistributed weed biological control agents. Second, to determine the effects of agent taxon and geographic areas on the probability of NTA, the categories of plant species attacked, whether NTA cases were predicted/predictable, and the persistence and severity of attack. And, finally, to provide recommendations for further improving the environmental safety of weed biological control.

Methods

source data

We utilized the most recent edition of *Biological Control of Weeds: A World Catalogue of Agents and Their Target Weeds* (Winston et al. 2014) as a basis for our review. This catalog summarizes all releases of weed biological control agents made globally and is the primary resource of weed biocontrol practitioners or anyone searching information on weed biocontrol agents and their target weeds. Based on the catalog, we identified all instances where weed biological control agents were intentionally released or actively redistributed until 2008 (inclusive). Although the catalog includes releases made until 1 January 2013, the most recent release to result in NTA was made in 2008, and we assumed that for later releases likely insufficient time had passed for NTA to occur or information to be published. Releases were treated as separate cases when one of the following conditions was met: a release of the same agent occurred in different countries; a release of the same agent was made in the same country but from a different source location; and a release of the same agent was made in the same country from the same source location, but on a different target weed.

After weed biocontrol agents were intentionally released in one country, some spread naturally or were accidentally transported into neighboring countries (Winston et al. 2014). These instances were included in the analysis because natural or accidental spread into new countries may result in new opportunities for NTA.

All records of NTA included in Winston et al. (2014) were collated along with NTA data summarized in previous reviews: Funasaki et al. (1988), McFadyen (1998), Pemberton (2000), Fowler et al. (2000a, 2004), Blossey et al. (2001), Paynter et al. (2004), Waipara et al. (2009), Barton (2012), and Suckling and Sforza (2014). In addition, we included data from MSc and PhD theses, unpublished reports, and personal communications with individual researchers for those cases where information was missing or unclear. Finally, the CAB Abstracts database (https://www.cabi.org/publishing-products/online-information-resources/cab-abstracts) was queried using the terms “nontarget effects” and “biological weed control,” but that search did not yield any additional results. Although we believe that by using the method above we produced the most thorough dataset on direct NTA of weed biological control agents worldwide, we cannot be certain to have captured all cases where NTA occurs.

Defining Nontarget Attack (NTA)

NTA has been defined in different ways (see Pemberton 2000; Fowler et al. 2004; Suckling and Sforza 2014). The following criteria were utilized to identify and categorize all cases of NTA analyzed in this review. First, we included all cases in which NTA occurred on native plant species as well as on beneficial species (both native and exotic). The latter encompassed crops, ornamentals, and plants with other economic or beneficial uses (e.g., timber production). We excluded cases in which agents exclusively attacked exotic invasive plant species that are in the same genus or tribe as the target weed. And we only included cases in which NTA occurred under natural conditions in the field following release. Excluded were cases where attack was found only in the laboratory or in experimental postrelease field trials.

There are likely instances of NTA occurring in countries where the details have never been documented. This is particularly likely for generalist insect herbivores released early in the history of weed biocontrol. In these instances, we likely underestimated NTA because we only included documented cases. Likewise, there are instances where we overestimated NTA. For example, when a biocontrol agent was released against four target weeds in one country and resulted in NTA, it was usually impossible to identify which of the releases led to the NTA. Consequently, the observed NTA was recorded for all four releases. We also included three cases in which NTA occurred but could not be definitively attributed to the biocontrol agent in question (*Ophiomyia camarae* Spencer, *Cheilosia grossa* (Fallén), and *Pyropteron doryliformis* (Ochsenheimer); for details see Appendix 1). In two instances where sibling biocontrol species were introduced combined (*Chrysolina hyperici* (Forster)—*C. quadrigemina* (Suffrian) and *Neochetina bruchi* Hustache—*N. eichhorniae* Warner), damage could not be attributed to one or the other species, and again NTA was attributed to both species.

Predictability and Persistence of NTA

We defined NTA as *predicted/predictable* if, based on information available prior to the release of the respective biocontrol agent, NTA was to be expected and did occur postrelease. For cases in which plant species suffered NTA, but were not included in prerelease host range testing, the NTA was categorized as *not predicted/predictable*. In cases where it was unclear whether a particular species had been included in prerelease testing, this information was extrapolated from host range data for other biocontrol agents of the same target weed during the same time period, as far as such information was available, otherwise we assumed that the plant species had not been tested. We estimated the persistence of NTA based on whether NTA was collateral damage, spillover, or sustained attack.

Collateral damage is herein defined as nontarget feeding following outbreaks of released biocontrol agents and subsequent depletion of target weed populations. Collateral damage typically occurs on plant species growing in close proximity (less than 50 m) to the target weed, or within dispersal distance of the biocontrol agent, but that are unrelated to the targeted weed taxon. As such, the affected species are typically not tested prior to the release of the agent, and NTA is typically not predictable. Because the biocontrol agents cannot develop on these unrelated plant species, collateral damage lacks persistence and is always short-lived (a few days to a couple of weeks). Collateral damage is therefore unlikely to cause noteworthy negative effects to nontarget plant species.

Spillover NTA also occurs at high biocontrol agent densities and on nontarget plant species growing in proximity to the target weed or within dispersal distance of the biocontrol agent. Unlike collateral damage, spillover NTA affects confamilial species on which the biocontrol agent can typically develop fully or to some degree. However, biocontrol agents do not sustain populations on the nontarget plant species, and NTA does not persist in the absence of the target weed. Spillover NTA will decline if populations of both the target weed and biocontrol agents decline. Spillover NTA can lead to negative effects at the individual plant level, but has thus far not been recorded to lead to negative consequences at the population level of nontarget species (e.g., Blossey et al. 2001; McFadyen et al. 2002; Center 2004; Taylor et al. 2007; Paynter et al. 2008a; Manners et al. 2011; Catton et al. 2015). However, only few studies have investigated population-level effects of spillover (Baker et al. 2004, 2008; Catton et al. 2015, 2016).

Sustained NTA occurs when the biocontrol agent is able to fully develop and sustain populations on the nontarget plant species, regardless of the presence or absence of the target weed. In other words, the nontarget plant species can serve as an alternative (albeit often suboptimal) host for the biological control agent. Similar to spillover NTA, sustained NTA affects confamilial nontarget species. In a few cases, limited information available made differentiating between spillover and sustained NTA difficult. If the biocontrol agent colonized geographically isolated populations of a nontarget species, we considered this an indication for sustained attack (e.g., Dodge 2005; Heystek 2006). When the agent had an oligophagous host range during prerelease investigations, we also assumed that NTA attack was sustained. Of all three NTA categories, sustained attack is the most likely to lead to negative effects at the population level and to persist independent of the target plant (Zimmermann et al. 2000; Louda et al. 2005). Cases where information was insufficient to determine which of the three persistence categories applied were assigned to the category "unknown."

