CHAPTER 1

History of Classical Biological Control in the United States

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INTRODUCTION

Each year in the United States, pest insects and plants cause millions of dollars of damage to agriculture, forestry, and infrastructure; they also threaten native biodiversity, alter ecosystem services, and affect human health (DiTomaso, 2000; Pimentel et al., 2005; Pyšek et al., 2012). While some pest species are native to the United States, many of the worst pests are not. Insect pests are frequently introduced inadvertently as stowaways in or among imported material, especially wood or living plants. Plant pests (weeds) can be introduced as contaminants of soil, hay, or seed mixes, but many were, and still are, introduced intentionally for agriculture, horticulture, or the aquarium trade, with their subsequent establishment and invasion of natural systems. Several factors may contribute to an introduced species becoming invasive, including favorable habitat and climatic conditions, less competition for resources, and fewer natural enemies to keep the pest population in check compared to its native range (Williamson, 1996).

In the United States, invasive pests are managed in a variety of ways, including treating insects and weeds with pesticides, physically controlling weeds though cutting, mowing, or roguing, suppressing insects and weeds by manipulating the crop or surrounding vegetation or using livestock for targeted grazing (known as cultural control), or manipulating their natural enemies (known as biological control). One type of biological control is called classical biological control, which is the regulation of an invasive pest's population by importing its specialized natural enemies (e.g., parasitoids, predators, herbivores, or pathogens) from the pest's native range for this purpose. The hope and expectation of classical biocontrol is for introduced natural enemies to establish in their new environment and increase in abundance to levels that inflict sufficient damage to target pests to reduce the target's impact and abundance until they are a less important pest or a non-pest. For example, in the last 20–30 years, birch trees in Alaska began being attacked by several invasive leaf-mining sawflies. These sawflies reduce the leaf area in the tree canopy, causing tree growth rates to drop. One such sawfly illustrates the process of classical insect control. The amber-marked

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birch leafminer (*Profenusa thomsoni*) was first noticed in Southeast Alaska in the late 1990s. By 2006, 70% of the leaves on Alaskan white birch (*Betula neoalaskana*, the dominant forest tree around Anchorage) were mined by *P. thomsoni*. This caused tree growth to decline by ca 25% (Van Driesche et al., unpub data). In 2004, the parasitoid *Lathrolestes thomsoni* was introduced to Alaska from Alberta, although it is likely native to Europe. Within 15 years, the parasitoid had increased leafminer mortality from approximately 30 to 70%, and the percentage of leaves mined dropped from 70% in 2006 to 9% in 2019 (Andersen et al., 2021). At this latter low level, the leafminer has only a small effect on tree growth. Most importantly, this change is permanent and does not require any ongoing control efforts to maintain leafminer suppression. Classical biological control has ecologically reconstructed the food web of this pest in Alaska with the addition of a new parasitoid that strongly attacks the pest.

Control of invasive insects and weeds through classical biological control can benefit crop production (Nechols et al., 1995), rangeland forage (Sheley et al., 2011), forests (Van Driesche and Reardon, 2016), native biodiversity (Van Driesche et al., 2010; Van Driesche and Reardon, 2017), infrastructure (Coetzee et al., 2009), and human health (Van den Bosch, 1976). Classical biological control moves through well-established steps to identify and introduce natural enemies likely to be both effective against their target pests and present little risk to native and/or desirable species (Harley and Forno, 1992; Van Driesche and Reardon, 2004; Van Driesche et al., 2008, see pp. 127–133). In the remainder of this chapter, we discuss the history of classical biological control in the United States, how biocontrol programs are currently executed, and some of the benefits obtained from classical biocontrol in the United States. Throughout the rest of this book, we use case studies to document the beneficial contributions of classical biocontrol to the economy and environment of the United States.

