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Biological control of invasive plants in California's Delta: Past, present, and future

PAUL D. PRATT, PATRICK M. MORAN, MICHAEL J. PITCAIRN, ANGELICA REDDY, AND JON O'BRIEN*

ABSTRACT

Implementation of weed biological control in the Sacramento–San Joaquin River Delta (the Delta) began in 1982 with the introduction of three natural enemies of waterhyacinth [*Eichhornia crassipes* (Mart.) Solms].The chevroned waterhyacinth weevil (*Neochetina bruchi* Hustache) is widely distributed in the Delta, the mottled waterhyacinth weevil (*Neochetina eichhorniae* Warren) is rare, and the waterhyacinth moth (*Niphograpta albiguttalis* Warren) failed to establish. Renewed interest in biological control led to the release of the waterhyacinth planthopper (*Megamelus scutellaris* Berg), assessments of cold-hardy biotypes of the *Neochetina* weevils, and research on stem-mining flies in the genus *Thrypticus*. New biological control research also focuses on nonnative waterprimrose (*Ludwigia* spp.), including host-range testing of the thrips *Liothrips ludwigi* Zamar as well as additional surveys for natural enemies of waterprimrose species in the plants' native range. Research on Brazilian egeria (*Egeria densa* Planchon) led to evaluation of the leaf-mining fly (*Hydrellia egeriae* Rodrigues) and additional surveys in the plant's native range. Biological control of giant reed (*Arundo donax* L.) has involved the release of a shoot-galling arundo wasp (*Tetramesa romana* Walker) and an armored scale [*Rhizaspidiotus donacis* (Leonardi)]. Both insects are established at locations upstream of or in the Delta. Future prospects include the introduction of the arundo leaf-mining midge (*Lasioptera donacis* Coutin). Alligatorweed [*Alternanthera philoxeroides* (Mart.) Griseb.] was recently discovered in the Delta for the first time, and efforts are underway to introduce the alligatorweed flea beetle (*Agasicles hygrophila* Selman and Vogt) as well as the alligatorweed thrips (*Amynothrips andersoni* O'Neill). While weed suppression remains elusive, the importance of biological control in the Delta is expected to increase as stakeholders seek treatment alternatives.

Key words: biocontrol, California, integrated weed management, natural enemies, weed.

*First, second, and fourth authors: Research Leader, Research Entomologist, Entomologist, U.S. Department of Agriculture–Agricultural Research Service, Western Regional Research Center, Invasive Species and Pollinator Health Research Unit, 800 Buchanan St., Albany, CA 94710. Third author: Senior Environmental Scientist, Biological Control Program, California Department of Food and Agriculture, 3288 Meadowview Road, Sacramento, CA 95832. Fifth author: Aquatic Invasive Species Control Program, Division of Boating and Waterways, California Department of Parks and Recreation, Sacramento, CA 95814. Corresponding author's E-mail: Paul.Pratt@usda.gov. Received for publication August 30, 2019 and in revised form July 1, 2020.

INTRODUCTION

The implementation of biological control to suppress invasive plant populations has a long history in California. The first recorded use of weed biological control is attributed to Harry S. Smith, who in 1940 collected the native scale *Dactylopius tomentosus* (Lam.) feeding on pricklypear (*Opuntia* spp.) growing in southern California and transferred the insects to weedy but native pricklypear on Santa Cruz Island (Goeden et al. 1967). The first implementation of classical biological control, or the introduction of foreign natural enemies to control foreign weeds, targeted common St. Johnswort (*Hypericum perforatum* L.) invading rangelands and pastures of northern California (Holloway 1964). The Eurasian St. Johnswort leaf beetle [*Chrysolina hyperici* (Foster)] was released in 1945 and the subsequent herbivory from this and other agents resulted in the landscape-level suppression of common St. Johnswort (Huffaker and Kennett 1959). This early example of successful weed biological control in California served as a landmark case study for the potential benefits of this weed management approach worldwide. Today, it is recognized that biological control of invasive weeds can be a safe, cost-efficient, and effective technique contributing to integrated weed management efforts (Van Driesche et al. 2010, Hinz et al. 2019, 2020).

Since the 1940s, a total of 77 species of biological control agents have been introduced in California to aid in the control of 39 weed species (Pitcairn 2018). Of the targeted weeds, only eight occur in aquatic or riparian environments, and these invasive plants experience among the lowest levels of control from introduced natural enemies (Pitcairn 2018). The disparity between the availability of effective biological control tools and the magnitude of weed invasions in the state's freshwater systems is concerning.

The California Sacramento–San Joaquin River Delta (hereafter Delta) is the largest freshwater estuary in the Western United States and the hub of California's water supply (reviewed in Moran et al. 2020). State and federal aqueducts provide water for a Delta agricultural economy of $800 million, statewide irrigated agriculture of over $30 billion, and part of the water supply for 27 million people (DiGennaro et al. 2012, Dettinger et al. 2015). The environmentally sensitive habitats that comprise the Delta and adjoining San Francisco Bay are collectively one of the most invaded estuaries in the world, with over 234 introduced species and an additional 125 cryptogenic species in the system (Cohen and Carlton 1998). Invasive aquatic weed species pose one of the most significant threats to water resources and natural habitats in the Delta. Aquatic weeds and associated pests threaten $300 million in Delta recreational boating and tourism, and commercial navigation to the shipping ports of Stockton and Sacramento, which handle five million tons of cargo per year (DSC 2013). Aside from the negative impacts of invasive plants on commerce and water availability, the Delta also provides habitat for threatened and endangered fish and a wide range of plant and animal life (Toft et al. 2003, Greenfield et al. 2006).

Mitigation of the negative effects of exotic plants has relied primarily on the application of herbicides, mechanical removal, or shredding vegetation in situ (Greenfield et al. 2006, 2007; companion articles in this issue). These conventional approaches are effective at reducing biomass but can be costly, and implementation has been difficult due to regulatory restrictions to safeguard listed endangered species (Caudill et al 2020, Moran et al. 2020). Treatments are currently limited by permitting restrictions to 22% of the Delta, but realized treatment coverage is often markedly less, representing a small proportion of the total invaded habitat. The authority to treat invasive plants in the Delta is further restricted to weeds occurring in what are termed navigable waterways, resulting in weed refuges in small tributaries, canals, or shallow wetlands. Additionally, public concern over the use of herbicides in these critical waterways is increasing (Mao et al. 2018).