Agent Release History

Host-specificity screening methods have undergone significant changes since the inception of classical weed biocontrol, effectively splitting the discipline into three distinct eras: until 1960, either no host-specificity testing was done or the emphasis was to ensure crop species were not attacked (Harris and Zwölfer 1968; Goeden 1988); 1961–1990 saw an increase in testing plants closely related to the target weed to determine the actual host range of the biocontrol agent, but these were typically selected from the area of origin of the target weed (Harris and Zwölfer 1968; Wapshere 1974); and from approximately 1990 onward, changing social and economic values have resulted in the increasing inclusion of species native to the introduced range in host-specificity testing and coincided with the introduction of new legislation, such as the Biological Control Act (1984) in Australia, the Environment Conservation Act (1989) in South Africa, and the National Environmental Policy Act (enacted in 1970, but policies implemented in the 1990s) in the U.S. (Sheppard et al. 2003). In parallel, the increasing availability of molecular tools improved our understanding of phylogenetic relationships of target weeds and native species, aiding the selection of plants for testing (Fowler et al. 2004; Briese 2005; Gaskin et al. 2011; Hinz et al. 2014). Cases of NTA were analyzed by release year to identify patterns in the proportion of cases occurring in each time period.

Releases and Cases of NTA By Country/Geographic Region

To relate the incidence of NTA to countries/geographical regions of agent release, we created 11 main geographic divisions. We first separated the five main countries/geographic regions historically and currently most active in weed biological control: Australia, Hawaii, New Zealand (NZ), North America (NA, including Canada, U.S., Mexico, and Central America), and South Africa. Other geographic divisions included Asia, the rest of Africa (including Ascension Island, Madagascar, Mauritius, and St. Helena), Oceania (including Melanesia, Micronesia, and Polynesia), the Caribbean Islands, South America, and Eurasia (including the Soviet Union in its post-1980 boundaries, e.g., including Kazakhstan).

Statistical Analysis

Both the proportion of agents and releases causing NTA per era and the proportion of taxa released with NTA were analyzed using binary logistic regressions, while the proportion of agents causing sustained NTA over eras was analyzed using a generalized linear mixed model assuming a binary response. The relationship between agent abundance and the number causing NTA was analyzed with a χ^2-test. All analysis was done in SPSS 9.4 (IBM Corporation 2013).

Results

The earliest release of a weed biocontrol agent was the scale insect *Dactylopius ceylonicus* (Green) in 1795, mistakenly believed to be the closely related *D. coccus* Costa used in dye production. This insect was subsequently intentionally redistributed throughout India and Sri Lanka from 1863 and 1865, respectively, for the control of invasive *Opuntia* species (Tryon 1910; Goeden 1978). Between 1863 and 2008, when the latest release causing NTA was made, 457 biocontrol agent species were intentionally introduced in a total of 1517 release events (Winston et al. 2014:Table 1).

NTA by agent species

Of these 457 agents, 60 (13.1%) were recorded attacking nontarget species in the field (for details see Appendix 2, available at https://www.journals.uchicago.edu/loi/qrb). This includes all nontarget attacks, temporally and spatially limited collateral damage, spillover, and sustained attack. The proportion of agent species causing NTA has declined by nearly 50% from 18.2 to 9.9% ($\chi^2 = 3.51$, df = 2, $P = 0.061$), from the first (until 1960) to the third (1991–2008) era, despite an increase in the number of biocontrol agent species released (Figure 1a).

Of the 457 agents, 67 (14.7%) spread naturally or were accidentally moved to other countries (Winston et al. 2014:Table 3); of these, 14 (20.9%) have caused NTA (Appendix 3, available at https://www.journals.uchicago.edu/loi/qrb). Of the 14, eight also caused NTA in the country where they had originally been released. Winston et al. (2014) included 19 additional agents in their Table 3 that have never been intentionally released anywhere, but that were accidentally introduced and

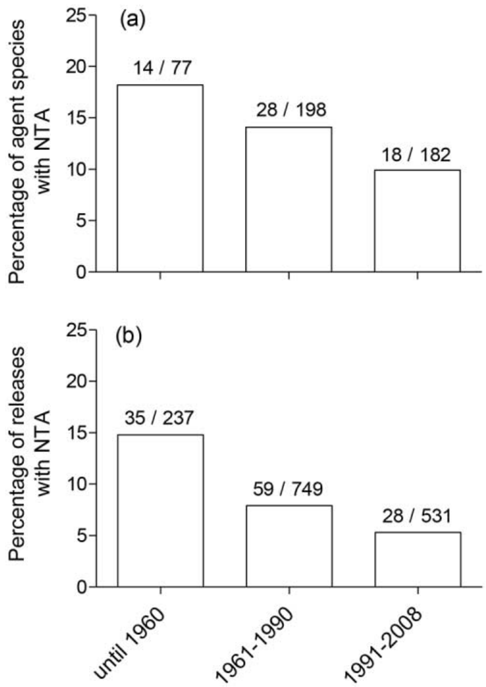

FIGURE 1. THE DECLINE OF NONTARGET ATTACK OVER TIME

Percentage of (a) intentionally released weed biological control agents and (b) agent releases causing nontarget attack during three different time periods. For (a) the year an agent species was first released was used. See the section titled Methods for details. Numbers on top of bars are the number of agent species or releases causing NTA/total number of agent species released or total number of releases.

have since been actively redistributed and utilized as biological control agents in their adventive countries. Of these, three—*Acentria ephemerella* (Denis & Schiffmüller), *Phenacoccus parvus* Morrison, and Rose Rosette disease—have caused NTA (15.8%).

NTA By Agent Taxonomy

The 457 biocontrol agents intentionally introduced until 2008 included 416 species of insects in eight orders, 29 fungal pathogens, 10 mite species, and two species of nematodes. No NTA was recorded for the small number of insect species (n = 6) released in the orders Heteroptera, Orthoptera, and Thysanoptera or for mites or nematodes. Only one fungal pathogen was documented causing NTA (*Puccinia spegazzinii* de Toni;

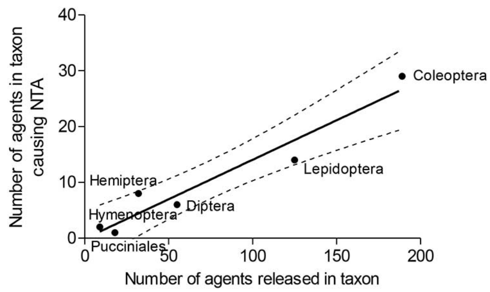

FIGURE 2. NONTARGET ATTACK IN RELATION TO AGENT TAXON

Relationship between the number of biological weed control agents released in each taxon and the number of agents in this taxon causing nontarget attack. Dotted lines signify 95% confidence interval (CI).