HISTORY OF CLASSICAL BIOLOGICAL CONTROL IN THE UNITED STATES

The five most active countries carrying out classical biological control programs (for both insects and weeds) have long been the United States, Australia, South Africa, Canada, and New Zealand. Classical biocontrol projects affect not only the country initiating the work, but they often lead to adoption in other regions as well (Day et al., 2020). Consequently, documenting the history and outcomes of classical biocontrol programs is important for the successful and safe implementation of this discipline worldwide. Australia, Canada, New Zealand, and South Africa have periodically produced summaries of the classical biocontrol programs undertaken in their countries (e.g., Anon., 1971; Kelleher and Hulme, 1984; Cameron et al., 1989; Waterhouse and Sands, 2001; Mason and Huber, 2002; Julien et al., 2012; Mason and Gillespie, 2013; Ferguson et al., 2021; Zachariades, 2021). The United States lags in this effort, with most of its program reviews either being outdated (Clausen, 1978) or only regional in coverage (e.g., Funasaki et al., 1988; Nafus and Schreiner, 1989; Frank and McCoy, 1993, 2007; Barbosa et al., 1994; Nechols et al., 1995). The content presented in the remainder of this book partially fills this gap for the United States by highlighting the successful use of classical insect and weed biological control in selected projects since 1985.

Insect Biological Control

Classical biocontrol of insects in the United States stretches from 1888 with the successful suppression of cottony cushion scale (*Icerya purchasi*) that saved the fledgling citrus industry of the new state of California (Caltagirone and Doutt, 1989), to the current efforts against emerald ash borer (*Agrilus planipennis*) to restore ash stands across two thirds of the country to a better condition, protecting forest productivity and biodiversity (Duan et al., 2014; Bauer et al., 2015; Duan et al., 2021).

For the United States as a whole, the number of projects of classical insect biocontrol declined sharply from 1985 through 2018 (Van Driesche et al., 2018, 2020a) (**Fig. 1**). Despite this decline, classical biocontrol of insects has made a significant contribution in combating a series of invasive species and reducing the damage they caused to crops, forests, and/or biodiversity. The purpose of this book is to illustrate that value and suggest that this decline in use of classical biological control runs counter to the continued invasions of many high-profile insect pests that have occurred in this same period, such as emerald ash borer (*A. planipennis*), spotted wing drosophila (*Drosophila suzukii*), brown marmorated stink bug (*Halyomorpha halys*), and spotted lantern fly (*Lycorma delicatula*), among others.

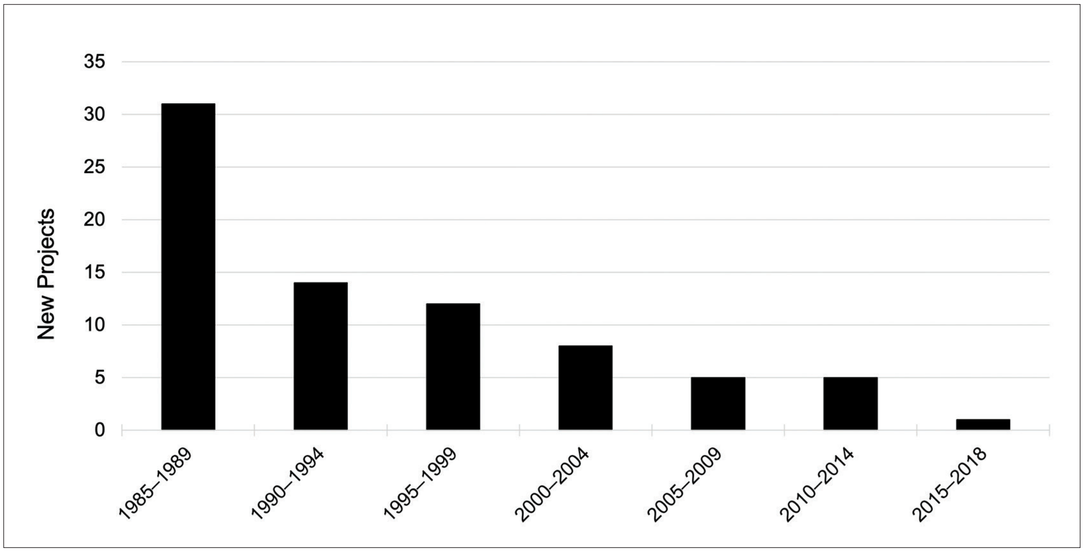

Figure 1. Number of projects of classical biological control of invasive insects from 1985 to 2018, in 5-year periods (apart from final interval), showing an 83.9% decline through 2014. (modified from Van Driesche et al., 2020a)