Renewed demand for weed management tools, including biological control, from stakeholders and the general public arose from an intense drought that spanned 2012 to 2015. Slower-than-typical water flows, lower water levels, and associated warmer water temperatures during this period contributed to weed outbreaks that affected the Delta's many functions (Moran et al. 2020). Past implementation of biological control for aquatic and riparian weeds in the Delta has been limited to water hyacinth, and control has been elusive (Stewart et al. 1988, Moran et al. 2016, Akers et al. 2017). The benefits of biological control, therefore, remain largely unrealized for the critical water resources of the Delta (Laćan and Resh 2016).

An inherent advantage of biological control includes the self-dispersing behaviors of natural enemies. Introduced herbivores are expected to spread to even the smallest weed patches and are not subject to spatial or temporal use restrictions as their conventional counterparts (Van Driesche et al. 2008). Because successful biological control agents are also persistent in the environment, repeated site visits for follow-up treatments are rarely necessary. While these attributes are attractive to weed managers, there are few biological control options that target invasive plants in aquatic environments. Can biological control play a greater role in Delta weed management efforts (Reeves and Lorch 2012)? We address this question by reviewing the history of biological control in the Delta, the status of programs currently in development, and future opportunities for weed biological control in this complex system.

WATERHYACINTH

Past

Waterhyacinth [*Eichhornia crassipes* (Mart.) Solms] is a floating aquatic weed recognized as one of the world's worst invasive plants (Villamagna and Murphy 2010). Similarly, waterhyacinth has long been considered the most problematic weed in the Delta (Spencer and Ksander 2004). The plant was first documented in the Delta in 1904, but it became a widely recognized weed in the mid-1970s to 1980s (Stewart et al. 1988, Toft et al. 2003, DBW 2012). Waterhyacinth grows abundantly in the Delta, where it forms dense floating mats that negatively affect the ecology, economy, infrastructure, and recreational services of the invaded areas (Toft et al. 2003, Villamagna and Murphy 2010, see companion papers in this volume).

A biological control program targeting waterhyacinth was initiated by the U.S. Department of Agriculture–Agricultural Research Service (USDA-ARS) in the 1960s to mitigate the effects of invasion in Florida and other Gulf Coast states of the southern United States (Bennett and Zwölfer 1968). Three biological control agents, including two weevil species—mottled waterhyacinth weevil (*Neochetina eichhorniae* Warner) and chevroned waterhyacinth weevil (*Neochetina bruchi* Hustache)—and the waterhyacinth moth (*Niphograpta albiguttalis* Warren), were imported from Argentina and evaluated in Florida during the1960s (Center 1994). Both waterhyacinth weevil species are similar in appearance and behavior. Nocturnal adults feed on the lamina and occasionally on the petiole of waterhyacinth foliage, resulting in characteristic scarring. Adults may lay up to 200 eggs, which are inserted into the petiole or lamina (Center et al. 2002). Larvae tunnel into the petiole, feeding internally as they move towards the rhizome. Larvae complete three instars before migrating below the water surface to pupate among the root hairs. Adult waterhyacinth moths range in color from gold to brown or grey and, like the waterhyacinth weevil adults, are nocturnal (Center et al. 2002). Adults only survive for about a week, during which females lay an average of 450 eggs. These eggs are creamy-white and larvae emerge a few days after oviposition. Brown larvae develop through five instars, feeding initially on the surface of leaves but later tunneling into petioles where pupation occurs.

Following regulatory approvals, the mottled waterhyacinth weevil was released in Florida in 1972, the chevroned waterhyacinth weevil in 1974, and the waterhyacinth moth in 1977 (Center et al. 2002). This effort resulted in the successful establishment of all three insects and collectively, along with the unintentionally introduced orobatid mite (*Orthogalumna terrebretalis* Wallwork) and a generalist moth, reduced waterhyacinth plant size ca. 50% in Florida (Tipping et al. 2014a). These biological control agents were transferred worldwide in the late 1970s and 1980s, with significant levels of control and marked reduction in population growth rates of waterhyacinth in areas of Australia, China, East Africa, India, South Africa (Julien 2001), and Mexico (Aguilar et al. 2003). This program was also implemented in waterhyacinth-infested waters of the Delta in the early 1980s, representing the first time weed biological control was used in this system. The two weevils, chevroned waterhyacinth weevil and mottled waterhyacinth weevil, were collected from Texas and released in 1982 (Stewart et al. 1988). The waterhyacinth moth was collected from established populations in Florida and Louisiana and released in 1984 (Stewart et al. 1988). Initial postrelease evaluations revealed that all three species had established in the Delta (Stewart et al. 1988), but a survey in 2002, two decades after release, indicated that only one weevil species, chevroned waterhyacinth weevil, persisted (Akers et al. 2017). General assessments suggested that damage caused by chevroned waterhyacinth weevil was insufficient to regulate waterhyacinth populations (Spencer and Ksander 2004, Akers et al. 2017, Hopper et al. 2017, Pitcairn 2018).

A new waterhyacinth agent, the waterhyacinth planthopper (*Megamelus scutellaris* Berg), was evaluated and approved for release in the United States in 2010 (Tipping et al. 2014b). The planthopper was first released in Florida in 2010; individuals from the Florida population were subsequently released in the Delta and its associated tributaries by scientists with the California Department of Food and Agriculture (CDFA) in 2011. Subsequent postrelease surveys confirmed establishment of the waterhyacinth planthopper in a single tributary in Folsom, CA, that feeds via the American River and Sacramento River into the Delta (Moran et al. 2016). The waterhyacinth planthopper is a small (ca. 3-mm adult) insect, with adults occurring as both brachypterous (short-winged) nonflying and macropterous (large-winged, flying) forms. Insects jump distances many times their size and can disperse at least 50 m in one field season (Moran et al. 2016). Females lay eggs in small wounds that they make in the petiole and lamina of waterhyacinth leaves (Sosa et al. 2005), and each female can produce ca. 50 eggs in its lifespan of several weeks (Tipping et al. 2011). The entire life cycle takes 25 to 40 d under field conditions (Sosa et al. 2005, Foley et al. 2016).