Figure 2). Among the five insect orders, the mites and the fungal pathogens with NTA, the percentage of agents causing NTA did not differ ($\chi^2 = 6.09$, df = 5, $P = 0.297$) and linearly increased with the number of agents released within each taxon (Figure 2; linear regression: $r = 0.965$.; n = 6; $P < 0.001$). For the taxa with most released agents (Coleoptera, Lepidoptera, and Diptera), NTA ranged between 11–15% (Figure 2).

Countries/Regions of Release and NTA

The number of agents with NTA per country/geographic region increased with the total number of agents released in the country/geographic region (Figure 3a; linear regression: $r = 0.786$; n = 11; $P = 0.004$). One notable exception to this is Australia, which has a similar number of agents causing NTA as Hawaii and South Africa, but which has released more than twice the number of agents as Hawaii and South Africa (Figure 3a). Oceania also had lower than average proportions of agents causing NTA, while North America shows higher than average NTA (Figure 3a). In South America and Eurasia, no NTA has been recorded to date, but only 14 and 11 agents were released in those regions until 2008, respectively.

Persistence and Severity of Observed NTA

The majority of NTA was categorized as spillover and sustained NTA (Figure 4). Collateral NTA was relatively equally distributed

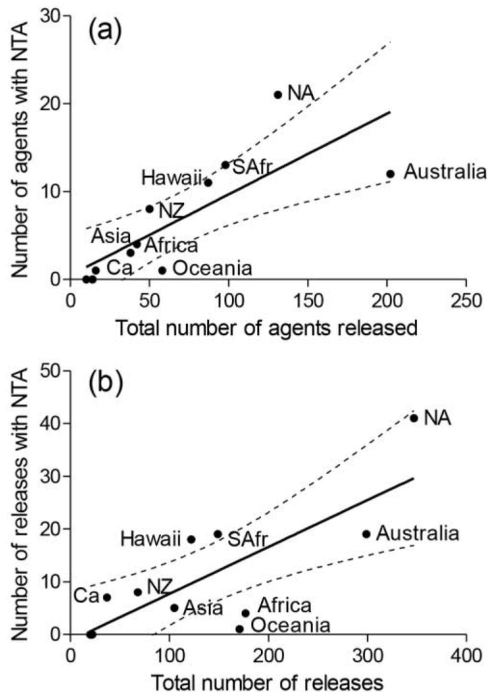

FIGURE 3. NONTARGET ATTACK IN RELATION TO COUNTRY/REGION OF RELEASE

Relationship between (a) the total number of biological weed control agents released in each country/region and the number of agents causing nontarget attack, and (b) the total number of agent releases in each country/region and the number of releases leading to NTA. Ca: Caribbean; NA: North America; NZ: New Zealand; SAfr: South Africa. No NTA is recorded from Eurasia and South America. Dotted lines signify 95% CI.

over the three time periods defined, while the proportion of agents causing sustained NTA differed among time periods and declined over time ($F_{2,70} = 4.11$, $P = 0.021$; Figure 4). Only two agents released during 1991–2008 caused sustained NTA: *Cydia succedana* (Denis & Schiffermüller) and *Aconophora compessa*, released in 1992 and 1995, respectively (for more information, see Appendixes 1 and 2).

NTA BY RELEASE

Because some agents were released in several different countries or against several different target weeds, the average NTA rate per release is lower than the average proportion of agents causing NTA. Of 1517 releases made using the 457 agent species until 2008

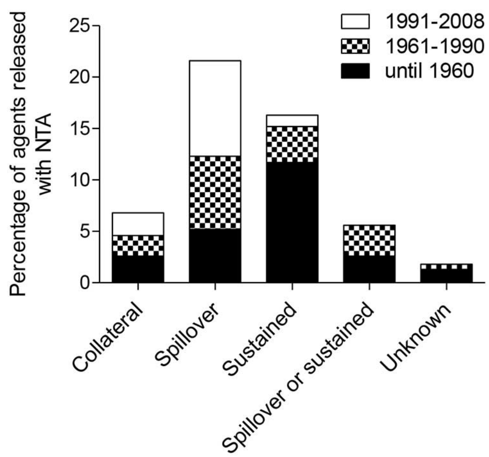

FIGURE 4. SEVERITY AND PERSISTENCE OF NONTARGET ATTACK OVER TIME

Percentage of agents released causing nontarget attack in five different nontarget attack categories over three different time periods. See the section titled Methods for a detailed definition of NTA categories and time periods.

(Winston et al. 2014:Table 1), 122 (8.0%) led to NTA. The proportion of releases leading to NTA significantly decreased over time ($\chi^2 = 17.57$, df = 2, $P < 0.001$), from 14.8 to 5.3%, despite an increase in the number of releases (Figure 1b).

In the few instances where certain agents caused different types of NTA from the same release, those were further split, resulting in 132 "unique" NTA cases (from 60 agent species). For example, the sap-sucking bug *Aconophora compressa* was released only once in Australia in 1995, but it has since caused unpredicted collateral NTA, predicted spillover NTA, and unpredicted sustained NTA to different nontarget plant species, leading to three "unique" NTA cases. Analyses based on the 132 unique NTA cases are specifically mentioned in the following sections.

Countries/Regions of Release and NTA

Similar to the number of agents released per country/geographic region, there was also a positive relationship between the total number of releases per country/geographic region and the number of releases causing NTA (Figure 3b; linear regression: $r = 0.774$; n = 11; P = 0.005). Differences between Australia and North America were no longer significant. There was lower than average NTA in Africa (excluding South Africa) and Oceania, and slightly higher than average NTA occurred per release in Hawaii and South Africa (Figure 3b).

NTA By Agent Abundance at the Release Site

Winston et al. (2014) includes the general abundance of the released agents in crude qualitative categories, defined as "high": agent is present with multiple individuals on most or all target plants examined in the region of interest; "moderate": agent is present on many but not all target plants in the region of interest, but with few individuals per plant; and "low": agent is present on some plants in the region of interest, but infrequently encountered. Although it may seem logical to assume that agents with the highest abundance in the field might have the highest probability of causing NTA, this was not the case. Of the 1517 releases recorded until 2008, 336 resulted in high abundances of the released agent; of these, 13.7% (n = 46) caused NTA. Of the 316 releases resulting in moderate-to-low agent abundance, 13.4% (n = 39) caused NTA ($\chi^2 = 0.261$; $P = 0.609$).

Categories of Plant Species Attacked

Of the 132 unique NTA cases, 50% of NTA occurred on one-to-two plant species, 31% on three-to-six species, and 19% on more than six species. Forty-five percent occurred on plant species in the same genus as the target, and 76% were in the same family. Of the 32 NTA instances where this was not the case, 19 were due to collateral damage on completely unrelated plants. In the remaining 13 cases, the NTA on unrelated species can be explained by five polyphagous agents being released against *Lantana camara* L. between 1902 and 1960 with little to no host-specificity testing.