Weed Biological Control

The first weed targeted for biological control in the United States was *Lantana camara* in Hawaii. Beginning in 1902, 14 natural enemies were released throughout the islands to reduce the damage this species caused in pastures and native forests (Conant et al., 2013). Most of these natural enemies either failed to establish or had only slight impacts on *L. camara*, and the weed continues to be a problem at many sites (Winston et al., 2021). In the continental United States, the first weed biocontrol releases were made in 1945 when *Chrysolina* beetles were released against common St. Johnswort, *Hypericum perforatum*, in six western states (Holloway and Huffaker, 1952). In California, these beetles were highly effective at reducing *H. perforatum* infestations, and this program became one of the most famous examples of successful classical weed biocontrol (**Fig. 2**). Grateful landowners even erected a monument in honor of the beetles that saved their rangelands, and the weed is still considered under complete control in California 75 years later (Pitcairn, 2018).

Figure 2. *Hypericum perforatum* invasion in California (a) before *Chrysolina* spp. introductions; (b) after *Chrysolina* spp. introductions; (c) monument in honor of *Chrysolina* spp. (a–c: USDA-ARS European Biological Control Laboratory, Bugwood.org CC BY 3.0 US)

Through the year 2020, 211 species of natural enemies had been released against 83 weed species in the United States (including the continental U.S., Hawaii, and overseas U.S. territories). The number of new weed biocontrol agent species introduced to the United States and its territories peaked from 1985 to 1999 (**Fig. 3**). Similar to the pattern in insect classical biological control, the number of new species introduced as weed biocontrol agents has decreased steadily since 1994 (Winston et al., 2021).

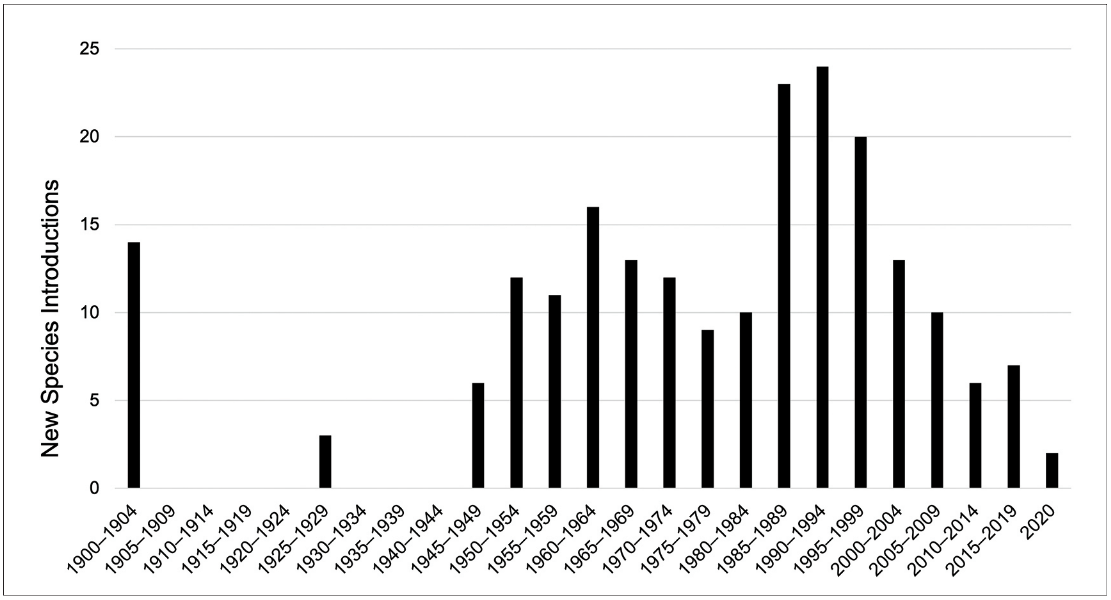

Figure 3. Numbers of new species of weed biocontrol agents introduced against weeds in the United States and its overseas territories from 1902–2020, in 5-year periods (apart from final interval). (Winston et al., 2021)

WHO RUNS CLASSICAL BIOLOGICAL CONTROL PROGRAMS?