Adults and nymphs of the waterhyacinth planthopper feed mostly on phloem tissues (Hernández et al. 2011). Heavy feeding damage can result in premature leaf death, reduced biomass and plant growth rate, and eventual death of entire plants (Sosa et al. 2007, Tipping et al. 2011, Fitzgerald and Tipping 2013). High densities of 100 planthoppers per plant or greater may be needed to achieve full impact (Fitzgerald and Tipping 2013). Recent evidence suggests that the waterhyacinth planthopper reduces leaf chlorophyll content (Miller et al. 2019). The realized impacts of the planthopper in the Delta may be negatively influenced by cooler temperatures experienced in the Delta as compared to Florida (May and Coetzee 2013, Moran et al. 2016).

Present

Previous assessments of the waterhyacinth biological control agents were limited both spatially and temporally. Additional surveys were conducted in 2015 to 2016, 34 yr after the initial releases, to provide greater insights to of the introduced herbivores' distribution and population dynamics in the greater Delta region (Hopper et al. 2017). This effort was also designed to investigate the spread of the waterhyacinth planthopper from its release site along a northern tributary as well as determine if other exotic natural enemies migrated to the Delta (Pratt and Center 2012). These surveys revealed three of the four previously released biological control agents are present in the sampled area. Over 3,000 weevils were collected and, based on molecular and morphological identifications, 96.6% were chevroned waterhyacinth weevils (Hopper et al. 2017). The weevil was recovered at all study sites, with densities reaching peak levels of five to six individuals per plant during late summer through early fall. Surprisingly, however, 3.4% of the adults collected were mottled waterhyacinth weevils, which were only found in tributaries flowing into the southern Delta from the San Joaquin River. The waterhyacinth planthopper was only found at the original site with no evidence of establishment or dispersal into the Delta. The waterhyacinth moth was absent from all samples, confirming previous reports of its failure to establish in the Delta (Stewart et al. 1988, Akers et al. 2017).

Densities of the weevils (primarily chevroned waterhyacinth weevil) in the Delta are not sufficiently high throughout the season to produce adequate damage and year-round control of waterhyacinth. These low densities may be due to the weevil's thermal limits, resulting in a lag phase between weed expansion in the spring and early summer and the population level response of the weevils to warming temperatures and increasing plant abundance. Similar dynamics have been observed with the current biological control agents of waterhyacinth in South Africa, as they do not appear to be well adapted to cold conditions at some high-altitude locations (Hill and Olckers 2001, May and Coetzee 2013). In the Delta, this climatic mismatch could be due to the source populations of the waterhyacinth weevil species released in the early 1980s. These populations were originally obtained from Wallisville, TX, and were the progeny of Florida populations that were originally derived from the insect's native range of Argentina in the 1970s (Stewart et al. 1988, Hopper et al. 2019). These source populations may have been preadapted for the warm temperatures in Florida and coastal Texas as rapid local evolution of environmental tolerance of biological control agents can occur (Szűcs et al. 2012, Griffith et al. 2019, Müller-Schärer et al 2020). Thus, waterhyacinth weevil species populations adapted to cooler climates in other regions, including parts of the native range, may have a greater tolerance to winter temperatures in the Delta. A similar situation was observed with the salvinia weevil (*Cyrtobagous salviniae* Calder & Sands) on giant salvinia (*Salvinia molesta* D. Mitch) (Russell et al. 2017).

In an effort to identify a more cold-tolerant biotype of mottled waterhyacinth weevil, we compared low-temperature performance of the current but rare Delta mottled waterhyacinth weevil population to three geographically distinct populations from its introduced (Australia and South Africa) and native (Uruguay) range. Results from developmental studies at average winter and fall temperatures experienced in the Delta suggest that immature stages of all populations died, and females stopped reproducing when maintained at winter (daily fluctuating range: 4 to 14 C, mean: 8.0 C) temperatures. All populations showed similar performance at fall temperatures (range: 13.2 to 28.7 C, mean: 20.5 C) but the Australian population had the highest intrinsic rate of increase, net reproductive rate, and doubling time, due to its longer oviposition period, and higher daily fecundity (2.1 ± 0.2 eggs d^{-1}). The Australian biotype produced twice as many eggs as the California population (1.0 ± 0.2 eggs d^{-1}) when maintained at fall temperatures (Reddy et al. 2018). These data suggest that the Australian population may be better adapted to cooler climates such as those in the Delta despite lower genetic diversity compared to the populations in the Delta and native range (Hopper et al. 2019).

Arguably, more is known concerning the host range of mottled waterhyacinth weevil than any other biological control agent (Julien et al. 1999). If biotypes with unique introduction histories experience dissimilar population growth rates, then do they also express different host-range preferences? To determine if the genetic bottlenecks inherent in importation procedures and selection pressures in Australia resulted in differential host use patterns, additional host range testing is underway to quantify the weevil's diet breadth in relation to published data for this species. These data will be compiled for a release permit request to justify the introduction of the mottled waterhyacinth weevil from Australia into northern California with the expectation that this new biotype that appears to be better adapted to cooler climates will improve biological control of waterhyacinth in the Delta.

The waterhyacinth planthopper was released at one site in the southern Delta in 2011 to 2012, but widespread Delta releases were delayed due to permitting requirements that included tests to evaluate the toxicological effects and physical choking hazards of feeding on the planthopper by listed fish species, Delta smelt (*Hypomesus transpacificus* McAllister) and winter-run Chinook salmon [*Oncorhynchus tshawytscha* (Walbaum)], using rainbow trout (*Oncorhynchus mykiss* Walbaum) as a surrogate for testing). These tests indicated that the insects did not affect fish survival or growth. Therefore, the planthopper was released at 19 sites in 2018 but was recovered at only one site in the spring of 2019. The planthopper was released at 11 sites that same year and was recovered at three sites in the spring of 2020 (P. Moran, unpublished data). Sites with more stable waterhyacinth populations are receiving large numbers of additional planthoppers in 2020.