Some biological control agents attacked more than one category of nontarget plant (e.g., natives, crops, ornamentals, plants with other economic uses such as timber production, and exotics), resulting in a total of 178 NTA cases of attack across all plant categories. In approximately half of these cases (n = 83), the plants attacked were natives. Similar proportions of crop species, ornamentals, and exotics were attacked (12.9–16.3% of NTA cases), while 9.6% of cases affected plants with other economic uses.

Predictability of Observed NTA

Of the 132 unique NTA cases, 70 (53%) were predicted/predictable based on prerelease host range data. For 21 of the 70 predicted cases, *the extent* of NTA was, however, not predicted. Nineteen of these 21 cases pertained to the release of *Rhinocyllus conicus* (Frölich), *Trichosirocalus horridus* (Panzer), and *Larinus carlinae* (Olivier) (= *L. planus* (Fabricius)) on thistle species in North America.

In 58 of the 62 "not predicted" cases (93.5%), the respective nontarget plant species had not been tested prerelease, and 51 of the 62 cases (82%) were associated with releases that occurred prior to 1990. The four cases that were not predicted, but where plant species had been tested prerelease are: attack by *Zygogramma bicolorata* Pallister on sunflower (*Helianthus annuus* L.); attack by the seed-feeding beetle *Bruchidius villosus* (Fabricius) on tree lucerne (*Chamaecytisus palmensis* (Christ)); attack by the pod-mining tortricid moth *Cydia succedana* on three other exotics; and attack of the gall wasp *Trichilogaster acaciaelongifoliae* on the exotic but commercially used *Acacia melanoxylon* R. Br. For more details see Appendix 1.

Persistence and Severity of Observed NTA

Of the 132 unique NTA cases, 14.4% were collateral damage, 43.9% spillover, and 32.6% sustained attack. In line with our definition, all collateral damage was on plant species not closely related to the target (i.e., in different families), and most were unpredicted cases on nontarget species not tested prerelease (Figure 5). Most spillover and sustained NTA cases were on species in the same family as the target (Figure 5a). The 10 cases of sustained NTA where plant species were not confamilial to the target weed (Figure 5a) were due to the release of oligo- to polyphagous species in the early era of weed biocontrol when few plant species (especially confamilials) were tested prerelease (Figures 5b and 5c). For 10

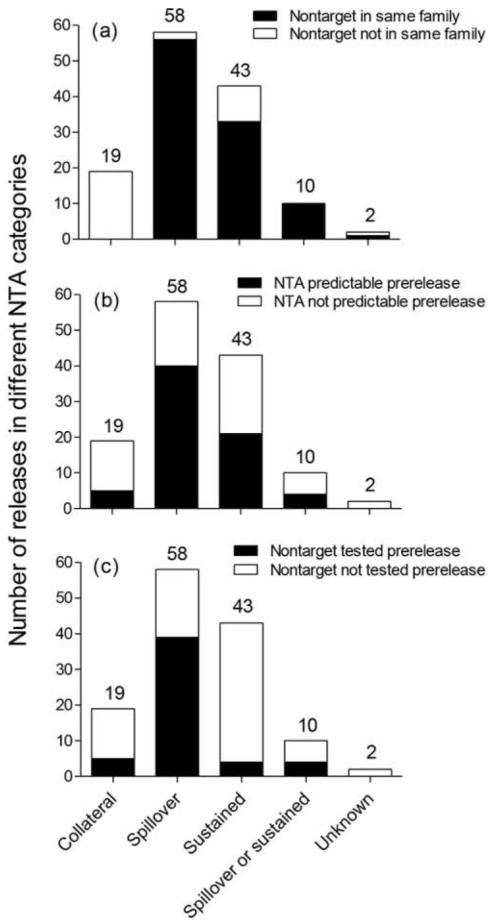

FIGURE 5. FURTHER SEPARATING THE FIVE NONTARGET ATTACK CATEGORIES ACCORDING TO THREE DIFFERENT CRITERIA

Number of biocontrol releases causing nontarget attack in five different nontarget attack categories. Presented with regard to (a) whether or not the nontarget plant was in the same family as the target plant, (b) whether or not NTA was predicted/predictable, and (c) whether or not the nontarget plant had been tested prerelease. See the section titled Methods for a detailed definition of categories. Numbers on top of bars are the total number of NTA cases in each category.

cases we could not clearly determine whether they were spillover or sustained NTA, and two cases could not be allocated to any of the categories.

Discussion

NTA over time and accuracy of current host range testing methods

One of the main results of this review is the fact that since the beginning of classical biological control in the 19th century, the proportion of intentionally released agents causing NTA declined from 18.2% in the period until the 1960s to 9.9% in the period 1991–2008 (Figure 1a). This trend was also true for the proportion of releases causing NTA, despite an increase in the number of agents released and releases made (Figure 1b). The decline either suggests that methods to determine the environmental safety of weed biological control agents prior to their release have improved over time, or that regulations to import exotic biocontrol agents have become stricter, or a combination of both. We anticipate that progress in research and technology will continue to improve environmental safety assessment methods in biological control (see the section titled Recommendations).

Two additional outcomes of this review support the notion that current methods to determine the host range of classical weed biological control agents are generally accurate. First, the majority of NTA cases (76%) occurred on congeners or confamilials of the target weed, and this proportion increased from 50% prior to 1960 to 85% for the period 1991–2008. The remaining cases were either due to collateral damage or to agents being released prior to 1960, when host range testing did not systematically include close relatives from the introduced range. The data confirm the validity of the centrifugal phylogenetic approach for the selection of test plant species (Wapshere 1974). This approach predicts that species more closely related to the target weed are more likely to be attacked than more distantly related species since they share traits important for the host selection and acceptance behavior of specialized herbivores. Second, the probability of released agents causing NTA appears to be independent of their abundance. This means that the host range of agents can be reliably predicted prerelease, even if agent populations become significantly more abundant postrelease, which is the desired outcome of biocontrol introductions. This finding excludes those cases where outbreak densities of agents may lead to temporally restricted collateral damage on plants completely unrelated plants to the target weed (see below). A similar trend of an increase in the level of specificity of released agents has been reported for parasitoids released for arthropod biocontrol between 1985 and 2015 (Van Driesche and Hoddle 2017).