A Description of the Process

Classical biological control programs begin with exploration for specialized natural enemies affecting an invasive pest in its area of origin. This process includes physical surveys for natural enemies attacking the target pest in its native range, as well as any relevant published literature. In both activities, emphasis is placed on natural enemies that feed on or develop on only the target pest or a few related species; such agents are said to show high host specificity and have narrow host ranges. Potential biocontrol agents identified during foreign exploration are then subjected to testing to show they are relatively host specific (Van Driesche and Reardon, 2004; USDA-APHIS, 2019) and potentially effective. The results of this testing are reviewed at several stages during the agent approval process, which are described in greater detail below. After a biocontrol agent is approved for introduction into the United States, it is released in the field. In ideal situations, biocontrol agent release sites are monitored before, during, and for several years after releases to gather data demonstrating the impacts of the release.

Introducing new classical biocontrol agents to the United States is a lengthy (3–5 years for parasitoids and predators, and 5–10 years for weed biocontrol agents) and expensive process, and many groups are often involved in the various stages of this process. Funding for many programs is obtained from federal or state government agencies because the pests targeted affect several sectors, and the development of safe biocontrol agents is for the general good of society. In some programs, however, funding has been provided entirely by private groups (e.g., ranchers or grower associations looking for solutions to their worst pest problems). Although some foreign exploration and host-specificity testing are conducted by scientists working for federal or state government agencies, there are also several private science firms and individual scientists worldwide who contribute to this part of the process. After an agent is approved for release in the United States, it is most often released in the field by the individual or agency who successfully petitioned for its approval. If the agent successfully establishes and/or large populations are easily propagated in the field or laboratory, surplus individuals are then shared with other federal, state, or private groups or individuals to increase the release and distribution of the new natural enemy over a wider area. While there are some private companies that charge for the collection or propagation of biocontrol agents, most federal, state, and country programs make every effort to distribute these natural enemies free of charge. Monitoring of biocontrol agent releases is initially conducted by the individual or agency who made the first release, but as the natural enemy becomes more widely established, other agencies and citizen scientists are frequently included in monitoring efforts to track establishment, spread, and impact on the target pest.

Regulations for Approving Classical Biocontrol Agents

Federal laws and regulations are in place to identify and avoid potential risks to native or desirable plants or animals that could result from organisms introduced to manage insect pests and weeds (USDA-APHIS, 2019; Van Driesche et al., 2020b). The U.S. Department of Agriculture's Animal and Plant Health Inspection Service–Plant Protection and Quarantine (USDA-APHIS-PPQ) is the federal agency responsible for authorizing the importation of biocontrol agents into the United States (under 7 CFR 330) as well as providing host specificity testing guidelines (USDA-APHIS, 2019). The regulation of classical biocontrol agents in the United States proceeds in two steps. The first step is the issuance of an importation permit to move the discovered natural enemies to a certified quarantine facility where their host specificity and efficacy can be studied. In phase two, following the completion of quarantine host specificity and efficacy studies, the concerned person or agency submits a written petition to USDA-APHIS-PPQ to request permission or approval of environmental releases of the candidate agent.

Upon receipt of a release petition, USDA-APHIS-PPQ proceeds down two different pathways, dependent upon whether the biocontrol agent being petitioned is for an insect or weed pest. For insect classical biocontrol agents, USDA-APHIS-PPQ will first seek reviews and comments from the North American Plant Protection Organization (NAPPO), which is a phytosanitary standard-setting organization whose mission is to provide a forum for public and private sectors in Canada, the United States, and Mexico to collaborate in the development of science-based standards intended to protect agricultural, forest and other plant resources against regulated plant pests, while facilitating trade. Based on comments and reviews from NAPPO, USDA-APHIS-PPQ will conduct an Environment Impact Assessment (EA), in which the characteristics of the potential agent, its host range, the need for the introduction, and any likely side effects are discussed. If the conclusions of the EA are favorable, USDA-APHIS-PPQ then submits the release petition for publication in the Federal Register for public comments. The agency then responds to public comments and reaches its decision, which, if positive, is called a FONSI (Finding of No Significant Impact), and a release permit is issued.