Future

Research plans for waterhyacinth biological control include both short- and long-term objectives. One short-term research priority is to investigate approaches that can facilitate the establishment of the waterhyacinth moth in the Delta. Populations of the moth from more northerly, and possibly cooler, regions of its distribution in the United States may possess more cold-hardy alleles that would foster establishment of the moth in northern California. Phases of the planned research include the importation of the waterhyacinth moth into California, establishing a laboratory colony, assessing the risk of moths to threatened and endangered species in consultation with regulatory agencies, mass rearing, release, and monitoring for persistence in the Delta. Should these additional efforts fail to establish a persistent population capable of controlling the weed, additional research on acquiring new genetic material from Argentina that is more suitable for the Delta's environmental conditions will be needed (Reddy et al. 2018, Cozad et al. 2019, Griffith et al. 2019). Alternatively, directed selection for cold hardiness in the laboratory may yield better-acclimated individuals for climates at the weed's geographic margins.

Additional biological control agents may also be considered. The orobatid mite (*Orthogalumna terrebretalis* Wallwork) is established in various regions of the southeastern United States and may be a useful biological control agent in the Delta. The mite appears to be an accidental introduction and may have accompanied the plant when first propagated as an ornamental (Cordo and DeLoach 1976). The impact of the mite and its host range remains largely unexplored (Tipping et al. 2014a). Similarly, small flies in the genus *Thrypticus* may also be effective at suppressing waterhyacinth in the Delta. Two species, *Thrypticus truncatus* Bickel & Hernández and *Thrypticus sagittatus* Bickel & Hernández, are only known from waterhyacinth and are expected to be highly specific (Bickel and Hernández 2004, Hernández 2008). The flies mine the petioles of waterhyacinth and may facilitate infections by resident pathogens. While critical foundational research on the biology and identification of these *Thrypticus* species has been reported, rearing methodologies and host specificity testing is still needed.

Examination of the role of pathogens may prove beneficial in increasing the effectiveness of the biological control agents. In the southeastern United States, feeding by waterhyacinth weevil species facilitates fungal colonization of waterhyacinth tissues and provides additive increases in plant mortality over the impact of insect feeding alone (Charudattan et al. 1978, 1985; Moran 2005). It may be worthwhile to examine fungi with known high pathogenicity on waterhyacinth in other areas of the United States and determine their use in the Delta.

BRAZILIAN EGERIA

Past and present

Brazilian egeria (*Egeria densa* Planchon) is a native of South America that has been disseminated widely through the aquarium trade. It is considered an invasive weed in areas of North America, Australasia, Asia, Europe, and South Africa (Gassmann et al. 2006). Dense submerged stands of the weed displace native species, limit navigation, disrupt irrigation systems, and interfere with recreational water uses (Anderson 1990, DBW 2006, Yarrow et al. 2009). This is particularly true in the Delta, where Brazilian egeria is considered by some water managers as the aquatic weed of greatest concern (Durand et al. 2016).

Surveys for natural enemies of Brazilian egeria began in the plant's native range of Argentina in 2005 (Cabrera Walsh et al. 2013). The first herbivore selected for evaluation was a new species of stem-mining fly: the leaf-mining fly (*Hydrellia egeriae* Rodrigues). Adult females of the leaf-mining fly oviposit on Brazilian egeria leaves exposed above the water surface, and the larvae mine leaves as well as stems (Cabrera Walsh et al. 2013). Congeners of the leaf-mining fly have a narrow host range and are used as biological control agents of another related aquatic weed, hydrilla [*Hydrilla verticillata* (L.f.) Royle] (Grodowitz, et al. 1997, Bownes 2014). However, recent evidence demonstrated that the North American native and close relative common elodea (*Elodea canadensis* Michaux) falls within the physiological host range of the leaf-mining fly (Pratt et al. 2019). Host-range tests indicated that larvae survived better when feeding on the target weed, suggesting that Brazilian egeria may be a developmentally superior host over common elodea. Females reared on common elodea, however, had similar fecundity when compared to those reared on Brazilian egeria (Pratt et al. 2019). Both Brazilian egeria and common elodea are sympatric in many California waterbodies and elsewhere across the southern United States, which increases risk of nontarget feeding. These data indicate that the host range of the leaf-mining fly, under artificial controlled (laboratory) conditions, is too broad to be considered as a biological control agent of Brazilian egeria in the United States.

Future

Multiple surveys for natural enemies of Brazilian egeria have resulted in few herbivores beyond the leaf-mining fly. Collaborators suggest that there are few suitable candidate agents among the known herbivores of Brazilian egeria and additional surveys in new regions of the plant's native range are needed. Expanded surveys should also include plant pathogens. The poor prospect for biological control is particularly concerning when considering the magnitude of the Brazilian egeria invasion in the Delta and beyond (Moran et al. 2020).

GIANT REED

Past

The giant reed, or arundo (*Arundo donax* L.), is a large (to 8 m tall) nonnative, perennial invasive grass that occupies over 5,000 ha of canal banks and riparian areas in California (Going and Dudley 2008, Cal-IPC 2020). Giant reed consumes and wastes scarce water resources (Moore et al. 2016), fuels fires in riparian corridors (Coffman et al. 2010), alters water flow and sediment deposition patterns (Cal-IPC 2020), and reduces plant and animal biodiversity (Herrera and Dudley 2003, Quinn and Holt 2008, Rubio et al. 2014). Giant reed is often managed with chemical and/or mechanical control methods (DiTomaso et al. 2013), but additional tools to improve weed suppression over large invaded regions will aid in the area-wide management of the exotic plant.