Predictability of NTA

Approximately one-half of the 132 unique NTA cases identified in this review were predicted/predictable. This proportion is lower than we expected but can be explained by the fact that for most of the *unpredicted* cases (93.5%), respective nontarget plant species had not been tested prerelease, preventing prediction. There were only four cases of *unpredicted* NTA, where the respective nontarget plant species *had* been tested prerelease, and all four of these releases were made prior to 1992. We assume that most "*unpredicted*" cases would have been predictable, had the plant species been included in host range tests. The proportion of NTA on plant species not tested prerelease declined from 54% in the period 1961–1990 to 16% in the period 1991–2008, while the predicted NTA cases increased from 33% to 70%, suggesting improved selection of test plant species and host range testing methods.

For 21 cases, we concluded that the extent of NTA was underestimated. In many of these cases, results from field host range surveys in the area of origin were not fully recognized, or surveys conducted prerelease were not sufficiently thorough. The latter appears to be true for *A. compressa*, where in surveys in its area of origin, postrelease, the insect was found on species of several different plant families (Manners et al. 2011). All four agents (*R. conicus*, *L. carlinae*, *C. grossa* (Fallén) (= *C. corydon* (Harris)), and *T. horridus* Panzer) released during the 1960s–1990s to control invasive thistles in the genera *Cirsium* and *Carduus* in North America were recorded to develop on several different genera within the same tribe, Cardueae, during field and literature surveys in their native European range (Zwölfer 1967; Ward et al. 1974; Rizza et al. 1988; McClay 1990). Limited host range tests conducted at the time with native *Cirsium* species—at least for *L. carlinae* and *C. grossa*—indicated attack on native thistle species would be unlikely, and the insects were released (Rizza et al. 1988; McClay 1990). Although NTA by *C. grossa* on native thistles is strongly assumed (but not conclusively demonstrated, Eric Coombs, pers. comm.), NTA by the other three thistle agents has been well documented (Gassmann and Louda 2001; Louda and O'Brien 2002; Takahashi et al. 2009). The results of field host range surveys for *B. villosus* (F.) were confused by taxonomy of the species and therefore not fully recognized (Andy Sheppard, pers. comm.). In its native range, this beetle was found on species belonging to tribes other than the target *Cytisus scoparius* (L.) Link (Sheppard et al. 2006). Such data would today either cause direct elimination of the species as a prospective agent—at least for release in countries where close relatives exist—or trigger molecular analyses of specimens reared from different field hosts to determine genetic variability or existence of cryptic species (Gaskin et al. 2011).

Data on the field host range of a potential agent in its area of origin can, however, also provide important indications for its environmental safety in the introduced range. For instance, data on the field host range was one important argument for releasing three chrysomelid beetles in the genera *Leptinotarsa* and *Gratiana* for the biological control of two exotic invasive nightshades (*Solanum* spp.) in South Africa (Hill and Hulley 1995; Olckers et al. 1995). All three beetles developed on several native South African *Solanum* species and on cultivated eggplant (*Solanum melongena* L.) under laboratory conditions, but *Solanum* species fed upon in cage tests had never been observed as hosts in the field where they co-occur with *S. melongena* (Olckers et al. 1995), and none of the beetles had ever been recorded as a pest of eggplant in their native range. Of the three species, *Leptinotarsa texana* Schaeffer is now highly abundant and exerts heavy and widespread impact on the target *Solanum elaeagnifolium* Cav. in South Africa (Winston et al. 2014). Only one incidence of NTA of *L. texana* on a private eggplant patch has been recorded to date (Terence Olckers, pers. comm.).

In only four of the 62 *unpredicted* NTA cases (or 0.3% of all intentional releases worldwide) were the affected nontarget plant species tested prerelease. That they were nevertheless attacked postrelease can either be explained by the fact that: a population other than the one tested was released, coupled with asynchrony between the agent and the target weed (*C. succedana*); testing methods were insufficient (*B. villosus* and *T. acaciaelongifoliae*); or NTA feeding was stimulated by host pollen landing on the nontarget plant (*Z. bicolorata*; for more detailed information see Appendix 1). In all four cases, the resulting NTA was either collateral damage, spillover that ceased as target weed and agent densities declined, or occurred on other exotic species. None of the four cases led to any significant negative impacts on the involved nontargets (Dhileepan and Strathie 2009; Fiona Impson, pers. comm.; John Hoffmann, pers. comm.; Quentin Paynter, pers. comm.).

PERSISTENCE AND SEVERITY OF NTA

Fourteen percent (n = 19) of all NTA cases identified in this review were collateral damage, i.e., only 1.3% of all intentional releases worldwide. Although collateral damage, by definition, cannot lead to long-term negative effects on the attacked nontarget plant species, some of these temporary outbreaks have been of concern to the public and have shed a negative light on biocontrol: for instance, the attack of *A. compressa* in Australia on fiddlewood and other plants (Palmer 2004) or, more recently, the outbreak of *Ga-*

lerucella spp. in Oregon, where beetles were temporarily abundant in residential areas, feeding on roses and other ornamentals (Eric Coombs, pers. comm.). These events may be prevented by avoiding biocontrol releases on weed populations adjacent to residential areas. In addition, public education and awareness efforts could help mitigate negative reactions by the public.

Forty-four percent (n = 58) of all NTA cases analyzed in this review are classified as spillover, which equates to 3.8% of all intentional releases worldwide. To the best of our knowledge, spillover damage has thus far not led to negative consequences at the population level of a nontarget species. A typical spillover scenario has recently been described for the weevil *Mogulones crucifer* (Pallas), released for the biological control of *Cynoglossum officinale* L. in 1997 in Canada. Sites with naturally occurring populations of the nontarget plant *Hackelia micrantha* (Eastw.) J.L. growing interspersed with the target weed *C. officinale* or in the absence of the target weed were monitored for three years after release of *M. crucifer* (Catton et al. 2015). Although NTA on *H. micrantha* occurred, attack did not persist at sites without the target weed, and matrix population models showed that *M. crucifer* attack depressed only the population growth rate of the target *C. officinale* (but not *H. micrantha*) below the population replacement level (Catton et al. 2016). For further examples of spillover NTA see Appendix 2.