For weed classical biocontrol agents, USDA-APHIS-PPQ first seeks reviews and comments from the Technical Advisory Group (TAG) for Biological Control Agents of Weeds, which is an expert committee with representatives from U.S. federal regulatory, tribal, resource management, and environmental protection agencies, as well as regulatory counterparts from Canada and Mexico. Following positive recommendations from the TAG, USDA-APHIS-PPQ then prepares a Biological Assessment that is shared with the U.S. Fish and Wildlife Service. If the latter agency agrees that there are sufficient data to demonstrate the candidate weed biocontrol agent is safe to threatened and endangered species, and if they concur with the proposed release, they provide a Letter of Concurrence to that effect. USDA-APHIS-PPQ then prepares an EA (similar to the process for insect biocontrol agents), but they then share the EA with Native American tribes in areas within the range of the target plant as a Tribal Consultation. Following this step, the process is identical to that of insect biocontrol agents in that USDA-APHIS-PPQ publishes the petition in the Federal Register for public comments, prepares a FONSI in the event of a positive decision, and issues a release permit. In addition, some states have their own approval process to permit field release of weed biocontrol agents.

Regulations for the introduction of new species for classical biocontrol have increased over time and are now the most stringent and comprehensive for any species introduced to the U.S. for any purpose, including species introduced for use commercially for horticulture, as pets, or in aquaculture (Van Driesche et al., 2020b).

HOW SUCCESSFUL HAS CLASSICAL BIOLOGICAL CONTROL BEEN?

Complete control of an invasive pest occurs when the pest population is reduced below an ecologically or economic threshold and is maintained at that level with no additional controls (Coetzee et al., 2009). However, even partial control of a pest population may be considered a success if the pest's negative impacts on society or nature are reduced, along with a reduced frequency or need for other control methods (Schwarzlaender et al., 2018). Worldwide up to about 2007, Van Driesche et al. (2008) determined from multiple sources that about 60% of all insect biocontrol projects had a positive effect, reducing the pest either partially or completely. Control was complete in 17% of the projects targeting insects, and partial control was achieved in 43% of the projects. More recently for the United States alone, Van Driesche et al. (2020a) found that for 75 projects against invasive insects carried out from 1985 to about 2015, 50% had positive effects (partial or complete control), fluctuating between 40 and 60% per 5-year period (**Fig. 4**).

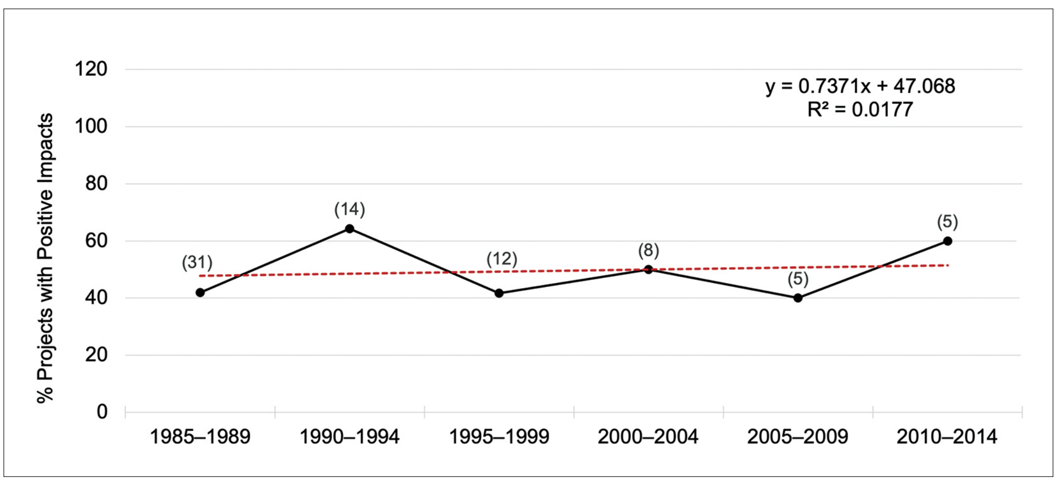

Figure 4. Trend in the percentage of U.S. insect classical biocontrol projects that, summed over each 5 year period, had a positive impact on their target pest in the United States and U.S. overseas areas. (modified from Van Driesche et al., 2020a)

For weed biocontrol, the most recent worldwide analysis of biocontrol programs (Schwarzlaender et al., 2018) further separated partial control into 'slight' and 'medium'. Of all weed species for which impact could be categorized, 65.7% of release programs worldwide resulted in medium to complete control. For weed biocontrol in the United States (and U.S. overseas territories), the percent of new biocontrol agent species introductions (not projects, but single agents) resulting in medium to complete control of their target weed averaged 44.6% per 5-year period since 1902 (**Fig. 5**; Winston et al., 2021).