Two insects have been released for biological control of giant reed, with U.S. releases occurring first in the Lower Rio Grande Basin along the Texas–Mexico border between 2009 and 2013. The shoot tip–galling arundo wasp (*Tetramesa romana* Walker) can feed and reproduce only on giant reed (Goolsby and Moran 2009). Adult females live ca. 1 wk and lay eggs inside giant reed shoot tips; each female can produce an average of 26 eggs (Moran and Goolsby 2009). This wasp completes its life cycle parthenogenetically (females produce fertile eggs without mating) in 40 to 70 d under variable (15 to 30 C) conditions. Larvae feed on gall tissue and complete three immature stages, pupate inside galls, and chew round "exit holes" in the stem galls. These holes are a recognizable sign of population establishment in the field. The wasp is well established along at least 600 km of the Lower Rio Grande in Texas (Goolsby et al. 2014, Marshall et al. 2018). The wasp stunts main shoot growth (Goolsby et al. 2009) and has reduced live giant reed biomass by 30 to 40% (Goolsby et al. 2016), leading to increases in the diversity of other plants by 2- to 3-fold (Moran et al. 2017).

The second giant reed biocontrol agent is the armored scale [*Rhizaspidiotus donacis* (Leonardi)]. Females produce live "crawlers" that feed on vascular tissues on rhizomes and the bases of shoots and shoot buds (Goolsby et al. 2009). Crawlers settle on rhizomes or shoots and become immobile, completing two immature life stages. Short-lived adult males emerge after 2 mo and mate with females, which continue to feed and expand, producing a new generation of crawlers. The life cycle from crawler emergence to reproductive female adult takes about 6 mo (Moran and Goolsby 2010). First released in Texas, the armored scale has established populations and reduced giant reed live biomass 50% at two sites there, expanding the level of damage beyond that exerted by the wasp alone (Goolsby and Moran 2019). The arundo wasp was first released in the northern Sacramento River watershed in 2010 by CDFA (Pitcairn 2018) and both the wasp and scale in 2013 by USDA (Goolsby and Moran 2019). Arundo wasps can be released either as adult females or as galled stems moved to field sites. The arundo armored scale can be released as neonate crawlers isolated from females, or by propagating females on potted giant reed "microplants" for 6 mo in a greenhouse and then planting adjacent to giant reed field populations (Villarreal et al. 2016).

Present

In 2017 to 2018, the arundo wasp and armored scale were released at nine sites: three in the northern Sacramento River watershed, three in the southern San Joaquin watershed, and three in the western Delta. Surveys in 2019 indicated establishment of the arundo wasp in one site in each of the two regions upstream of the Delta, with galls found 100 m or more from release plots (P. Moran, unpub. data). Additional releases in the Delta are ongoing. Surveys for the armored scale consisted of excising a rhizome sample adjacent to the release point and dissecting to determine the number of adult females and crawlers. Reproductive armored scales are present at all of the upstream sites and at two Delta sites.

Impact assessments of the giant reed biocontrol agents are ongoing. Damage caused by the wasp can be quantified by counting wasp exit holes on main and lateral shoots (e.g., Marshall et al. 2018) and number of large galls on main stems. Damage of the armored scale can be seen as distorted, "witch's broom" side shoots indicative of heavy infestation (Goolsby et al. 2011) and by searching for immobile, immature "whitecap" scales (mostly males) on the leaf collars. Impact of biological control of giant reed in the Delta is expected to consist of reduction of live giant reed shoot density and size or biomass (Moran et al. 2017, Goolsby and Moran 2019), as well as increases in diversity and abundance of other plant species.

Future

In addition to the wasp and scale impact assessments noted above, releases of one new agent is planned. The arundo leaf-mining midge (*Lasioptera donacis* Coutin) was permitted for release in the United States in 2017. This midge carries a globally distributed saprophytic fungus as it lays eggs in holes or cracks in giant reed leaf sheaths, and larvae complete three immature stages feeding on the fungus and decaying leaf tissues (Goolsby et al. 2017). Difficulties were encountered rearing this agent outside of quarantine, so additional research is needed to investigate rearing methods in preparation for field releases in the Delta.

WATER PRIMROSES

Past

Exotic water primroses (*Ludwigia* spp.) have invaded aquatic and riparian ecosystems worldwide (EPPO 2011, Thouvenot et al. 2013). Their rapid growth impacts ecological processes in aquatic ecosystems, displacing desired native wildlife and vegetation (Lambert et al. 2010, Grewell et al. 2016). The plants form dense mats over the water surface that constrain navigation and interfere with recreational activities, irrigation, drainage, and agricultural production (Thouvenot et al. 2013, Grewell et al. 2016). In the United States, four exotic *Ludwigia* taxa include water primrose [*Ludwigia hexapetala* (Hook. & Arn) Zardini, H. Y. Gu, & P.H. Raven], creeping water primrose [*Ludwigia peploides* (Kunth) Raven subsp. *peploides*] and floating primrose-willow [*L. peploides* (Kunth) Raven subsp. *montevidensis* (Spreng.) Raven], and Uruguay waterprimrose [*Ludwigia grandiflora* (Michx.) Greuter & Burdet]. All four have naturalized and become invasive in aquatic systems (Reddy et al. 2020). The most problematic taxa is water primrose, which continues to spread aggressively throughout watersheds in coastal southeastern, Gulf of Mexico, and Pacific western states despite control efforts.

Manual, mechanical, and chemical control methods have been used to manage *Ludwigia* spp. with variable results (Meisler 2009, EPPO 2011, Thouvenot et al. 2013, Hussner et al. 2016). Mechanical devices can produce a high number of fragmented pieces that can reinfest or disperse downstream (Skaer Thomason et al. 2018). Chemical control has shown efficacy (Thouvenot et al. 2013, Grewell et al. 2016) but can be nonselective. Stakeholders have called for classical biological control as a management option for invasive *Ludwigia* taxa, particularly in watersheds where access for management is limited.

The four exotic *Ludwigia* taxa as well as the native *Ludwigia peploides* subsp. *glabrescens* (Kuntze) Raven collectively belong to the same section *Jussiaea*. A suitable biological control agent must be host-specific to one or more of the four target weeds, but not utilize the closely related *L. peploides* subsp. *glabrescens*. Similarly, risk to the > 28 U.S. native *Ludwigia* species (but in different taxonomic sections than the target taxa) must be quantified for candidate biological control agents.