Thirty-three percent (n = 43) of all NTA cases were sustained, which equates to 2.8% of all intentional releases. Sustained attack is more concerning than the other categories of NTA, and their proportion was higher than expected based on previous reviews (McFadyen 1998; Blossey et al. 2001; Suckling and Sforza 2014). Of the 43 cases identified, 21 were caused by five oligophagous agents for which NTA was predicted or predictable (Figure 5b), albeit not necessarily to the extent to which it was observed. For an additional 20 of the 43 sustained NTA cases, the attacked nontarget species had not been tested prerelease. The remaining two cases (*B. villosus* and *C. succedana*) are part of the four "false negatives" described above. Of the 18 biocontrol agents responsible for the 43 sustained NTA cases, all were released prior to 1996. The proportion of agents causing sustained NTA declined from 12% prior to 1960 to 1% in the period 1991–2008 (Figure 4). Based on data available to date, only two agents causing sustained NTA, or 0.4% of all agents intentionally released, have the potential to generate population-level impacts on nontargets. These are the seed-feeding weevils *R. conicus* and *L. carlinae* that attack *Cirsium pitcheri* (Torr. ex Eaton) Torr. & A. Gray, federally listed as threatened in the U.S. and Canada (Louda et al. 2005; Havens et al. 2012) and *R. conicus* attacking *C. canescens*, a sparse species native to North America (Rose et al. 2005). In the 1960s, when *R. conicus* was investigated as a potential biological control agent for invasive *Cirsium* spp. and *Carduus* spp. thistles in North America, testing of native species was not a requirement. Only one native *Cirsium* species was therefore tested, and that species was only included in adult feeding trials (Zwölfer 1967). This would, of course, not be acceptable today. *L. carlinae* is thought to have entered the U.S. accidentally in the 1960s and was actively redistributed for *C. arvense* control (Havens et al. 2012). After host range tests were conducted in Canada using five native *Cirsium* species, *L. carlinae* was deliberately released in Canada in 1990 (McClay 1990; Winston et al. 2014). Subsequently, the weevils have been found attacking several native *Cirsium* species, including *C. pitcheri*. Based on demographic plant population models, both *R. conicus* and *L. carlinae* are predicted to reduce the population growth rate and time to extinction of *C. pitcheri* and *R. conicus* also of *C. canescens* (Louda et al. 2005; Rose et al. 2005; Havens et al. 2012).

The only other case we are aware of in which a biological control agent threatens the survival of a threatened or endangered (T&E) species involves *Cactoblastis cactorum* (Berg). This moth is a classic case for an agent intentionally released in one region, leading to NTA in another region for which it was not intended. *C. cactorum* was deliberately released on islands in the Caribbean in 1957 for the control of native *Opuntia* species. From there, it either moved naturally on its own or was accidentally introduced via the plant nursery trade from the Dominican Republic to Florida, where it is threatening native *Opuntia*, including the critically endangered *Opuntia spinosissima* (Martyn) Mill. (Pemberton 1995; Zimmermann et al. 2000; Stiling et al. 2004). Although the release of *C. cactorum* into the Caribbean was a legal action of sovereign countries at the time, in hindsight, the moth should never have been introduced there. First, its likely dispersal to the U.S. should have been anticipated and, second, biological control of native plants that are considered weeds using exotic herbivores is now considered to be unwise (Pemberton 1985). Overall, our results confirm other accounts that reported that less than 1% of all weed biocontrol releases led to severe negative impacts on nontarget species (Sheppard et al. 2003; Suckling and Sforza 2014).

differences by country/region

In some regions of the world there are fewer NTA occurrences than expected based on the number of agents released and/or releases made (Figure 3). Less frequent NTA in Africa and Oceania may be the result of less intense NTA monitoring in these regions due to limited infrastructure, resources, and training (Dovey et al. 2004) or to the fact that these regions implemented several "repeat" projects using agents that had already been successfully and safely used in other regions (Schwarzländer et al. 2018). This is not likely the case for Australia where similar low frequencies of NTA have been recorded compared to other regions. There, a phylogenetically more distinct flora, especially compared to North America, may partly explain lower percentage of NTA. For example, of all releases leading to NTA in Australia and North America, 48% and 87%, respectively, resulted in NTA to natives. In addition, the percentage of NTA cases where plants in the same family were attacked was 53% in Australia versus 89% in North America. On the other hand, similar patterns were not found for New Zealand and Hawaii, which also have quite unique floras. The full reasons for the lower than average rate of NTA in Australia therefore remain unclear, although the higher than average number of agents with NTA in North America is likely influenced by the greater number of native congeners.

nta on native species

Of the 60 agents we found to be associated with NTA, 42 attacked natives. This equates to 9.2% of the total 457 agents intentionally released worldwide, which is less than the proportion described by Pemberton (2000), who found that 15 of the 117 agents analyzed (or 12.8%) caused NTA on native species. Pemberton (2000) included introductions until 1994. Repeating the same analysis using only the regions/countries Pemberton included (Hawaii, the continental U.S., and the Caribbean), but with our updated data set including releases until 2008, resulted in 9.5% of agents causing NTA on natives (20 of 211 released). This may be considered another indication that host-specificity testing methods have improved since Pemberton's analysis, reducing NTA incidence rates on native plants. Pemberton (2000) also found that only one biocontrol agent attacked a native plant unrelated to the target (*Teleonemia scrupulosa* on *Myoporum sandwicense*; 1/117 = 0.85%). Excluding collateral damage, since Pemberton (2000) only included cases in which the agents were able to complete their life cycle on the nontarget, we did not find any additional agents attacking native plants unrelated to the target (1/457 = 0.2%). Pemberton (2000) and others (Suckling and Sforza 2014) concluded from these results that NTA can be reduced by choosing weed targets with no or only few native congeners. Although we agree with this general concept, many target weeds with numerous native confamilials (e.g., Brassicaceae, Fabaceae, Asteraceae, and Poaceae) are very widespread and economically and/or ecologically damaging and lack effective conventional control means. Classical biological control is in some cases the sole remaining potential control strategy for these invasive species. In addition, past examples have shown that even target weeds with numerous native congeners can be safely managed using classical biological control (Baker and Webber 2008; Casagrande et al. 2018 and references therein).

potential indirect nontarget effects and agent effectiveness

Even if biological control introductions do not lead to direct NTA, indirect effects can occur (Pearson and Callaway 2003). Indirect interactions have been recorded via resource competition (Louda et al. 1997), apparent competition (Carvalheiro et al. 2008), second-order apparent competition (Pearson and Callaway 2008), and ecological replacement (Pearson and Callaway 2003; Dudley and Bean 2012). However, only few examples are documented for weed biological control, and we therefore refrained from including them in our review.

Potential indirect effects are even harder to predict than direct NTA. It has been proposed that studying food webs in the native range of the biocontrol agent prior to release could predict the structure of food webs in the introduced range postrelease (Veldtman et al. 2011). In addition, both Pearson and Callaway (2003) and Carvalheiro et al. (2008) suggested that ineffective biocontrol agents that are unable to reduce target weed densities and that remain highly abundant are the most likely source of indirect effects. Assuring agent effectiveness prior to release should therefore be another important criterion in the risk assessment of biocontrol agents (McEvoy and Coombs 1999; Pearson and Callaway 2003; Shea et al. 2005).

Summary and Conclusions

1. The proportion of intentionally released weed biocontrol agents causing NTA declined from 18.2% in the period until the 1960s to 9.9% in the period 1991–2008, and the proportion of releases causing NTA decreased in the same periods from 14.8 to 5.3%. In addition, the proportion of agents causing sustained attacked declined from 12 to 1%. This either suggests that methods to determine the host range of agents prior to release have improved over time, or that import regulations have become stricter, or a combination of both.