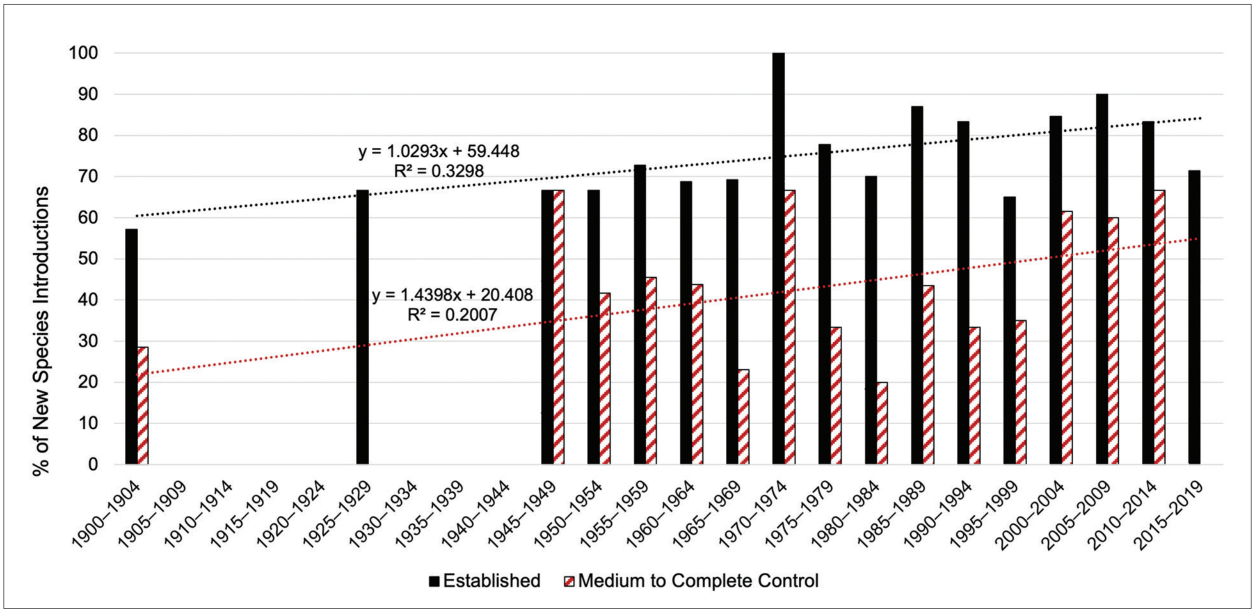

Figure 5. Trend in the percentage of U.S. weed biocontrol agent species introductions resulting in medium to complete control of their target weed per 5-year period (including overseas areas). (Winston et al., 2021)

For both insects and weeds, many advancements have been made in the discipline of classical biocontrol in recent decades. These include an increased awareness of the potential of negative direct and indirect effects of natural enemy releases, tightened introduction regulations, increased emphasis on demonstrating natural enemy impacts before release, advances in pre-release host-specificity testing methodologies, and development of molecular tools that clarify evolutionary relationships of target pests. Some of these changes have led to fewer releases of new natural enemy species in recent years (**Fig. 3**). Comparing **Figures 3** and **5** demonstrates an important trend that while the number of weed biocontrol agent species has decreased since 1999, the percent of species establishing and causing medium to complete control of their target weeds has increased since then.