The first foreign exploration and field host range evaluation of insect herbivores on *Ludwigia* spp. were conducted in the 1970s in Argentina by Cordo and DeLoach (1982a, b). A second survey was conducted by Hernández and Cabrera Walsh (2014), who documented 19 insect species, across 6 feeding guilds, feeding on water primrose (*L. hexapetala*). Of these species, only two species were also found on Uruguay waterprimrose and one on creeping water primrose. The list of promising biological control agents included a thrips (*Liothrips ludwigi* Zamar), six stem-boring beetle species [*Merocnemus binotatus* (Boheman) and five *Tyloderma* spp.], and one fruit-feeding beetle (*Tyloderma nigromaculatum* Hustahe).

The first species formally evaluated as a biological control agent of exotic *Ludwigia* species was *Liothrips ludwigi*, a cell-content feeder that attacks and breeds in *Ludwigia* apical buds. Host range studies conducted by scientists at the Fundacion para el Estudio de Especies Invasivas (FuEDEI) showed that *Liothrips ludwigi* nymphs completed development on water primrose (*L. hexapetala*), Uruguay waterprimrose (*L. grandiflora*), floating primrose-willow (*L. peploides* subsp. *montevidensis*), and *L. peploides* subsp. *glabrescens* (Cabrera Walsh 2015). Results from recent host-range studies conducted by USDA scientists confirmed these results and expanded the list of acceptable host plant species to include creeping water primrose (*L. peploides* subsp. *peploides*) and three *Ludwigia* species native to the United States: floating waterprimrose (*Ludwigia repens* Frost), waterpurslane [*Ludwigia palustris* (L.) Elliott], bushy waterprimrose (*Ludwigia alternifolia* L.). These results indicate the thrips is unsuitable for release in the Delta and research efforts were redirected to other candidates.

Present

In 2019, FuEDEI and USDA scientists, in collaboration with Uruguay's Instituto National de Investigacion Agropecuaria (INIA), conducted additional surveys in Argentina and Uruguay. Scientists reviewed *Ludwigia* species for herbivores in two provinces of Argentina (Buenos Aires and Entre Ríos) and five departments in Uruguay (Colonia, San José, Maldonado, Rocha, and Treinta y Tres). Two *Tyloderma* species were collected in Uruguay and imported to the USDA quarantine facility in Albany, CA. Adults of the fruit-feeding weevil *T. nigromaculatum* feed on leaf margins, creating crescent-shaped marks around the leaf perimeter. The adult oviposits its eggs at the base of the sepals of flower buds and spent flowers. Complete larval development occurs inside the fruit where it feeds on developing seeds. Efforts are underway to colonize this species in the laboratory. The second *Tyloderma* weevil has yet to be identified but adults feed on all leaf stages, resulting in discrete holes in the lamina. Females oviposit singly where the petiole meets the lamina. Neonate larvae tunnel through the leaf petiole to the stem where they develop and pupate.

The resulting adult emerges from the stem by cutting a circular exit hole. Initial evidence suggests that feeding by the stem-mining and fruit-feeding weevils can be debilitating to host plants but it remains unclear if the insects are sufficiently host specific for introduction in the Delta and other regions of the United States affected by *Ludwigia* invasions.

Future

Recent surveys of water primrose species in Argentina and Uruguay by FuEDEI, INIA, and the USDA resulted in the observation of numerous herbivorous insects, including the *Tyloderma* spp. weevils described above (Cordo and DeLoach 1982a), but also new candidates not discovered previously (Hernandez and Cabrera Walsh 2014). The USDA and INIA collaborators recently received a Uruguayan export permit for additional species that are expected to be investigated as biological control agents, including the weevil *Sudauleutes bosqui* Hutache, multiple *Lysathia* beetle species, and an unidentified lepidopteran (Hernandez and Cabrera Walsh 2014). In addition to exotic herbivores, select native herbivores have been observed attacking exotic water primroses. Transitory but at times dramatic levels of herbivory has been recorded by larvae and adults of the water-primrose flea beetle *Lysathia ludoviciana* Fall on Uruguay waterprimrose (*L. grandiflora*) in Alabama (McGregor et al. 1996) and the crepe myrtle flea beetle (*Altica litigata* Fall) on water primrose (*L. hexapetala*) in California (Carruthers et al. 2011). Research is needed to determine if early-season inoculative or inundative releases of these insects will yield meaningful suppression of the target weeds in the Delta. Population buildup of these native herbivores on exotic plants may be of concern as outbreak densities can cause disproportionate effects on the herbivore's native host(s) as they disperse from the target weed.

ALLIGATORWEED

Past

Alligatorweed [*Alternanthera philoxeroides* (Mart.) Griseb] is a native of South America that grows both as a terrestrial and an aquatic plant. Alligatorweed can reproduce both sexually and vegetatively but, like many of the weeds discussed here, the primary mode of dispersal is via buoyant stem fragments that are carried with the water. Fragments readily root in wet soil and may grow in terrestrial areas of riparian habitats. Stems also expand across the surface of the water and form roots at the nodes. Alligatorweed invades riparian and aquatic habitats worldwide (Sosa et al. 2008). In the United States, alligatorweed is historically a pest of the southeastern states from Virginia south to Texas but the species has also been recognized as an invasive plant in southern California since the 1970s (Reed 1970). Alligatorweed was first observed in California in 1946 near Rio Hondo, Los Angeles County. Herbarium records over the next 30 yr report the plant in various locations between San Diego and Ventura counties. A second population was observed in the 1970s ca. 200 km north of Los Angeles, near the towns of Porterville and Visalia in Tulare County. The presence of alligatorweed in central and southern California has been of concern, but invasions in California were thought to be restricted by highly channelized and managed water delivery systems in southern California and the Central Valley, and thus spread of the weed would be limited by the region's xeric environment. In 2017, however, multiple small patches of alligatorweed were discovered in the Delta, where the complex matrix of natural wetlands, human-altered sloughs, and tributaries is likely to facilitate large-scale invasion of critical habitats. Recent evidence suggests that several incipient populations exist in the Delta and are likely to continue to spread into the system from upstream sources (Walden et al. 2019). This recent invasion and associated negative ecological impacts of the exotic weed has led to stakeholder requests to implement biological control of the incipient weed.