2. The accurate prediction of NTA is largely a function of the inclusion of respective nontarget plant species in prerelease testing. Our findings strongly suggest that appropriate selection of test species could have avoided greater than 90% of unpredicted NTA.

3. In less than 1% of all intentional releases worldwide were "false negative" predictions made based on prerelease testing (i.e., nontarget attack occurred although the respective plant species were tested prerelease).

4. Seventy-six percent of NTA cases occurred on confamilials of the target weed, and this proportion increased from 50% prior to 1960 to 85% for the period 1991–2008. The instances where this was not the case were either due to collateral damage or the release of poly- or oligophagous agents prior to 1960.

5. Based on current data available, less than 1% of all intentional releases worldwide have the potential to lead to negative effects at the population level of nontarget species.

6. The field host range of a candidate biocontrol agent in its native range needs to be recognized as an important factor when determining its likely environmental safety postrelease.

Recommendations

Our summary and conclusions lead to the following recommendations.

going one step further in host range testing

As indicated under point 1 above, both the incidence of NTA and its severity have declined over time. In order to continue this trend, recent research not only attempts to determine the host range of candidate biocontrol agents, but also tries to understand the mechanisms underlying the differences in performance on field and nontarget hosts, as influenced by secondary plant chemistry or other factors (Wheeler 2005; Kirk et al. 2012; Wheeler et al. 2014) and to study the physiological and chemical basis for the host finding and host selection behavior of agents (Beck et al. 2008a; Kafle 2016; Park et al. 2018; and/or see Catton et al. 2014 for postrelease data). Combined, these research approaches should significantly increase the already good predictive power of nontarget plant attack. The aforementioned approaches can also assist in the testing of plant species that are rare and protected and for which there are no propagules available or those that are difficult to propagate. For instance, two recent studies at the University of Idaho used field-collected volatile organic compounds of federally listed threatened or endangered species to test the host finding and acceptance behavior of one candidate weed biocontrol agent and one already released agent (Kafle 2016; Park et al. 2018).

avoiding "false negatives"

Only four agents caused NTA despite the respective plant species being tested prerelease (points 2 and 3 above). Nevertheless, it is important to understand the underlying reasons and prevent such cases from occurring in the future. In two of the cases (involving *B. villosus* and *T. acaciaelongifoliae*), only choice tests were conducted prerelease (Van den Berg 1980; Syrett and O'Donnell 1987). However, asynchrony between the activity period of the released agent and the appropriate life stage of the target plant species can lead to no-choice situations in the field. This is especially true for seed feeders, which depend on a relatively ephemeral resource (Fowler et al. 2000b; Paynter et al. 2008a). Three of the four "false negative" cases are seed feeders (*B. villosus, C. succedana*, and *T. acaciaelongifoliae*). We therefore recommend no-choice tests be preferentially conducted to determine the fundamental host range of biocontrol agents prerelease. Because many insects need to feed on the pollen or sap of their host plant or a suitable alternative host to develop their ovaries and mature eggs (Schwarzländer et al. 1996), we also recommend conducting oogenesis tests on especially critical plant species. This will indicate whether potential NTA postrelease is likely to be mere spillover or whether sustained attack is possible (but see also Paynter et al. 2008b). The case of *C. succedana* also highlights the importance to only release the agent population that was used in host range tests.

choosing the right plants for testing

Point 4 above affirms the rationale for the centrifugal phylogenetic approach (Wapshere 1974) to select plants for testing and supports the notion that its application has been steadily improved with the advancements of molecular tools that clarify evolutionary relationships within target plant families (Briese 2005; Gaskin et al. 2011). We therefore recommend obtaining the latest family phylogeny when selecting plants for host range tests. Should the phylogeny not include all important plant species, genera, or tribes known in a family (based on traditional taxonomy), their sequences could be obtained by sampling or from commonly accessible databases (e.g., GenBank) and be built into the existing phylogenetic tree.

It is also recommended that phylogenies of the candidate agent and its congeners be studied to determine how host associations have evolved, especially where different host races exist within a species considered for biological control (Briese 1996; Briese et al. 1996; Toševski et al. 2014, 2015). Host range trials should therefore include plant species known to be exploited by closely related insect species (Wapshere 1974; Madeira et al. 2008).

the importance of determining the field host range of agents in the native range

Literature data on the field host range of natural enemies associated with a target weed are used as a first step to prioritize the most host-specific agents during a new project. Because such data are not always available, field surveys on the target and related species are usually the second step to determine the likely specificity of an agent. Although field surveys in the area of origin of the target have the obvious disadvantage that potential attack on plant species solely occurring in the invaded range cannot be determined, they do provide the best indication of the realized host range of the agent under natural conditions (see point 6 above). For instance, *A. compressa*, released in Australia to control *L. camara* agg., was found to cause unpredicted NTA on *Citharexylum spinosum* L. (fiddlewood), a popular ornamental. Later, more thorough field surveys in Mexico, the area of origin of *A. compressa*, revealed its low-density presence on fiddlewood (Manners et al. 2011). Had this been known prior to release, fiddlewood would most likely have been tested, and the NTA would have been predicted.

CONDUCTING POSTRELEASE MONITORING

Systematic postrelease monitoring efforts surveying likely nontarget plant species based on prerelease testing are still rare. Too often NTA records are based on coincidental observations, which may trigger more thorough follow-up investigations. It is therefore possible that proportions of NTA reported here are—at least in some cases—an underestimate of their actual occurrence. New Zealand is likely the country with the most thorough surveys for NTA worldwide (Fowler et al. 2000a, 2004; Paynter et al. 2004, 2018; Waipara et al. 2009). Based on the 50 agents intentionally released in New Zealand until 2008, we calculated that 16% (eight agents) caused NTA. However, only 33 of the 50 agents have been systematically surveyed, and so Paynter et al. (2018) calculated that 24% of agents are known to attack nontarget plants. Unfortunately, exact numbers of systematically surveyed agents are currently not available from other regions. Nonetheless, we believe that major impacts on nontarget plants, especially on rare and endangered species, would have been observed and reported, at least in the most active countries in weed biocontrol.

To reliably detect population-level NTA in postrelease monitoring surveys, multiple years of monitoring need to be conducted. Ideally this would either include years when the agent is at outbreak densities in the same nontarget population (Baker et al. 2004; Baker and Webber 2008) or monitoring data needs to be combined with a plant modeling approach (Louda et al. 2005; Catton et al. 2016). An alternative, more cost-effective approach may be manipulative experiments postrelease, which have the additional advantage of allowing cause and effect relationships to be established between NTA and potential population-level consequences (Catton et al. 2015, 2016). Or, test plant species expected to be attacked based on prerelease studies can be exposed to the agent in common garden or open-field tests in the area of introduction (Center et al. 2007; Moran et al. 2009; Pratt et al. 2009; Frye et al. 2010). Results of these experiments have shown that prerelease predictions on the risk of potential nontarget attack were accurate to conservative.