ECONOMIC AND ECOLOGICAL BENEFITS

Economic Benefits

Measurement of the economic benefits of classical biocontrol is most common for pests affecting agriculture or horticulture because benefits are readily expressed in terms of dollars saved (e.g., increases in productivity or yield, lower control costs, lower expenses for other work such as removal of dead landscape trees, etc.). The ratio of project benefits to project costs is the commonly used measure of the economic value of classical biocontrol projects against agricultural pests. If pests are strongly suppressed, benefits continue to grow indefinitely as more years of reduced pest pressure accumulate. Estimates for benefit/cost ratios have ranged from 1.4:1 for white wax scale (*Ceroplastes destructor*) in Australia (Tisdell, 1990) to 4331:1 for the golden wattle (*Acacia pycnantha*) project in South Africa (van Wilgen et al., 2004). Some examples specifically for the United States include the project against mole crickets (Gryllotalpidae spp.) in Florida, which had a benefit: cost ratio of 52:1 (Mhina et al., 2016), and the project against the ash whitefly (*Siphoninus phillyreae*) in California, which had a ratio of 270:1 (Jetter et al., 1997). In Oregon, biological control of the weed tansy ragwort (*Jacobaea vulgaris*) produced a benefit: cost ratio of 13:1 (Coombs et al., 1996), though the overall savings across the United States and Canada is likely an order of magnitude higher considering the number of states and provinces initially heavily infested with the weed. The biological control of the weed leafy spurge (*Euphorbia virgata*) across the United States and Canada has delivered a benefit: cost ration of between 8.6:1 and 56:1 (Cock et al., 2015).

More recent studies demonstrate that worldwide, the economic benefits of classical biocontrol projects are very large relative to costs and that these returns grow substantially over time as the benefits of avoided negative impacts or costs accumulate (van Wilgen et al., 2020). This allows agencies engaged in classical biological control to have strong, positive net effects on society even though only roughly 60% of classical biocontrol programs have succeeded in partially or completely controlling their target pest. For comparison, many municipal infrastructure projects are funded if they have benefits that only slightly exceed costs (in the range of 1.1:1 to 2:1), yet these activities are seen as good public investments.

Ecological Benefits

Ecological benefits of classical biocontrol of insects (see Van Driesche et al., 2010 for review) and weeds (e.g., de Lange and van Wilgen, 2010; van Wilgen et al., 2020) are very real and significant but are harder to quantify, and less attention has been paid to this matter than for agricultural pests. In some cases, the benefits can be measured in terms of dollars, as for example the impacts on South Africa of control of woody acacias and other tree species (van Wilgen et al., 2004; Moran and Hoffmann, 2012), but this is often not the case. Impacts are often studied in terms of restoration of affected native species or degraded habitats or an increase in biodiversity (de Lange and van Wilgen, 2010; Coetzee et al., 2020). In some cases, benefits can be measured as conservation of valuable ecosystem services (see pp. S21–23, Van Driesche et al., 2010) or resources such as water (van Wilgen et al., 2004; Arp et al., 2017). However, it is not always possible to assign monetary or ecological units of value to the environmental benefits achieved through classical biocontrol. For example, control of erythrina gall wasp in Hawaii has likely saved the endemic wiliwili tree, *Erythrina sandwicensis*, from extinction, thus preserving the dominant tree of native Hawaii dry forests (Kaufman et al., 2020), but there is no obvious way to measure those benefits in terms of dollars. Similarly, biocontrol control of the invasive swamp tree *Melaleuca quinquenervia* has been an important part of the efforts to restore the Everglades National Park and other areas of south Florida, preserving the open glades that define many of the area's most characteristic habitats (Center et al., 2012). In the Galapagos National Park, a world conservation interest of the highest order, the successful biological control of the polyphagous invasive scale *Icerya purchasi* protected many native plants, including both rare endemics and foundational species that create key habitats such as mangrove swamps (Calderón Alvarez et al., 2012; Hoddle et al., 2013). As our understanding and ability to quantify the ecological harm of invasive pests increase (Vilà and Hulme, 2017), so too will our ability to quantify the ecological benefits of classical biocontrol in natural environments.

CONCLUSIONS

In the United States, invasive insects and plants cause millions of dollars of damage annually both economically and ecologically. Continuing globalization and increasing international trade will likely result in more invasive species becoming established, exacerbating their impacts and the need for management solutions. Classical biological control is one important tool for reducing the negative impacts caused by invasive pests. Since 1888 when it was first applied in the United States, the discipline of classical biocontrol has grown and evolved. Under strict regulations and with improvements in testing practices, classical biocontrol has emerged as an effective and sustainable method for the long-term management of invasive pests. Subsequent chapters of this book illustrate the important role biocontrol has played in the control of invasive pests over the past 30 years. Its benefits are illustrated with a series of detailed case studies of invasive insects and weeds in the United States.

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