Alligatorweed has been a target for weed biological control since the 1960s, with the first exploration for natural enemies conducted by the USDA-ARS scientist G. Vogt in 1960 and 1961. Three insects became the focus of researchers in Argentina and the United States: the leaf-feeding alligatorweed flea beetle (*Agasicles hygrophila* Selman and Vogt, the stem and foliar-feeding alligatorweed thrips (*Amynothrips andersoni* O'Neill), and the alligatorweed stem-borer moth *Arcola* (as *Vogtia*) *malloi* (Pastrana) (Vogt 1973, Coulson 1977, Buckingham 2002). Host-range testing indicated that all three herbivores are largely host-specific and posed little risk to native flora or agricultural crops of the United States (Maddox et al. 1971, Coulson 1977). Based on these data, approval to introduce the three insects was acquired from both federal and state regulators. Individuals of all three species were collected near Buenos Aires, Argentina, and shipped to the USDA-ARS Albany, CA, quarantine facility for rearing and redistribution throughout the United States.

The first release of alligatorweed flea beetles in the United States was made in California in 1964, with nearly 500 adults introduced at the Los Angeles County alligatorweed infestation (Coulson 1977). Additional releases of nearly 5,500 alligatorweed flea beetle adults were made from 1964 to 1969 at both the Los Angeles and Tulare county sites. Despite these efforts, the beetles failed to persist at either site. There is some evidence that the beetles successfully overwintered from 1967 to 1968 but failed to survive the following winter (Goeden and Ricker 1971). Similarly, 480 alligatorweed thrips adults were released at the Los Angeles County site during the summer of 1967 but there is no evidence that the insects established. The alligatorweed stem-borer moth was released near the city of La Mirada, CA, in September of 1976. Between 60 and 70 gravid females were introduced but alligatorweed plants at the site were chemically treated and the population failed to establish (Richmond 1977). These results stand in stark contrast to the successful establishment and control achieved by the suite of herbivores in many regions of the southern United States, where suppression of alligatorweed remains one of the most compelling examples of successful biological control of an aquatic weed worldwide (Buckingham 2002). Explanations for the failure of these insects to persist following releases in the 1960s and 1970s in California, however, may have relevance to biological control of the weed in the Delta today.

Early in the alligatorweed biocontrol program it was understood that successful overwintering of alligatorweed flea beetles and resulting weed control was influenced by temperature, with the failures attributed to regions with average minimum winter temperatures below 9 C (Coulson 1977). Mean low temperatures for the Los Angeles County, Tulare County, and Delta sites are consistently below this minimum. Low temperatures likely explain the failure of the alligatorweed flea beetles to establish but also indicates that future releases of the flea beetle in the Delta are unlikely to result in a persistent population. However, the alligatorweed flea beetle has completed numerous generations in the southeastern United States since its introduction and selection may have occurred. Therefore, cold-tolerant alleles may be more common in individuals sourced from cooler regions of the insect's introduced range that may facilitate establishment in California's Delta. In addition, it remains unclear what are the climatic limits of alligatorweed thrips and the alligatorweed stem-borer moth. Therefore, new permits to introduce all three natural enemies have been acquired and a suite of laboratory tests and field releases are currently underway.

Present

A source population of alligatorweed flea beetles was collected near the town of Gramercy, LA, and shipped to the Albany, CA, quarantine facility in May 2019. The insects were removed from quarantine after completing one generation in containment, confirming the identification, and screening for pathogens (microsporidia). Approximately 500 alligatorweed flea beetle individuals of all stages were reintroduced in Tulare County in June 2019 as a sentinel field colony for future releases in the Delta. Regular sampling of the insect's population dynamics at the site were conducted throughout the summer. Flea beetle population densities at the Tulare County site remained low throughout the summer but it is too early to determine if the insects will successfully overwinter in the field. A similar effort of first releasing the alligatorweed thrips and alligatorweed stem-borer moth at the Tulare County site as a precursor to releases in the Delta are underway. However, releases of biological control agents in the Delta are complicated by the additional steps of review and approval from federal agencies responsible for enforcing the Endangered Species Act (Moran et al. 2020). Current research focuses on risk assessments to quantify the influence of consuming candidate insects on the growth and survival of threatened species.

Future

In addition to redistributing existing alligatorweed biological control agents from the southeastern United States to the Delta, other biotypes of known natural enemies may also aid in the suppression of the new Delta invader. While the authors are optimistic, establishment of the three alligatorweed biological control agents permitted for release in the United States remains uncertain based on prior establishment attempts (Coulson 1977). Therefore, new biotypes of these insects in their native South American ranges may be better matched climatically to the Delta's cool winters and warm summers. A new suite of host-range testing will be needed, ideally including species tested in the original assessments in the 1960s, to confirm the host ranges of these new biotypes are similarly narrow as those approved for release previously. In addition to new biotypes of existing agents, other exotic natural enemies not previously considered for biological control are of interest. Another South American flea beetle, *Disonycha argentinensis* Jacoby, was investigated by Australian scientists for introduction into Queensland for control of alligatorweed in 1980 but failed to establish (Julien et al. 2012). In contrast to the alligatorweed flea beetle, which pupates in the hollow stem of its host, *D. argentinensis* pupates in the soil and may be less affected by stems that are filled with arenchyma when the plant is growing terrestrially. Host specificity testing is needed to determine if this herbivore is suitable for introduction into the Delta and other locations where the current introduced herbivores do not provide adequate control. It should also be noted that other alligatorweed natural enemies, including several never considered in the 1960s, have yet to be evaluated as possible agents.