Thorough postrelease monitoring in combination with prerelease host-specificity testing can also be a powerful tool to further advance the predictability of host use of biocontrol agents. Paynter et al. (2015) developed a model to predict nontarget use of weed biocontrol agents released in New Zealand, based on their relative performance on the respective nontarget plant species in prerelease laboratory tests. Similar models could be developed for other regions, and these should be compared with results from open-field tests to examine their usefulness in predicting NTA postrelease. An effort is currently underway to compile similar data for agents released in the U.S. (Fritzi Grevstad, pers. comm.). In summary, systematic postrelease monitoring should be considered *as* important as prerelease host-specificity testing and should be an integral part of any weed biocontrol project.

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APPENDIX 1

Selection of NTA cases

We also included three cases in which NTA occurred but could not conclusively be attributed to the biocontrol agent in question. These include:

1. *Ophiomyia camarae* Spencer on native *Lippia* species in South Africa, which may have been caused by an indigenous leaf-mining moth (Heystek 2006; Urban et al. 2011);
2. Larvae of a syrphid species were found in the native North American *Cirsium brevistylum* Cronquist in the Douglas County area, Oregon (Eric Coombs, pers. comm.). Although they could not be reared to adult to confirm species identity, there are no known syrphids that occur in native thistles in Oregon. It is therefore likely that attack was caused by the syrphid *Cheilosia grossa* (Fallén) (= *Cheilosia corydon*), originally released for the control of *Carduus* spp. in the U.S.;
3. Mining damage was found during surveys for nontarget attack in the two native Australian species *Rumex brownii* Campd. and *R. dumosus* A. Cunn. ex Meisn. Although no larvae could be recovered, damage was consistent with larval feeding of the sesiid *Pyropteron doryliformis* (Ochsenheimer) (Dianne B. J. Taylor, pers. comm.), released for the control of *Rumex* spp. in 1989.

The Four "False Negative" Cases

1. The defoliating chrysomelid beetle *Zygogramma bicolorata* Pallister introduced for the biological control of *Parthenium hysterophorus* L. into India was observed to feed on tender leaves of sunflower (*Helianthus annuus* L.). This was completely unexpected, since no feeding or even nibbling occurred on any of the sunflower varieties exposed during prerelease host-specificity tests, and larvae are unable to develop on sunflower (Jayanth et al. 1993). Subsequent studies demonstrated that the nontarget feeding was stimulated by windborne *P. hysterophorus* pollen deposited on the sunflower leaves (Jayanth et al. 1993). However, as weed abundance decreased, so did the nontarget feeding without any impact on crop yields.
2. The seed-feeding beetle *Bruchidius villosus* (Fabricius) was introduced from the U.K. into New Zealand for the biological control of *Cytisus scoparius* (L.) in 1987. In host-specificity tests conducted in 1985 in the U.K. and in quarantine in New Zealand, *B. villosus* females only laid eggs on *C. scoparius* and a few on the ornamental *Cytisus praecox* "Allgold," but larvae did not develop (Syrett and O'Donnell 1987). In 1999, *B. villosus* was found emerging from tree lucerne or tagasaste (*Chamaecytisus palmensis* (Christ) Bisby & K. Nicholls), a plant originating from the Canary Islands, grown in New Zealand as a fodder crop. Further studies showed that this plant was a suitable and commonly utilized alternative host for *B. villosus* (Syrett 1999 in Haines et al. 2004). However, *B. villosus* destroys a relatively low proportion of tagasaste seeds and is considered unlikely to be capable of inflicting population-level impacts on tagasaste in New Zealand (Quentin Paynter, pers. comm.). In the original tests under quarantine conditions in New Zealand, *C. palmensis* was only tested under choice conditions, i.e., in the presence of the target weed *C. scoparius* (L.), and only in two replicates. In 2001 and 2002, host-specificity tests were repeated, using, as far as possible, the same methods as utilized in 1985 (Haines et al. 2004). To see whether released beetles might have undergone host-range expansion, tests were conducted with beetles collected in New Zealand, and beetles from the original collection site in the U.K. Both populations accepted *Cytisus proliferus* for egg laying in choice tests, so host-range expansion was ruled out as a mechanism for explaining attack of *B. villosus* on this nontarget. Instead it was hypothesized that differences in the number of *B. villosus* tested (fewer adults were tested in fewer replicates in 1985) and the way beetles were held prior to tests (only on *C. scoparius* versus on both *C. scoparius* and *C. proliferus*) may explain the differences in test results (Haines et al. 2004).
3. The pod-mining tortricid moth *Cydia succedana* (Denis & Schiffermüller) was introduced into New Zealand in 1992 for the control of *Ulex europaeus* L. Contrary to results of prerelease host range testing (Hill and Gourlay 2002), the moth was found to persistently develop on several species of exotic Genisteae, *C. scoparius* (Scotch broom), *Genista monspessulana* (L.) L.A.S. Johnson (French broom), *Lupinus arboreus* Sims (tree lupine), and *Lotus penduculatus* Cav. (Loteae) six years after release (Withers et al. 2008; Quentin Paynter, pers. comm.). Subsequent investigations found that although the original host range tests were conducted on moths collected in the U.K., the population that was released into New Zealand also contained the progeny of moths collected in Portugal (Paynter et al. 2008b). Although molecular analysis did not indicate the release of a cryptic species, additional host range tests

showed that moths sourced from Portugal performed better on nontargets than moths originating from the U.K. It was concluded that the release of untested *C. succedana* sourced from Portugal, coupled with asynchrony between the flight period of the moth and gorse flowering explains the unanticipated NTA in New Zealand (Paynter et al. 2008b).

4. Lastly, the gall wasp *Trichilogaster acaciaelongifoliae* (Froggatt) was released in 1982 in South Africa for the control of *Acacia longifolia* (Andrews) Willd. At exceptionally high population levels, *T. acaciaelongifoliae* may colonize the exotic but commercially used *Acacia melanoxylon* R. Br. (Dennill et al. 1999). However, attack only lasted for a short time when the wasp was very abundant and galls that formed were underdeveloped; lately no attack on *A. melanoxylon* has been reported and it is therefore a classic case of spillover NTA (John Hoffmann, pers. comm.). When Van den Berg (1980) tested the wasp, he only saw females attempting to lay eggs in the axillary buds of *A. melanoxylon*, but no galls developed. It is unclear why. Potential explanations include the fact that only choice tests were conducted prerelease or that attack on the nontarget only occurs at outbreak densities of the wasp.