ADDITIONAL WEED TARGETS

Future

Interest in weed biological control for the management of exotic plants in the Delta, rejuvenated in part by the Delta Regional Areawide Aquatic Weed Project (DRAAWP; Moran et al. 2020), is expected to persist well into the future. Advances in research described above have spawned greater stakeholder support and facilitated the continued release and monitoring of agents. However, additional natural enemies are required for adequate control of these aquatic and riparian weeds. Continued invasion of the Delta and elsewhere in California by new aquatic weeds is also expected. Finally, exotic weeds already present in the Delta but of lower priority for management may benefit from initiating biological control research in the near term. Therefore, scientists who develop biological control and pest managers who implement these tactics must remain forward-thinking to meet future challenges.

Future research may focus on the development of a biological control program targeting South American sponge plant [*Limnobium laevigatum* (Humb. & Bonpl. Ex Willd.) Heine]. This species is a native of Central and South America but has been used extensively as an ornamental in aquascapes (Howard et al. 2016). It was first detected in ponds of the northern most counties of California in 2003 but the weed was discovered in both the northern and southern portions of the Delta between 2007 and 2010 (Anderson and Akers 2011). Sponge plant is a perennial that forms floating rosettes and reproduces from seed as well as vegetatively via runners that spread across the water's surface. Leaves possess a patch of spongy aerenchyma cells

Table 1. Biological control agents released against invasive weeds in the Sacramento–San Joaquin River Delta region.

Biological Control Agent	Target Weed	Year Released	Status in Delta	Reference
Chevroned waterhyacinth weevil	Waterhyacinth	1982	Widely established	Stewart et al. 1988
Mottled waterhyacinth weevil	Waterhyacinth	1982	Established but rare	Stewart et al. 1988
Waterhyacinth moth	Waterhyacinth	1984	Failed to establish	Stewart et al. 1988
Waterhyacinth planthopper	Waterhyacinth	2011	Established but rare	Moran et al. 2016
Arundo wasp	Giant reed	2010	Established but rare	Pitcairn 2018, Goolsby and Moran 2019
Arundo armored scale	Giant reed	2013	Established but rare	Pitcairn 2018, Goolsby Moran 2019

on their lower surface, which contributes to buoyancy and dispersal. Like many weed species discussed herein, rapid growth results in large mats that shade other plants and compromise habitat quality. The taxonomy of sponge plant is controversial and relevant to biological control. The plant has long been considered a subspecies of the North American native, American frogbit [*Limnobium spongia* (Bosc) Steud], based on flower morphology (Lowden 1992). More recently, however, authors have referred to sponge plant as a full species (Cook 1996, DiTomaso and Healy 2003, Jørgensen et al. 2013) but molecular comparisons are lacking. This close relationship may indicate that natural enemies from the weed's native range may also use the native American frogbit as a host, although this plant is not native to or known from California. As an alternative, host-specific American frogbit herbivores native to North America could be released as biological control agents of invasive populations of sponge plant in the Delta and elsewhere. Several authors have noted that the frog's bit weevil (*Bagous lunatoides* O'Brien) feeds as an adult on American frogbit in Florida and possibly other locations in the southeastern United States but the biology and larval host range of this species remain largely unknown (O'Brien and Marshall 1979, Haag et al. 1986, Harms and Grodowitz 2010). Center et al. (2002) suggests frog's bit weevil is host-specific, but others have recovered this species resting on floating pennywort (*Hydrocotyle ranunculoides* L.f.) and dense-flower knotweed (*Polygonum glabrum* Willd) (Harms and Grodowitz 2010, O'Brien and Marshall 1979). It is also likely that other natural enemies of American frogbit have yet to be discovered across the plant's more northerly range (Arkansas, Illinois, Missouri, Oklahoma), which may be more climatically similar to California. Based on published molecular phylogenies, close relatives that may be at most risk from American frogbit herbivores relocated from the eastern to western United States include American eelgrass (*Vallsineria americana* Michx.) (same clade as *Limnobium*) and *Elodea* spp. (different clade; Chen et al. 2012).

Synergies

Weed invasions in the Delta are not unlike those experienced in wetland habitats throughout the world, often with the same weed species occurring in like environments on multiple continents. Regional or international collaborations to develop weed biological control programs can be formed in response to these cosmopolitan invaders and, through information sharing and partitioning of labor, economies of scale can reduce program costs across multiple invaded ranges. For example, egeria is a severe problem in the Delta but is also weedy in South Africa. Information-sharing between collaborating countries facilitated the introduction of the leaf-mining fly in South Africa, where there are no native species (i.e., *Elodea*) within the herbivore's ecological host range (Smith et al. 2019). Similar collaborations with colleagues developing biological control on weeds like parrotfeather [*Myriophyllum aquaticum* (Vell.) Verdc.], Eurasian watermilfoil (*Myriophyllum spicatum* L.), hydrilla, and others may lead to expedited control benefits for weeds not profiled above.

CONCLUSIONS

Despite early examples of successful weed biological control in California, the discipline has yet to provide effective tools for management of invasive aquatic weeds in the Delta. To date, biological control efforts have resulted in the release of four insects targeting waterhyacinth and two insects that attack giant reed (Table 1). Postrelease assessments indicate that five of the six insects have established in or near the Delta. The two waterhyacinth weevils have not had sufficient impact on plant growth and survival; The other three agents (waterhyacinth planthopper and the two giant reed agents) have yet to reach their maximum distribution and stable densities so it may be too early to determine efficacy. One explanation for the limited control achieved thus far may relate to the practice of acquiring biological control agents originally developed and released in the southeastern United States and redistributing them to weed patches in the Delta. New efforts to improve the efficacy of existing and discover new agents focuses on developing natural enemies that are better suited for the Delta's climate. These new projects focus on sourcing agents from native ranges or the margins of introduced ranges that are similar climatically to those experienced in northern California (waterhyacinth, giant reed, alligatorweed). Additionally, new projects are targeting problematic weeds that have received little attention from the biological control community due to lower likelihood of success, based on the presence of native and sympatric congeners or close relatives (*Ludwigia* spp., Brazilian egeria, sponge plant, etc.). The importance of biological control within an integrated weed management approach in the Delta is expected to increase in the future as environmental restrictions and public opinions limit the use of herbicides as tools.

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